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Nonlinear Combination of Luminance Excursions During Flicker, Simultaneous Contrast, Afterimages and Binocular Fusion

STUART ANSTIS,*† ALAN HO*

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The changes in apparent brightness or color, induced into a test spot by a surround, can be greatly enhanced either by flickering the test spot between two luminances, or by binocularly fusing a pair of test spots of different luminances. Simultaneous contrast, in which a white surround makes a grey spot look darker, is greatly enhanced if the spot (not the surround) flickers between black and white. Colour contrast is likewise enhanced by chromatic flicker: on a blue surround, a grey spot looks slightly yellowish, but a yellow/blue flickering spot looks strongly yellow. Temporal successive contrasts, or negative afterimages, are also enhanced by flickering the test field. The negative afterimage of a half-white, half-black rectangle looked dark grey and light grey when projected on a grey test field, but it looked almost black and almost white when projected on a test field that flickered between black and white. Coloured negative afterimages were also enhanced by projecting them on a chromatic flickering test field. We examined the combination rules for pairs of luminances which were presented either successively as flicker or else dichoptically (and fused binocularly). The brightness averaging functions for spatial increments (light spots) on dark surrounds were quasi-linear for binocular fusion but quadratic for flicker. For spatial decrements (dark spots) on white surrounds, the brightness averaging functions were strongly nonlinear winner-take-all for both binocular fusion and flicker. We also found temporal analogues of Fechner's [(1860). *Elements of psychophysics*. New York: Holt, Rinehart, Winston, 1966] paradox and Levelt's [(1965). *British Journal of Psychology, 56,* 1–13] dichoptic contour effect. We conclude that the visual rules for combining luminance excursions, whether in flicker or binocular fusion, favour disproportionately the spot with the higher contrast. © 1998 Elsevier Science Ltd. All rights reserved.

Flicker simultaneous contrast afterimage brightness perception colour vision binocular fusion Fechner's paradox

INTRODUCTION

Our perception of the brightness of any single patch of a visual scene is not solely determined by the patch's physical luminance. Rather, the visual system interrogates the surrounding spatiotemporal luminance structure to provide some context within which to interpret the retinal image. Thus, the contrast, the difference between the patch and surround luminance (Whittle, 1992a, 1992b), is more important to perceived brightness than actual patch luminance. This idea can be traced back to Wallach (1976, 1963), who showed that a 1 $\mathrm{cd.m^{-2}}$ disk centred in a 3 $\mathrm{cd.m^{-2}}$ annulus, has the same subjective lightness as a 10 $\mathrm{cd.m^{-2}}$ disk centred in a 30 $\mathrm{cd.m^{-2}}$ annulus (the Ratio rule). Walraven (1976, 1977) showed that a green spot flashed up on a red surround looks not yellow but green, even though the red + green mixture seen in isolation would look yellow. The importance of context is very apparent in simultaneous contrast, where a grey spot looks darker on a light surround than on a dark surround (Heinemann, 1955; Reid & Shapley, 1989; Shevell, Holiday, & Whittle, 1992).

One of us (AH) noticed that *flickering the test field* (not the surround) *greatly enhances the effects of simultaneous contrast.* Thus a flickering test spot looks almost white on a dark surround and almost black on a light surround [Fig. 1(a, b)]. We could obtain this flicker-augmented contrast (FAC) effect from many different contrast displays [Fig. 1(d, e, f)]. The enhancement of contrast was vivid, striking and robust. As we shall see later, colour contrast can also be enhanced by applying chromatic flicker to the test spot, and so can successive contrast, namely negative afterimages of brightness and colour.

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*Department of Psychology, UC San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0109, U.S.A.

†To whom all correspondence should be addressed [*Tel*: 619 534 5456; *Fax*: 619 534 7190; *Email*: sanstis@ucsd.edu].

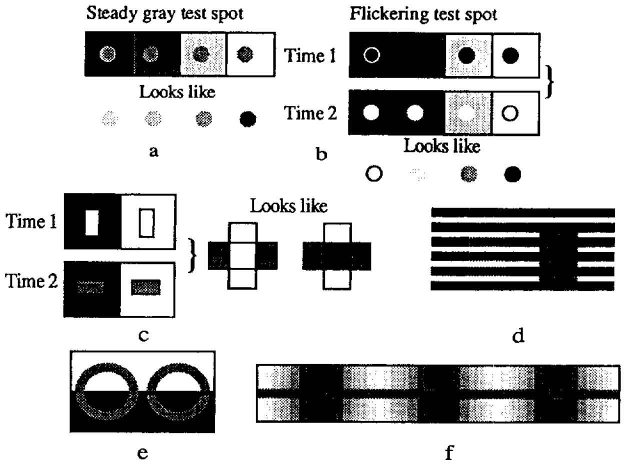

FIGURE 1. (a) Owing to simultaneous contrast, the grey spot on the dark surround looks lightest, and the spot on the light surround looks darkest. (b) Flickering the spots between black and white at 7–15 Hz augments simultaneous contrast. The flickering spot looks almost white on a dark surround and almost black on a light surround. (c) Light and dark phases of flicker need not be congruent. Other contrast displays that are augmented by flickering the test regions include: (d) White's effect (White, 1979); (e) Koffka's rings (Koffka, 1935); (f) induced grating (McCourt, 1982).

Heinemann (1955) found that simultaneous contrast affected spatial decrements far more strongly than spatial increments. He measured the brightness induced into a test spot by a surrounding annulus, finding that a dark annulus had almost no effect on the subjective brightness of the test spot. However, as the surround luminance came closer to and then exceeded the test spot luminance, the subjective brightness of the test spot fell off steeply. Thus, dark surrounds do not make light spots look any (or much) lighter but light surrounds do make dark spots look even darker. Schirillo & Shevell (1996) examined the brightness induced into grey spots by checkerboard surrounds.

Simultaneous contrast is usually attributed to lateral inhibition in cells with spatially opponent receptive fields (Diamond, 1960; Ratliff, 1965; Shapley, Caelli, Grossberg, Morgan, & Rentschler, 1990; Nabet & Pinter, 1991), although successive contrast mediated by eye movements may contribute to the effect (Shapley & Enroth-Cugell, 1984). Higher level perceptual judgements of shadows and transparency may also play a part (Gilchrist, 1992; Adelson, 1993). We shall show in Experiments 2 and 3 that simultaneous contrast is much more pronounced for a flickering than for a grey test spot. However, our Experiment 5 will rule out any direct role for lateral inhibition or brightness induction. Instead, we shall attribute flicker-augmented contrast (FAC) to the visual system's tendency to overweight high contrast edges. Thus, when a spot flickers between light and dark on a white surround, the dark phase has much higher contrast than the light phase so it predominates and makes the spot look very dark. On a black surround the light phase predominates and makes the spot look very light.

There have been several studies on flickering the surround and the test spot. Magnussen & Glad (1975b) exposed a steady test spot against a flickering surround and noted that the luminance of the test spot appeared to be modulated in counterphase: when the surround grew brighter the test spot looked darker. This happened only for flicker rates below 2.5 Hz (De Valois, Webster, De Valois, & Lingelbach, 1986).

When a spot flickers between black and white on a grey surround, say at 15 Hz, does one see the two spots in alternation, or does one spot predominate? The problem is to find a unitary description of a stream of time-varying events which are not fast enough to smear into a single luminance but not so slow that one can characterise separately the luminance of each temporal phase in sequence. One could postulate a sluggish channel which extracts time-averaged mean luminance plus brisk channels which report the flicker. Magnussen & Glad (1975a, 1975b, 1975c) obtained separate estimates of the apparent brightnesses of the dark phase and the light phase of a flickering spot when they made extensive measurements of the effects of steady surrounds upon brightness and darkness enhancement of flickering test spots (cf. also Harvey, 1970; Corwin & Giambalvo, 1974). They claimed that a point could be reached where the light and dark phases appeared to be simultaneously present, looking like a pulsating dark patch lying behind a pulsating light patch. Although the light and dark phases could be resolved in time only at low frequencies, the phases could be resolved in space at frequencies almost up to the fusion point. Observers were able to make independent lightness and darkness matches of the light and dark phases. Matches showed that the light phase looked apparently lighter and the dark phase looked apparently darker than a steady grey test spot of the same physical luminance. The brightness and darkness enhancement effect was greatest for flicker frequencies between 4 and 8 Hz. There was also a marked asymmetry between light and dark spots; the darkness enhancement was up to three times greater than the brightness enhancement.

Magnussen & Glad's results anticipate some of our own findings, but their observers were performing a different task from ours. Their observers were able to make separate matches of the apparent brightness of both the dark and light phases of the flickering spot. However, our observers were asked to match the unitary perceived brightness of the flickering test spots without perceptually separating out the light and dark phases. Our observers reported no difficulty in making judgements of the overall brightness of the flickering spot by lumping both phases together. Given the difference in brightness matching criterion, our results are not directly comparable with those of Magnussen & Glad. Macleod & He (1993) viewed a 10 cpd sinusoidal grating that alternated at 7–15 Hz with a grey field, in other words a grating that alternated in contrast between 100 and 0%. The perceived mean contrast was not 50% but about 80%. This anticipates some of our findings.

To understand why flickering the test stimulus increases perceived contrast, we measured the apparent brightness of the flickering test spot as a function of the test flicker amplitude and the surround luminance level.

METHODS

We used two kinds of display, both presented under computer control (Anstis, 1986; Anstis & Paradiso, 1989; Wenderoth, 1990). We initially demonstrated the visual phenomena, using a computer-controlled video projector, to a classroom full of naïve observers and obtained magnitude estimates (Experiments 1 and 11). All our other experiments were presented on a monitor screen. We collected magnitude estimates from naïve observers on an individual basis (Experiments 12 and 13). We also made more precise measurements with a matching method on a small number of trained observers (Experiments 2–10).

In our classroom projection experiments (1 and 11), the visual subtense of the stimuli varied with viewing distance. All our other experiments presented a test spot of 0.7 deg on a computer-controlled monitor screen. The spot was centred in a black or white annular surround 1.4 deg in outer diameter, with the rest of the screen black. There were two ways of judging the apparent brightness of the spot: observers adjusted a grey comparison spot to match the test spot by striking two computer keys which respectively brightened and dimmed the comparison spot; or observers simply selected, out of a spatial array of comparison spots of different luminances, the spot which best appeared to match the test spot. In the flicker experiments (Experiments 1–7 and 10), the test spot alternated between light and dark phases at a temporal rate of 15 Hz, except where stated otherwise. In the dichoptic experiments (Experiments 8 and 9) two test spots, one light and one dark, were presented dichoptically (one to each eye) and fused binocularly into a single spot by means of a prism stereoscope with a septum. In our colour experiments (4 and 7), the flicker rate was reduced to 7.5 Hz and the spots and surrounds were, of course, coloured instead of achromatic.

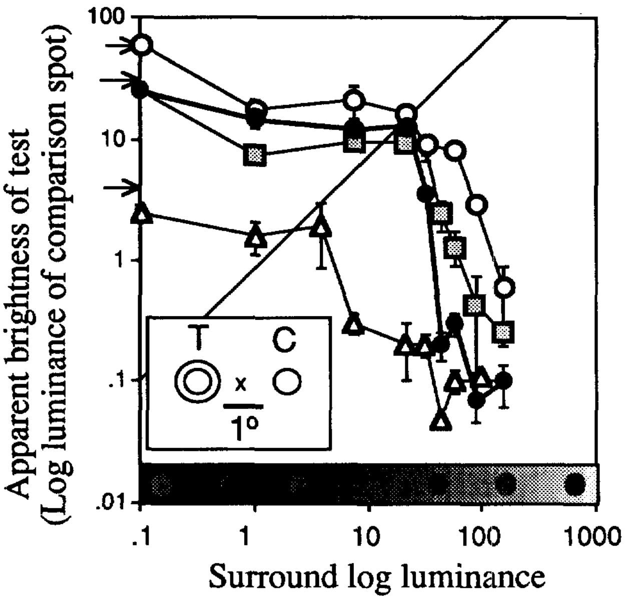

FIGURE 2. Heinemann (1955) curves. Stimulus, shown in inset, was a 0.7 deg test spot T in a 1.4 deg surround. Observer matched appearance of test spot by adjusting comparison spot C. When simultaneous contrast was induced into the spot the slope of the right-hand part of the curve was steeper for a flickering spot (filled circles) than for a white, grey or black test spot. The arrows on the left by the ordinate show the true luminance of each spot, and the oblique line of unit slope joins the points for which the spot and surround had the same luminance.

In Experiment 2, the test spot and the comparison spot were positioned so that their centres lay 1.25 deg to the left and right of a small fixation cross (Fig. 2, inset). The test spot was either grey or flickering at 15 Hz, but always had the same time-averaged luminance of 71 cd.m^{-2}. It was centred in an annulus of outer diameter 1.4 deg, whose steady luminance was preset by the experimenter. The rest of the screen was black. The observer adjusted the variable luminance of the comparison spot by striking two keys, until it appeared to match the subjective brightness of the test spot. All settings were recorded for later analysis. In Experiment 2 only, to avoid unwanted interactions between the two spots, the test spot and its surround were presented to the left eye only and the comparison spot to the right eye only, by means of a prism stereoscope and a septum. To prevent unwanted effects from variations in pupil size, the observer viewed the display through 2.5 mm diam. artificial pupils. In Experiments 1, 3–8 and 10–11 we used binocular viewing without artificial pupils. Experiments 8 and 9 used the prism stereoscope.

RESULTS

Experiment 1: Magnitude estimates of flicker-augmented contrast

We demonstrated flicker-augmented contrast (FAC) to a classroom of 55 naïve undergraduates, using a method of magnitude estimation. A video projector cast steady and flickering disks on to a large screen at the front of the room, and students rated the apparent brightness of each disk on a scale from 0 (black) to 100 (white) by writing numbers on a pre-printed form. The main effect was that a flickering disk looked lighter on a black surround, and darker on a white surround, than a steady grey disk.

The disk diameters (18 cm on the screen) ranged from 2.57 deg arc for students at the front of the class to 35 min arc for those at the back. Four disks were presented: a steady grey disk on a white and on a black surround, and a light/dark flickering disk on a white and on a black surround. Expressing all luminances as a percentage of white, where white (=100%) was 3.3 cd.m^{-2} on the projection screen, the luminances of the light and dark phases of the flickering disk were 20 and 80%, and the mid-grey steady disk was 50%.

All ratings were rescaled by subtracting 50 from them. Thus positive [negative] ratings indicate that subjects saw the disk as apparently lighter [darker] than the mid-grey surround. Results: Changing the surround from white to black had little effect on the estimated brightness of a steady grey disk, which was rated at −4.5 on a white surround and +3.7 on a black surround. However, it greatly affected the flickering disk, which fell to −13 on a white surround and rose to +14.4 on a black surround. Thus, the flickering disk looked much darker than the grey disk when on a white surround, and much lighter when on a black surround, and its estimated brightness changed by 27.4 units, more than three times greater than the 8.3 change in the grey disk. These results show that FAC was robustly visible to large groups of naïve observers, even in poorly controlled classroom conditions. Our next experiment measured FAC more precisely.

Experiment 2: Heinemann curves for flickering vs steady test spot

The subjective brightness (equivalent to comparison log luminance) of various test spots was measured as the surround luminance ranged from 0 to 180 cd.m^{-2} (Fig. 2: mean of two observers × 3 trials). We compared a spot flickering at 15 Hz with a grey spot of the same mean luminance. We also used a black spot and a white spot—the two components of the flickering spot. To anticipate, the flickering spot showed flicker-augmented contrast (FAC) in the form of a much steeper Heinemann curve for spatial decrements.

The upper, middle and bottom curves joined with thin lines are the data for a steady white, grey and black test spot, respectively. The arrows on the left by the ordinate show the true luminance of each spot, and the oblique line of unit slope joins the points for which the test spot had the same luminance as the surround. In the region below and to the right of this oblique line, the test spot was darker than the surround (a spatial decrement). For surrounds that were lighter than the test spot (upper left field), the test spot remained perceptually constant (Fig. 2). However, once the surround luminance reached and surpassed that of the test spot (lower right field) the test brightness fell off sharply, demonstrating the brightness contrast sketched in Fig. 1(b) and confirming Heinemann's (Heinemann (1955)) findings.

The filled circles joined by the thick line show the results for a spot that flickered in square-wave between black and white at 15 Hz. The flicker was clearly visible but observers had no trouble in reporting the spot's brightness. Note that the right-hand portion of this curve slopes much more steeply than for a steady black, grey or white test spot. This increased slope is a measure of FAC. On a dark surround the flickering spot looked lighter than the grey spot (left hand portion of curves in Fig. 2), but when the surround became brighter than the spot, the apparent brightness of the flickering spot fell precipitously until it looked almost as dark as the black spot (right hand portion of curves). Thus, soon after either a steady black or a flickering test spot (with a black component) was made a spatial decrement it was quickly driven to appear black.

Experiment 3: Effects of depth of modulation of the test flicker

The depth of flicker modulation, defined as $(L_{\max} - L_{\min})/(L_{\max}+L_{\min})$, was 0.99 for the flickering disk and 0.0 for the grey disk in Experiment 2. We now added two intermediate modulation depths, namely 0.38 and 0.66. All four modulation depths had the same time-averaged luminance of 71 cd.m^{-2}.

Results are shown in Fig. 3 (mean of 2 observers × 3 trials). Notice that deeper flicker gave stronger FAC (steeper curves in Fig. 3). A strongly flickering spot looked somewhat lighter than a grey spot on a dark surround (left-hand end of the curves), but lost brightness precipitously as the surround luminance increased, falling below the grey spot's curve and showing that any percentage of black in the test spot served to drive its appearance quickly toward black. The curve for the deepest flicker (0.99) does not fall below that for 0.66 flicker, presumably because of floor effects which prevent it from becoming blacker than black.

Experiment 4: Flicker-augmented colour contrast

We also observed phenomena of colour contrast which were analogous to our findings for brightness contrast (Walraven, 1976, 1977). A grey spot looks bluish (or yellowish) when placed on a yellow (or blue) surround, but this colour contrast increased dramatically when the test spot flickered at 7.5 Hz between blue and yellow, or, in general, between the hue of the inducing surround and

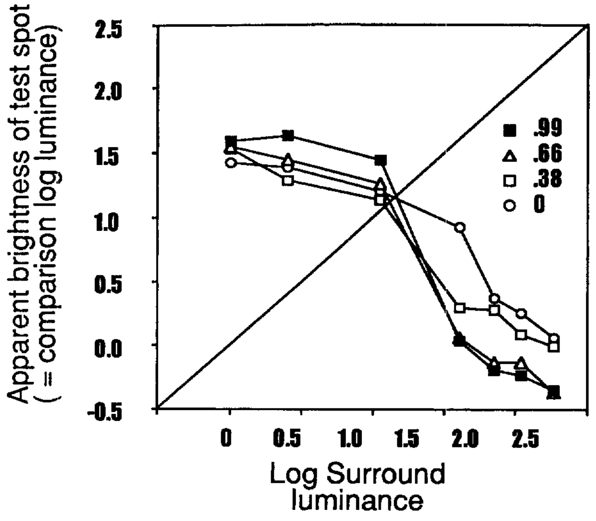

FIGURE 3. Amount of FAC depends upon depth of test flicker. Ordinates are the same as in Fig. 3. Slope of Heinemann functions was least for grey (open circles) and progressively greater for deeper flicker (0.38 = open squares; 0.66 = triangles; 0.99 = filled squares).

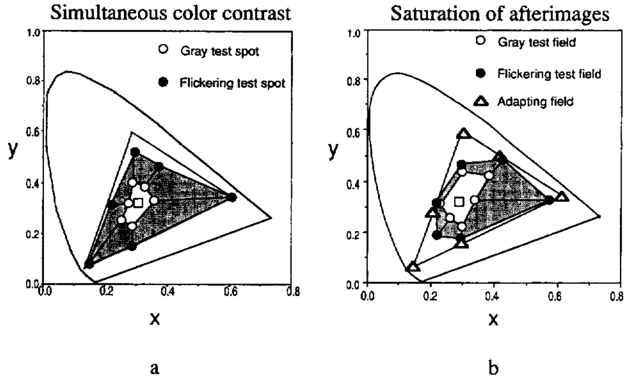

FIGURE 4. Colour contrast and coloured afterimages give broadly similar results. (a) A coloured surround induced only desaturated subjective colours into a grey test spot (open circles), but much more saturated colours into a chromatically flickering test spot (filled circles). (b) A coloured stimulus produced only weakly coloured negative afterimages on a grey test field (open circles), but much more saturated afterimages on a chromatically flickering test field (filled circles). Triangle shows range of colours available from TV screen phosphors.

its complementary colour. We used coloured annular surrounds, and the observer matched the test spot's subjective hue and saturation by adjusting the comparison spot along a colour axis that ran from blue through grey to yellow. The experiments were run for blue and yellow, for red and cyan, and for green and magenta. Colours were set to equiluminance beforehand, using a minimum flicker criterion (Wagner & Boynton, 1972). The x and y coordinates of the six stimulus surround colors are shown as triangles in the CIE plot of Fig. 4(b), and the resulting apparent hues induced into the test spots are shown as circles in Fig. 4(a).

Each coloured surround induced its complementary hue into the test spot [Fig. 4(a)]. These induced hues were weak for steady grey test spots (open circles) but were much more saturated (filled circles) for test spots that flickered between complementary hues. The shaded area shows the increase in chromatic contrast produced by flickering the test spot as compared with having a steady grey test spot.

How can we explain these results? In the Introduction, we attributed FAC for brightness to a disproportionate weighting of whichever flicker phase is higher in contrast. The same hypothesis could be extended to chromatic FAC, by taking cone contrast into account and adding the conjecture that the higher contrast phase would be overweighted independently within each cone class. To anticipate our experiments later on binocular fusion, the same cone-contrast hypothesis could also be applied to green and magenta spots which are presented dichoptically, instead of flickering. On a green (or magenta) surround we have noticed that the dichoptically fused spot looks apparently magenta (or green).

Experiment 5: Achromatic surrounds alter colour of a test spot

If FAC depends only upon disproportionate weighting of the higher contrast phase of a flickering spot, as we believe it does, then it should be possible to change the apparent colour of a flickering spot by varying the luminance of an achromatic surround. A test spot flickered at 7.5 Hz between two phases that differed in both hue and luminance, namely light green and dark magenta. The surround was achromatic, not coloured. On half the trials it was a very light grey (24.4 cd.m^{-2}), which was selected to be equiluminous with the green phase. On the other trials it was a dark grey (7.65 cd.m^{-2}), which was equiluminous with the magenta phase. These equiluminous points were established in preliminary work, using a minimum-border criterion (Wagner & Boynton, 1972). The idea was that on the dark surround the magenta would be equiluminous and therefore lacking in contrast and salience. So the visual system would downplay the magenta and perceive the flickering test spot as greenish. By a corresponding argument, on a light surround, the equiluminous green component would lose salience and the magenta component should dominate the percept.

Figure 5 plots the results in a CIE triangle (mean of 7 observers × 3 readings). The test spot flickered between the (light) green and (dark) magenta (open circles). On a dim surround which was equiluminous with the magenta, the flickering spot looked green (upper triangle), shifting upwards by 62% of the distance from grey to the green phase. On a light surround which was equiluminous with the green, the flickering spot looked strongly magenta

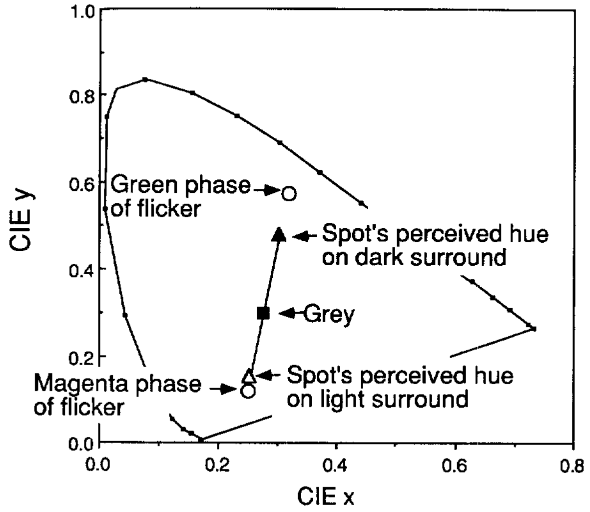

FIGURE 5. Lightness of an achromatic surround altered the perceived hue of a chromatic flickering spot. The test spot flickered between light green and dark magenta (open circles). On a dark grey surround (equiluminous with magenta) the spot looked green (upper triangle). On a light grey surround (equiluminous with green) the spot looked strongly magenta (lower triangle). This shows that the surround did not induce hues, but selected them from those available in the spot. The higher contrast phase determined the spot's appearance.

(lower triangle), shifting downwards by 87% of the distance from grey to the magenta phase. These results confirmed our contrast-weighting hypothesis. In a control condition the green and magenta were spatially mixed by a dithering technique to give a steady grey disk (solid square). Switching the surround from light to dim, which changed the apparent hue of the flickering spot, had no effect upon the apparent hue of this steady control spot.

When we first plotted Heinemann curves for a flickering test spot (Experiment 2) we believed that the test flicker was enhancing lateral inhibition. However, we have changed our minds, now that we know that the luminance of an achromatic surround controlled the apparent hue of the flickering spot. Clearly, the grey surround cannot be inducing any colours into the spot. Instead, it is selecting one of the colours that is already present in the spot, by reducing the salience of the spot's other colour. This shows that the visual system is favouring the temporal phase that has the higher contrast.

We now turned our attention from spatial interactions to temporal interactions between colours and luminance levels. We found that just as flickering the test regions enhanced simultaneous contrast, so it also enhanced the successive contrast phenomena otherwise known as afterimages.

Experiment 6: Flicker-augmented negative afterimages of luminance

Flickering the test field keeps afterimages visible for longer (Miles, 1915a, 1915b; Mooney, 1956), especially at low test frequencies (0.5–2 Hz) (Magnussen & Torjussen, 1974). We now report that test field flicker can also enhance the subjective contrast of afterimages. The observer adapted to a bipartite adapting field containing two panels, each 9.5 deg wide and 12 deg high. The inner edges of the two panels lay 0.5 deg to the left and right of the fixation point.

Figure 6(a) (inset) shows a black and a white adapting panel, with the test panels either grey or flickering (G/F) on different trials. In practice, we measured the afterimages from black and from white on different trials, so the left adapting panel was black, or white, and the right control panel was the same mid-grey as the surround. We used a "topping-up" adaptation method. Following an initial 30 s of adaptation, a bipartite test field was exposed for 1 s, then replaced by the adapting field for 5 s, and so on repetitively. The left test panel was mid-grey in control sessions and flickered between black and white in experimental sessions. This left panel looked lighter or darker owing to the previous adaptation to black or white. The luminance of the right test panel was adjusted by the observer, by striking two keys, until he or she was satisfied that this luminance matched the appearance of the negative afterimage in the left panel. All settings were recorded.

Results are shown in Fig. 6 (mean of 3 observers × 2 readings). Following adaptation to white (lower curve), a grey test panel looked somewhat darker and a flickering test panel looked much darker. Following adaptation to black (upper curve), a grey test panel looked somewhat lighter and a flickering test panel looked much lighter. Thus, the flickering test field greatly increased the apparent contrast of the negative afterimage.

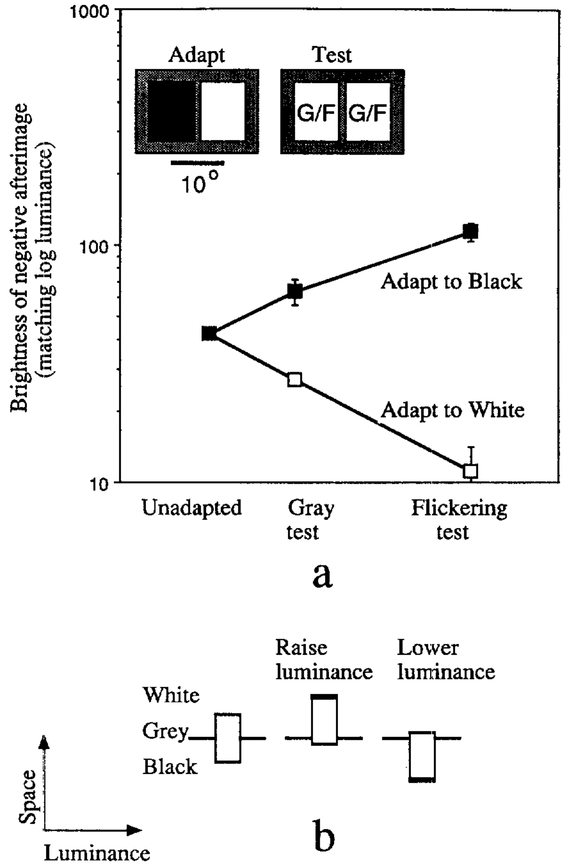

FIGURE 6. (a) Achromatic afterimages. Observers adapted to black or white stimuli (inset), and observed their afterimages on a test field that was grey (G) or flickering (F). Following adaptation to white [or black], the afterimage was much darker [or lighter] on a flickering test field than on a grey test field. Thus, test flicker increased the subjective contrast of afterimages. (b) Afterimage can be simulated by raising the luminance of both flicker components (centre) of the test field, thereby increasing the contrast of the lighter component (heavy line) which now dominates and makes the field look very light. Lowering the luminance (right) favours the darker component (heavy line) and the patch looks very dark.

In summary, flickering the test field enhanced not only simultaneous contrast but also successive contrast. We believe that the effects of a light or dark afterimage resemble viewing the flickering test field through a physical filter, since physically raising (or lowering) the luminance of both flicker components in the test field by an equal amount will necessarily move one of the components closer to the surround luminance, thereby reducing its contrast and favouring the other component. We simulated a light afterimage by adding equal luminance to both flicker components of the test field [Fig. 6(b)]. Result: the dark component lost contrast as the light component gained contrast against the mid-grey surround, and the flickering field looked much lighter.

We simulated a dark afterimage by darkening both components equally, so now the lighter component lost contrast as the dark component gained contrast and the flickering field looked much darker. The same luminance changes applied to a steady grey control patch had far less effect than on the flickering field. No actual afterimages were present during these simulations.

We conclude that the perceived change in the afterimages is really another demonstration of flicker-augmented simultaneous contrast.

Experiment 7: Flicker-augmented coloured afterimages

Coloured afterimages could also be enhanced. The adapting panels used in Experiment 6 were now coloured and the test field flickered between the adapting hue and its complement. The subjective hue and saturation of the afterimages were measured by the same matching procedure as before. Following adaptation to a bipartite coloured field that was blue on the left and yellow on the right, a uniform grey test field appeared weakly tinged with yellow on the left and blue on the right, owing to the presence of a negative coloured afterimage. If the observer re-adapted and now viewed a uniform test field that flickered between blue and yellow (not black and white), this flickering field appeared strongly yellow on the left and strongly blue on the right. Coloured afterimages were also augmented for the other colours we used, namely green and magenta, and red and cyan.

The adapting panel to the left of the fixation point was set on different runs to a saturated blue, yellow, red, cyan, green, or magenta. The CIE x and y coordinates of these adapting panels are shown as triangles in Fig. 4(b). The test panel on the left was either grey, or chromatically flickering between the adapting hue and its complement. Thus, for an adapting field that was blue or yellow, the test field on the left flickered between blue and yellow at 15 Hz (suprathreshold). The observer adjusted the matching panel on the right, using two computer keys, along a colour axis ranging from blue through grey to yellow, until it matched the subjective appearance of the negative coloured afterimage. On other runs, the observer adapted to green or to magenta (test field flickered between green and magenta), or to red or cyan (test field flickered between red and cyan).

Results are shown in Fig. 4(b) (mean of 3 observers × 2 trials). The negative coloured afterimage seen on the test field was always shifted toward the complement of the adapting hue. For instance, adaptation to blue [or yellow] gave a yellow [or blue] afterimage on a grey test field (open circles), but a much more saturated yellow [or blue] afterimage (filled circles) when the test field flickered between blue and yellow. Other colours gave similar results. For each pair of points connected by a line in Fig. 4(b), the test field differed but the adapting stimulus was exactly the same. The grey shaded region in Fig. 4(b) represents the increased saturation produced by flickering the test field. Results for colour contrast and for coloured afterimages were generally similar [cf. Figure 4(a) and (b)].

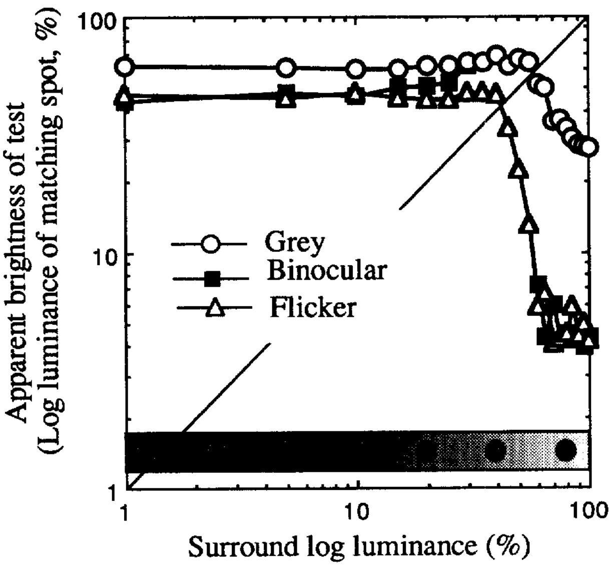

FIGURE 7. Results of Experiment 8 show that simultaneous contrast was only moderate for a grey test spot (circles) but was strongly augmented when two test luminances were presented either in alternation at 15 Hz (triangles) or dichoptically (filled squares). Conventions are the same as for Figs 2 and 3.

Flicker and binocular vision both combine two luminances. Flicker is not the only case in which the visual system combines or averages two brightness levels together. Another case is binocular fusion. We asked before: If a single disk flickers between light grey and dark grey, what is the perceived lightness of the flickering disk? We shall now ask: If the eyes binocularly fuse in a stereoscope a pair of disks, one light grey and the other dark grey, what is the perceived lightness of the fused disk? In what follows we shall compare the luminance combination rules for flicker and for binocular fusion, and we shall show that in different conditions the combination can be based upon linear averaging, quadratic averaging, or a winner-take-all rule. Quadratic and winner-take-all combinations imply a disproportionate weighting of the higher contrast component, which, we shall argue, is the basis of flicker- and binocular-augmented contrast. We have also discovered that two well known illusions of binocular vision, namely Fechner's paradox (Fechner, 1860) and Levelt's (Levelt, 1965) contour effect, have temporal analogs in the flicker domain. Lastly, most of these effects are robust enough to show to a classroom of naïve observers.

Experiment 8: Simultaneous contrast is augmented by flicker and by binocular fusion of unequal luminances

Experiment 8 shows that simultaneous contrast can be enhanced not only by flicker but also by binocular fusion of two unequal luminances. We compared the apparent brightness of a steady mid-grey disk, a flickering disk and a binocularly fused disk when these were seen against an annular surround which was varied in luminance over a 2 log unit range (Fig. 7). The disk diameter was always

0.7 deg and the annulus diameter was 1.4 deg of visual angle. Expressing the luminances as percentages of white, where white (=100%) was 64.8 cd.m^{-2}: the luminance of the surrounds ranged in 5% steps from 1 to 100%; the mid-grey disk was 50%; the flickering disk alternated between 20 and 80%, and the binocularly fused disk was 20% to one eye and 80% to the other eye. (Of course, the time average of 20 and 80% was equal to 50%). Free viewing with eye movements was permitted. To avoid eye bias, the luminance seen by each eye was switched on half the binocular trials, for a total of four readings per datum point. The observer matched the perceived lightness of the grey, flickering or binocularly fused test disks when seen against each luminance value of the surround, by striking two computer keys to adjust the luminance of a comparison spot until it appeared to match the test disk. The comparison disk was always presented against a black surround.

Results are plotted in Fig. 7, in which the conventions, though not the parameters, are the same as in Figs 2 and 3. Typical SE bars were smaller than the plotting symbols. Figure 7 shows that simultaneous lightness contrast was strongly enhanced by flickering or dichoptic presentation of a light/dark test spot. All three test spots were relatively unaffected by a dark surround (Heinemann, 1955), but when the surround luminance approached or exceeded that of the test spots, the perceived brightness of the spots started to fall (right-hand half of curves in Fig. 7). Whereas the steady grey test spot fell off by only 0.3 log units for our most luminous surround, the brightnesses of both the flickering and the binocularly fused test spots declined precipitously through one log unit. Thus, the effects of simultaneous contrast were tripled, either by presenting two test luminances dichoptically or by presenting them sequentially as flicker. It made little difference whether the two luminances were presented across eyes or across time. We conclude that in both cases the visual system systematically overweighted the spot that had the higher contrast.

Note that there is a gap in the results for binocular fusion (black squares) in Fig. 7, when the surround lay in the intermediate range (approximately 20–80%) for which the spot was a spatial increment in one eye and a spatial decrement in the other. In these conditions the observer reported strong binocular rivalry: the test spot's perceived brightness fluctuated considerably over time as first one eye then the other dominated the percept, making it impossible to find a unitary brightness match. We also noted a similar but weaker effect in the flickering spot, which acquired a lustrous or metallic appearance (Magnussen & Glad, 1975c) which we shall call monocular lustre. This was seen only when the two flicker phases straddled the surround luminance, so that the spot alternated between being an increment and a decrement. However, this monocular lustre was much weaker than binocular rivalrous lustre and did not preclude judgments of the unitary brightness of the flickering spot.

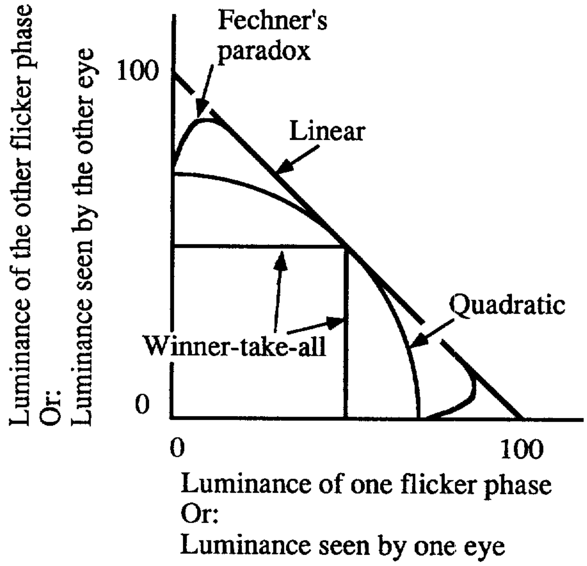

FIGURE 8. Possible functions when two luminances are combined include linear averaging, sometimes modified by Fechner's paradox near the axes: winner-take-all; and quadratic averaging (winner take most). Both phases receive equal weighting in linear averaging, but in all the other functions the higher contrast phase receives a disproportionate weighting.

For all three types of test spots—grey, flickering and binocularly fused—we found that decrements but not increments underwent strong brightness induction from a luminous surround. Schirillo & Shevell (1996) also found asymmetries between spatial increments and decrements when they compared the brightness induced into a grey test patch by a uniform surround vs a checkerboard surround.

Binocular brightness summation. Binocular summation has recently been ably reviewed by Howard & Rogers (1995), ch. 9. Levelt (1965) presented a 3 deg luminous disk to corresponding points on each eye. One disk was held at a fixed luminance while the subject varied the disk presented to the other eye to match a constant, binocular comparison disk. Standard and comparison disks were presented sequentially in the centre of the visual field. Some of the possible equal-brightness curves that one might expect to find in such an experiment are diagrammed in Fig. 8. The oblique line with a slope of -1 shows linear averaging. The brightness of the flickering spot depends on the mean of its two luminances, so the condition for constant brightness is: L_1+L_2 = constant.

When both phases of the test spot have the same luminance, the test and comparison spots are an identical steady grey. As the luminance of one test phase is increased, the luminance of the other phase would have to be decreased by the same amount to maintain the match with the comparison spot. This linear average applies an equal weighting to both components.

Another possibility is that the higher contrast phase of the flickering spot would receive a higher weighting than the lower contrast phase, and would predominate in the perceived brightness. This could happen in many possible ways, but Fig. 8 shows two simple ones. The circle centred on the origin in Fig. 8 would result from a process of quadratic averaging:

$$L_1^2 + L_2^2 = \text{constant}.$$

This gives a disproportionate weighting to the phase of the flickering spot that differs more from the surround, that is, the phase with the higher contrast (Engel, 1967, 1969, 1970; Curtis & Rule, 1978; Legge & Rubin, 1981). Legge (1984) presented binocularly fused, congruent gratings of different contrast to the two eyes. His results were well fitted by quadratic summation, which provided a good, first-order account of binocular summation in contrast detection, contrast discrimination, dichoptic masking, contrast matching, and reaction time studies. Legge presented a binocular energy-detector model based upon Green & Swets (1974), in which all information presented monocularly was funnelled through a single, binocular conduit.

Finally, the vertical and horizontal lines in Fig. 8 show a more strongly nonlinear "winner take all" function, in which the observer simply perceives the overall brightness of the flickering spot as equal to the higher-contrast phase. L_1 has the higher contrast and wins out along the vertical line, whereas L_2 has the higher contrast and wins out along the horizontal line. This is the most disproportionate weighting of all. It could perhaps be modelled as:

$$L_1^n + L_2^n = \text{constant}$$

where $n \gg 2$, but more conservatively it could be expressed simply as: $\max(L_1, L_2) = \text{constant}$

Levelt's results (1965) resembled the linear averaging straight line in Fig. 8, except that the ends of the lines hooked back near the axes, owing to Fechner's paradox. In Fechner's paradox, a light grey spot on a black surround seen by one eye looks darker when paired with a dim grey spot in the other eye than when paired with the black surround (no spot) in the other eye. Yet of course the mean of light grey + dark grey is higher than the mean of light grey + black. In this situation more luminance was required in the brighter disk to match the comparison stimulus when the dimmer disk was visible than when there was no stimulus in the other eye. Levelt explained his results by supposing that the binocular impression of brightness (B) was determined by the weighted sum of the luminances of the monocular stimuli:

$$B = w_l E_l + w_r E_r.$$

For instance, Fechner's paradox would arise if the zero-contrast (absent) disk in one eye received zero weighting, leaving the binocular impression of brightness to be determined entirely by the bright disk in the other eye. See also De Weert & Levelt (1974); Gilchrist & McIver (1985); Irtel (1986) and Gregson (1989).

Levelt assumed that dichoptic luminances rather than brightnesses were averaged, but Teller & Galanter (1967) showed that the brightness of dichoptically viewed patches varied with monocular brightness, not monocular luminance.

The physicist Erwin Schrödinger suggested (Schrödinger (1926)) that the weight assigned to each monocular input was the ratio of the signal strength from that eye to the sum of the strengths of the signals from both eyes. Macleod (1972) extended this idea by proposing that the strength of a neural signal is a logarithmic transform of the contrast. When he replotted Levelt's data on logarithmic coordinates he predicted, and obtained, a circle passing through (not centred on) the origin, showing that Levelt's data could be well fitted by Schrödinger's equations.

Experiment 9: Luminance combination rules compared for flicker and binocular fusion

We decided to compare the luminance combination rules for flicker and for binocular fusion by collecting equal-brightness curves. In Experiment 8 above, we used a fixed pair of luminance levels (20 and 80%) and adjusted a comparison disk to match. This time we used a fixed comparison disk of luminance L_0 and adjusted the pair of flickering (or binocularly fused) luminance levels L_1 and L_2 to match L_0.

The comparison disk, a steady grey spot of diameter 0.7 deg, was set to a fixed luminance L_0, say 50%. The flickering disk alternated between two luminances: L_1 (randomly selected from the set 0, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 95 and 100%) and a second luminance L_2, which the observer selected such that L_1 alternating with L_2 subjectively matched L_0. The surround for all the spots filled the rest of the screen and was black (0%) or white (100%) on alternate blocks of trials. Within each block, values of L_1 were selected randomly, and three readings were collected for each value. The entire procedure was repeated for four values of the comparison luminance L_0, namely 22, 33, 50 and 70%. This procedure gave pairs of luminances (L_1, L_2) which all subjectively equalled a fixed luminance L_0.

In the binocular conditions, the procedure was exactly the same, except that now each eye saw a separate disk presented on a split monitor screen. The disks had luminances L_1 and L_2 and were fused binocularly by means of a prism stereoscope aided by a sagittal septum. To avoid eye bias the luminances L_1 and L_2 were switched across eyes on half the trials, for a total of four readings per datum point. The comparison stimulus L_0 was always seen by both eyes.

In Fig. 9 we plot not the raw luminance values, L, but the luminance excursions (LEX). On a black surround LEX is simply the spatial increment L, and on a white surround it is the spatial decrement, namely (100% − L). Thus the luminance excursion LEX is equal to abs(L). Note that on a black surround luminance and contrast both increase in step with LEX, but on a white surround contrast increases with LEX but luminance decreases. For both spatial increments and decrements, the larger the LEX, the greater the contrast. Thus the spot luminance

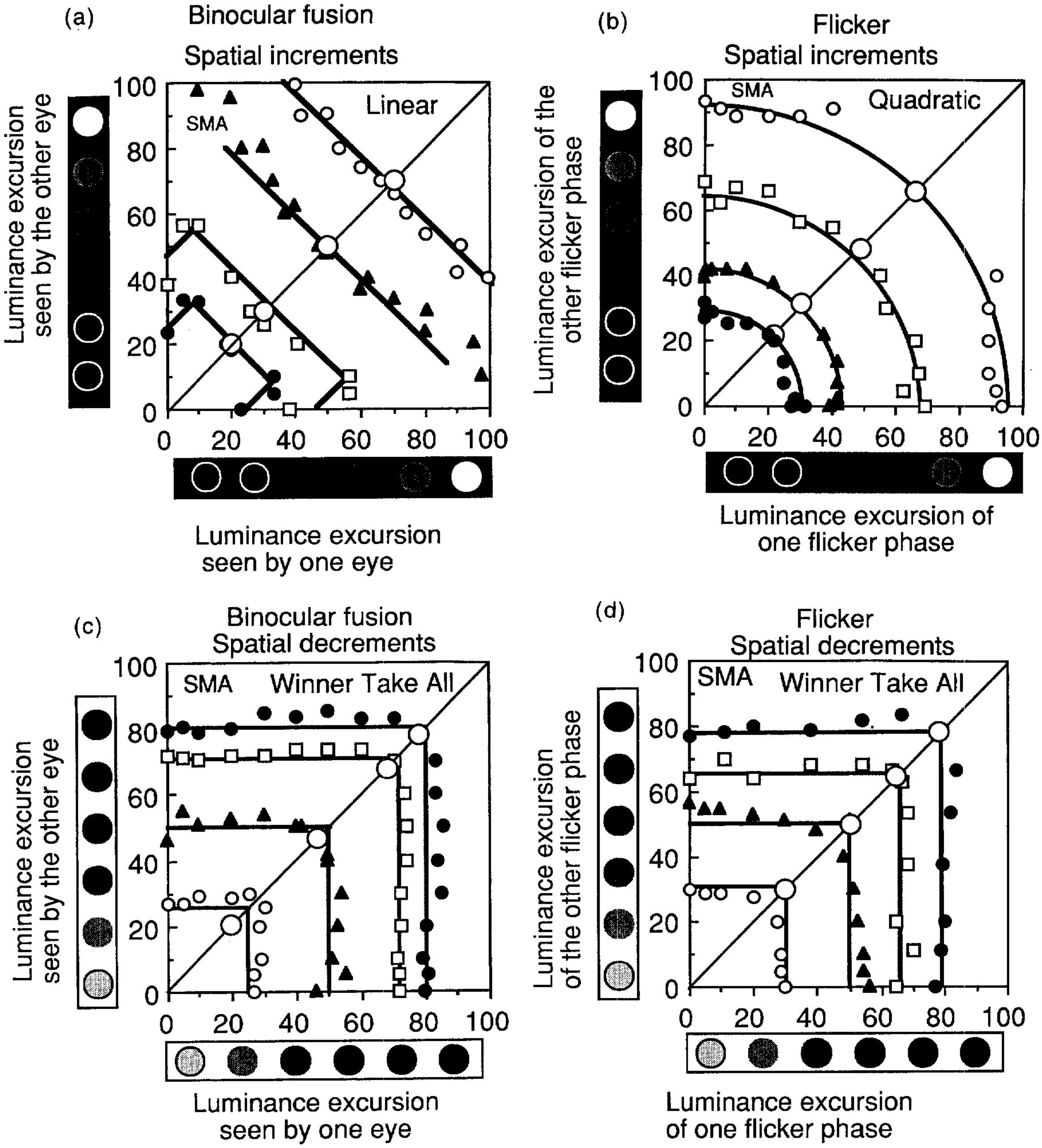

FIGURE 9. Results of Experiment 9 (observer SA). Luminance excursions (LEXs) (=spatial increments or decrements) which were set to match the appearance of pairs of LEXs. The four equal-brightness functions within each graph show the luminance combinations (LEX_1, LEX_2) that subjectively matched the four steady grey values of LEX_0 that lie on the positive diagonal (large circles), namely 22% (solid circles), 33% (squares), 50% (triangles) and 70% (open circles). (a) Binocularly fused light spots on a black surround show linear averaging (straight lines), modified by Fechner's paradox (lines hooked near axes). (b) Flickering light spots on a black surround show quadratic averaging (circular functions), modified by temporal Fechner's paradox (arcs hooked near axes). (c) Binocularly fused dark spots on a white surround show L-shaped winner take all functions. So do flickering dark spots on a white surround (d). Nonlinearities indicate overweighting of higher contrast spots.

increases from left to right on the x-axis for black surrounds, but decreases for white surrounds.

Results for two observers are plotted in Figs 9 and 10. Results are shown for flicker and binocular fusion, respectively, of light spots (spatial increments) on a black surround, and dark spots (spatial decrements) on a white surround, in the following order: (a) binocular light spots; (b) flickering light spots; (c) binocular dark spots; (d) flickering dark spots. Each graph contains four equal-brightness functions comprising the luminance combinations (LEX_1, LEX_2) that subjectively matched each of the four steady grey values of LEX_0 that lie on the positive diagonal (open circles). All data points are reflected about the positive diagonal. Look first at the binocular fusion results for light spots on a black surround [Fig. 9(a), Fig. 10(a)]. The oblique −45 deg lines indicate linear

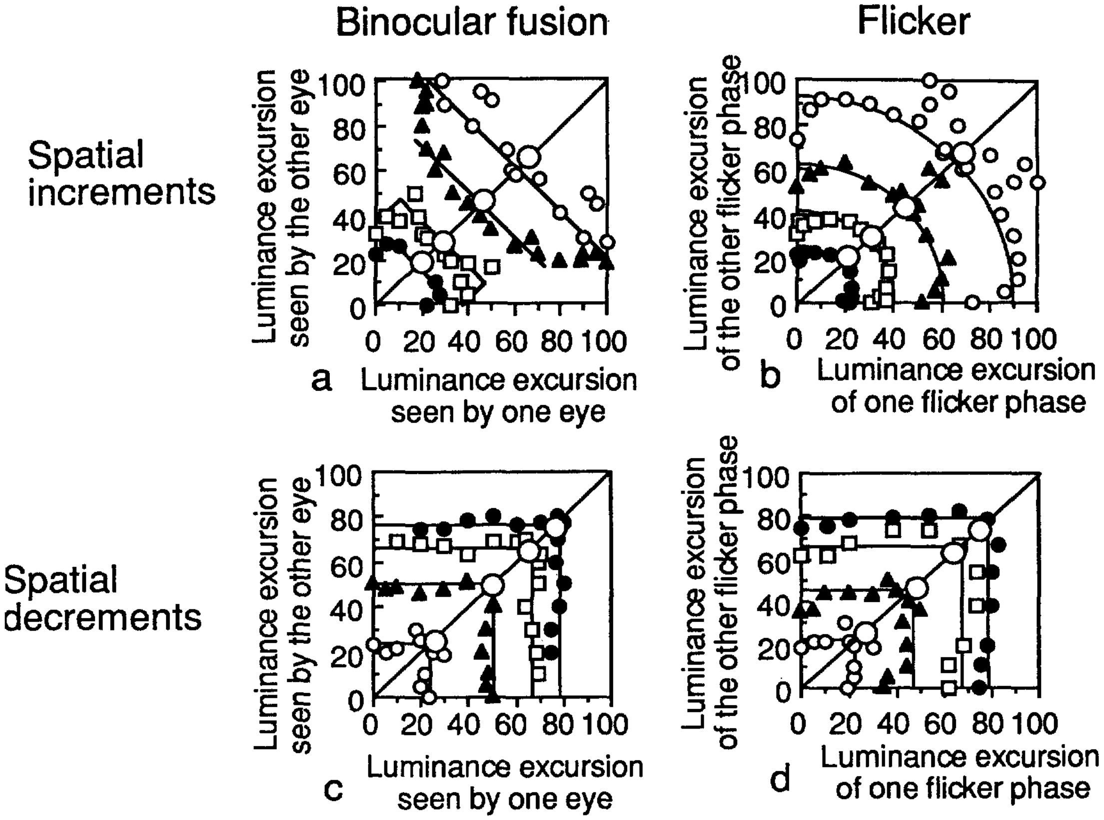

FIGURE 10. Same as Fig. 9, but results for observer KL.

averaging of the brightnesses seen by the two eyes. However, in the two lower left-hand curves the lines hook around near the *x* and *y* axes, reversing their slope. This indicates the presence of Fechner's paradox and confirm Levelt (1965), who used a 3 deg light disk on a dark surround. (The data are actually slightly concave upwards for 50% contrast, suggesting if anything a slight underweighting of higher contrasts. We cannot explain this.)

Now look at the results for flickering spatial increments on a black surround [Fig. 9(b), Fig. 10(b)]. The combination rules for flicker are different from those for binocular fusion. The circular equal-brightness functions centred on the origin betoken quadratic averaging of the two flicker phases ($\mathrm{LEX}_1^2 + \mathrm{LEX}_2^2$). This overweights the higher contrast of the two flicker phases, and this is the best description of flicker-augmented contrast.

However, flicker does share two interesting phenomena with binocular brightness fusion. First, the data curves in Fig. 10(b) for observer KL hook inwards at the ends, and this indicates that we have discovered a temporal analog of Fechner's paradox. This is to say that when a light grey disk LEX_1 alternated with a dark grey disk ($\mathrm{LEX}_2 > 0$) on a black surround, it looked darker than when it alternated with an empty black surround ($\mathrm{LEX}_2 = 0$). Yet the mean of light grey + dark grey is greater than the mean of light grey + black. Like Fechner's paradox, it can be explained by disproportionate weighting. Our second discovery is a temporal analog, which we shall describe later, of Levelt's contour effect.

The combination rules for spatial decrements on white surrounds [Fig. 9(c, d): Fig. 10(c, d), both for flicker and for binocular fusion, obey quite different functions from increments on black surrounds. For binocularly fused light spots on a black surround [Fig. 9(a), Fig. 10(a)] our results agree with Levelt (1965). Unlike Levelt, we also examined dark spots on a white surround [Fig. 9(c), Fig. 10(c)]. Here the equal-brightness functions were not straight −45 deg lines, but instead lay along a vertical and a horizontal line in an inverted L-shape. This is a pure winner-take-all strategy which massively overweighted the higher-contrast (not the higher-luminance) disk so that it determined the perceived brightness of the binocularly fused disk. Along the vertical line, $\mathrm{LEX}_1 > \mathrm{LEX}_2$, and the perceived brightness was equal to LEX_1. Along the horizontal line, $\mathrm{LEX}_1 < \mathrm{LEX}_2$, and the perceived brightness was equal to LEX_2. Dark spots on a white surround, both flickering and binocularly fused, showed the same L-shaped winner-take-all functions [Fig. 9(c, d): Fig. 10(c, d)].

In summary, the luminance combination rules for light spots were linear averaging for binocular fusion, and quadratic averaging for flicker. (Both were modified by Fechner's paradox, or its new temporal analog, at low contrast levels). For dark spots, whether fused or flickering, the rule was winner-take-all.

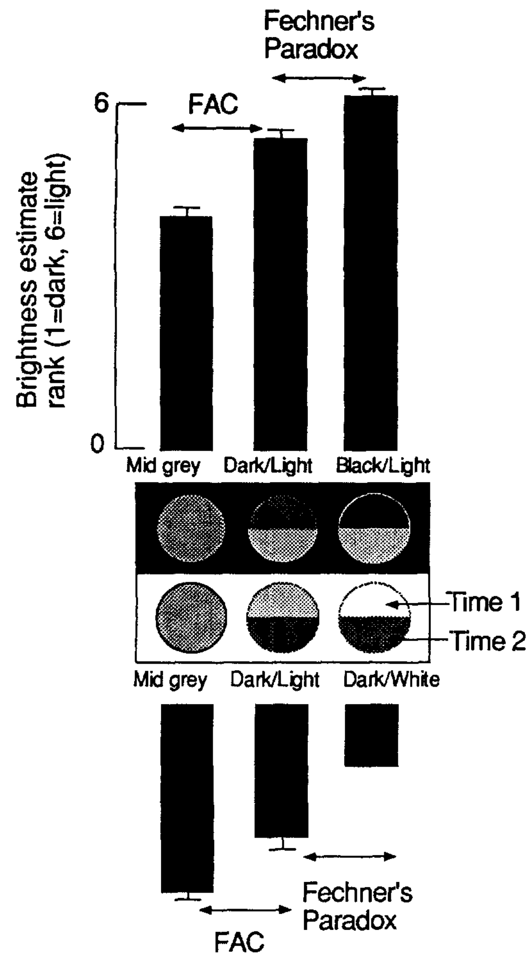

FIGURE 11. Demonstration of FAC and of temporal version of Fechner's paradox. All three disks looked brighter on a black surround (upper row) than on a white surround (lower row). The surrounds induced very little simultaneous contrast into the steady grey disks on the left. However, the simultaneous contrast was strongly augmented for the flickering disks in the middle. The surround made an even greater difference to the two right-hand disks (temporal analogue of Fechner's paradox, both for spatial increments and decrements). In the top row, the right hand disk that alternated between light and black (80 and 0%) looked paradoxically lighter than the middle disk which alternated between light and dark (80 and 20%). In the bottom row, the right-hand disk that alternated between dark and white (20 and 100%) looked paradoxically darker than the middle disk which alternated between dark and light (20 and 80%).

In the next section, Experiments 10 and 11 demonstrate two newly discovered flicker phenomena, namely temporal analogues of the binocular phenomena known as Fechner's (Fechner, 1860) paradox and Levelt's Levelt, 1965) contour effect.

Experiment 10: Temporal analogue of Fechner's (Fechner, 1860) paradox

Experiment 1 showed that a flickering spot lost far more brightness than did a steady grey disk when the surround changed from black to white. Our next new finding is that a light spot (80%) which alternated with no-spot (a featureless black region) on a black surround looked brighter than if it alternated with a dark (20%) spot. Yet the time-averaged luminance of 80 and 0% is, of course, lower than that of 80 and 20%. This paradoxical effect for flicker is the temporal analogue of Fechner's paradox of binocular fusion. We found a corresponding flicker effect for spatial decrements on a white surround: A dark spot (20%) that alternated with no-spot (a featureless white region) on a white surround looked darker than when it alternated with a light (80%) spot. Yet the time-averaged luminance of 20 and 100% is, of course, higher than that of 20% and 80%.

Results are shown in Fig. 11. Observers ($n = 26$) viewed six steady or flickering disks and estimated their brightness on a scale ranging from 0 (black) to 100 (white). To normalize against individual differences in the use of a magnitude scale, Fig. 11 shows the mean rankings for the six disks, not the raw scores. The surround was black for the three top disks and white for the three bottom disks.

Each whole disk alternated between two luminance levels, symbolised by the grey levels of the split halves. The two disks on the left were a uniform steady grey, the two disks in the middle alternated between light and dark (20 and 80%), and the two disks on the right alternated between a high contrast phase and no-disk. Thus, the top-right disk alternated between light (80%) and an empty black field, while the bottom-right disk alternated between dark (20%) and an empty white field.

The vertical bar next to each disk shows its mean estimated brightness. (The fact that the bars point up or down is of no significance; all that matters is the length of the line, and the longer the line, the brighter the disk was estimated to be.) Naturally, all the disks looked brighter on a black surround than on a white surround: the upper vertical lines are all longer than the lower lines. The surround induced very little simultaneous contrast into the steady grey disks on the left, in that the two left hand lines are of nearly equal length. However, the surround strongly affected the flickering disks in the middle, since the middle vertical line is much longer than the lower. This is an example of FAC. In addition, the surround made an even greater difference to the two right-hand disks, for which the upper and lower vertical lines differ even more in length than for the middle disks. This is the temporal analogue of Fechner's paradox, because in the top row, the right-hand disk that alternated between light and black (80 and 0%) looked lighter than the middle disk which alternated between light and dark (80 and 20%). Yet the time-averaged luminance of (80 and 0%) is lower than that of (80 and 20%). Conversely, in the bottom row, the right-hand disk that alternated between dark and white (20 and 100%) looked darker than the middle disk which alternated between dark and light (20 and 80%). Yet the time-averaged luminance of (20 and 100%) is higher than that of (20 and 80%). Thus, we found a temporal analogue of Fechner's paradox, both for spatial increments and decrements.

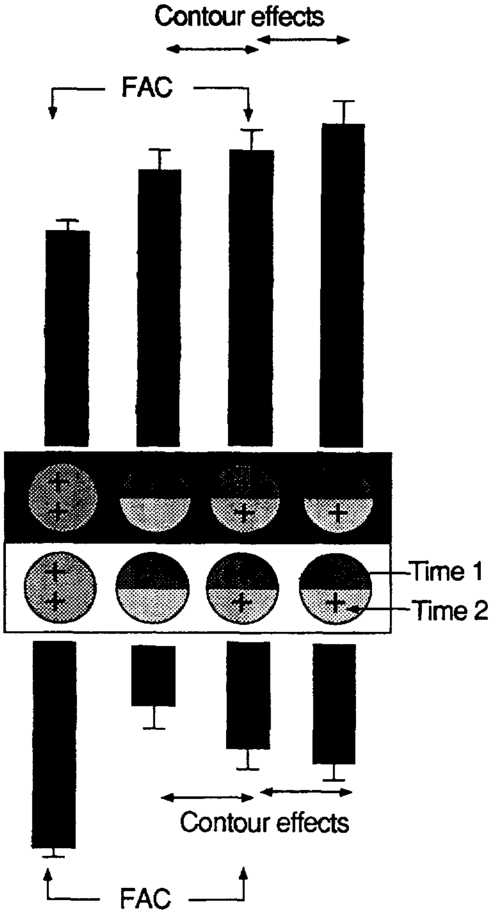

FIGURE 12. A white surround apparently darkened flickering disk 3 far more than the steady disk 1 (flicker-augmented contrast). Also, a comparison of disks 2, 3 and 4 shows a temporal analogue of Levelt's contour effect. A cross added to any phase increased the luminance weighting applied to that phase. Both in the top and bottom rows, adding a cross to the dark phase (disk 2) apparently darkened the flickering disk, whilst adding a cross to its light phase (disk 4) apparently lightened the disk.

Experiment 11: Temporal analogue of Levelt's (Levelt, 1965) contour effect

Contour is important for binocular brightness summation. Leibowitz & Walker (1956) found that the amount of binocular summation increased as the size of the stimulus was increased from 15 min arc to 1 deg, because larger areas have a smaller ratio of contour to area. Bolanowsky & Doty (1987) used brightness estimates to show that a binocular contourless Ganzfeld looked about twice as bright as a monocular Ganzfeld, so binocular summation of brightness was complete. For a 2 deg disk, binocular brightness was about the same as monocular brightness, as Levelt found. Similarly, Bourassa & Rule (1994) found that a contourless Ganzfeld produced much more binocular brightness summation and much less Fechner's paradox, compared with small targets with abrupt contours. This suggests a trade-off between suppressive and summative mechanisms in spatially tuned binocular cells. Levelt (1965) showed that a 3 deg light grey disk seen by one eye, and binocularly fused with a 3 deg dark grey disk seen by the other eye, looked mid-grey. When a 2 deg outline circle was superimposed on the light disk, the fused disk looked lighter. When the contour lay on the dark disk instead, the fused disk looked darker. Evidently the contoured disk was weighted more heavily than the contourless disk. This encouraged us to look for, and find, a temporal analogue of Levelt's contour effect in the flicker domain.

Figure 12 shows eight disks arranged in two rows against either a black or white background. As in Fig. 11, the split halves of each disk symbolise the two luminance phases between which the whole disk alternated. The lower row is like a photographic negative of the upper row. In addition, a tan-coloured cross was centred in the whole disk during certain phases. In each row, disk 1 was a steady grey (50%) whilst disks 2, 3 and 4 flickered between a light and a dark phase (80 and 20%). Disk 1 always had a steady cross visible throughout. Disk 2 had a cross centred in it only during the dark phase. Disk 3 had a cross visible throughout, during both phases, whilst Disk 4 had a cross only during the light phase.

Results (mean of 26 observers) are shown as a vertical bar next to each disk. A comparison of disks 1 and 3 shows a strong FAC effect, in that the presence of a white surround apparently darkened the flickering disk 3 far more than the steady disk 1. Also, a comparison of disks 2, 3 and 4 shows a temporal analogue of Levelt's contour effect. To summarise, a cross added to one phase increased the luminance weighting applied to that phase. Thus, in both the top and bottom rows, adding a cross to the dark phase (disk 2) apparently darkened the flickering disk, whilst adding a cross to its light phase (disk 4) produced an apparent lightening. We conclude that luminance weighting favours contoured over non-contoured regions. Presumably when the contours of a cross seen during one temporal phase are competing against a zero-contrast uncontoured region during the other phase, the cross has the higher contrast and hence wins out. Thus, our hypothesis, that a high-contrast edge wins out over a low-contrast or zero-contrast (invisible) edge which alternates with it over time, can explain our discovery of FAC and of the temporal versions of the Fechner and Levelt effects. Together, these phenomena demonstrate parallels between the rules of spatial luminance combination in binocular fusion and in temporal flicker.

There are two logical possibilities for the quadratic and winner-take-all functions in Fig. 9:

1. overweighting of high contrasts during combinations, as already suggested.
2. Alternatively, perhaps the visual system applies a nonlinear transform to stimulus contrast, followed by linear averaging.

But the fact that a disk's weighting is increased by a superimposed cross suggests that the bias towards the higher contrast phase does come from combination rules, not from nonlinear contrast response function.

DISCUSSION

Let us summarise our findings.

1. Simultaneous contrast, in which a white surround makes a grey spot look darker, was greatly enhanced by flickering the test spot between black and white. Colour contrast was likewise enhanced by flickering the spot, between (say) yellow and blue when the surround was yellow or blue.
2. Flickering the test field enhanced negative afterimages. For achromatic afterimages, the test field flickered between black and white: for coloured afterimages it flickered between (say) yellow and blue when the adapting field was yellow or blue.
3. We examined the combination rules for pairs of luminance excursions (abs[L]) which were presented either successively as flicker or else dichoptically (and fused binocularly). The contrast averaging functions for light spots on a dark surround were quasi-linear for binocular fusion but quadratic for flicker. For dark spots on a white surround they were strongly nonlinear winner-take-all for both binocular fusion and flicker. It is unclear why these functions are different, but each can be regarded as a nonlinear combination of two contrasts in which the spot with the higher contrast is weighted more strongly. Even the quasi-linear combination of binocular light spots is modified by nonlinearities near the axes which correspond to the phenomenon known as Fechner's (Fechner, 1860) paradox. This paradox itself is probably a nonlinear weighting in favour of higher contrast spots.
4. We also found temporal analogues in the flicker domain to Fechner's paradox and Levelt's (Levelt, 1965) dichoptic contour effect. We regard these as examples of nonlinear luminance combinations, favouring in both cases the spot with the higher contrast.
5. We have suggested that the visual rules for combining luminances, whether in flicker or binocular fusion, favour disproportionately the spot with the higher contrast. How well does this hypothesis hold up? The best test comes from the data in Experiment 9 which are plotted in Figs 9 and 10. In Figs 9 and 10, a linear slope indicates that all contrasts are weighted equally. Any convexity indicates that high and low contrasts are respectively over- and underweighted. Downward hooks near the axes show a zero weighting of zero contrasts (Fechner's paradox and its flicker analogue), while the circular function of quadratic averaging shows disproportionate weighting at all contrast levels. Finally, an L-shaped winner-take-all curve shows maximal overweighting of the higher contrast.

Our findings support the following luminance combination rules, as in point (3) above:

A. Light spots (spatial increments). Binocularly fused light spots undergo linear averaging, showing that all contrasts were weighted equally, except for Fechner's paradox, in which zero contrasts receive zero weighting. Flickering light spots undergo quadratic averaging, showing disproportionate weighting of higher contrasts.

B. Dark spots (spatial decrements), whether binocularly fused or flickering, undergo winner-take-all, showing 100% weighting of the higher contrast.

So our hypothesis of disproportionate weighting is confirmed as an explanation of flicker-augmented and binocular-augmented contrast, since in all the four cases in (A) and (B) the higher contrast stimulus was overweighted by the visual system. The different weighting functions for light vs dark spots may reflect some underlying asymmetry in the ON- and OFF-pathways which are thought to process light and dark spots (see Schiller, 1992; Smallman & Harris, 1996). However, it is not clear why flickering light spots are weighted differently from binocularly fused light spots.

We shall now compare our findings with the well known phenomenon of subtractive adaptation.

Multiplicative and subtractive adaptation

From starlight to sunlight, the visual world offers an intensity range of some 10 log units. Rods and cones have a far more limited response range, in the order of 2 or 3 log units (see Walraven, Enroth-Cugell, Hood, Macleod, & Schnapf, 1990). At least three mechanisms help to fill this sensitivity gap:

1. Compressive response nonlinearity (Macleod & He, 1993). This allows the visual system to respond over a wider intensity range, but at the price of losing intensity discrimination (dI/I) near the top of the operating range as the response curve flattens out.
2. Multiplicative adaptation, in which the whole response range slides up and down to match the current stimuli. Since this form of adaptation has an effect similar to putting a neutral density filter over the eye it has been termed "dark-glasses" adaptation by Macleod (1978).
3. Subtractive adaptation, which is thought to underlie brightness and colour induction, and was first suggested to explain the colour appearance of incremental lights (Jameson & Hurvich, 1964). This subtractive mechanism may be relevant to explaining our results.

Remarkably, the presence of a large adapting field has little effect on the appearance of a small incremental light. For example, a green patch of light on a larger, relatively intense red field is only slightly altered in hue by the presence of the red field. A large green patch combined with the same red surround would render the patch yellow or orange. When the green patch is smaller, it is as if the adapting field is discounted or subtracted from the response to the increment (Jameson & Hurvich, 1964; Shevell, 1978; Walraven, 1976). For reviews see Hood & Finkelstein (1986) and Walraven *et al.* (1990).

Thus, the visual system tends to discount large, steady backgrounds, so that brightness and colour appearance depend primarily on the added spatial and temporal transients. (The subtraction might be done by opponent receptive fields with on-centers and off-surrounds.) This is consistent with our finding that a flickering spot looks dark on a light surround, and light on a dark surround, because the flickering stimulus is similar to repeatedly flashed increments on a steady dark surround, and subtractive adaptation would make the increment appear lighter than a steady-state mixture. Similarly, a flashed green spot on a steady red background looks much greener than the physical (red + green) mixture seen in steady isolation would look, as shown by Walraven (1976), Walraven (1977) and Shevell (1978), and this is similar to the stimuli in our Experiment 4.

Our results extend this work in several directions. First, our flicker experiments examined the mixture of not one but two contrast components that both differed from the background. Thus, whereas earlier works have shown that a single spatial and temporal transient is readily perceived whilst its large, steady background is discounted, we have examined two spatiotemporal transients in alternation at the same location, and shown that the higher contrast transient conquers not only the background but also the competing, lower-contrast transient.

Subtractive adaptation can easily account for simultaneous contrast, both achromatic and chromatic. For instance, a grey spot will look darker in a white surround because subtractive adaptation deducts the luminance of the surround from the perceived brightness of the spot. However, subtractive adaptation cannot, by itself, explain why flickering the test spot increases the simultaneous contrast and makes the spot look darker still. For coloured spots and surrounds, subtractive chromatic adaptation could explain why a grey spot looks greenish when surrounded by magenta. But it cannot explain why the spot looks greener still when it flickers between green and magenta. This is brought out most clearly in Experiment 5, in which a spot flickered between light green and dark magenta. Compared with a large field that flickered between the same two colours, the spot looked more magenta when it was surrounded by a white background, and it looked greener when it was surrounded by a black background. These changes in the perceived hue of the spot cannot be explained by any subtraction of the achromatic (black or white) background. With these flickering spots, one could argue that some process of temporal differentiation is enhancing the subtractive process (Arend, 1973). But this does not explain the analogous effects which we showed in binocular fusion of steady grey disks, where there were no temporal transients. This brings us to one more point.

Our dichoptic experiments showed that binocular fusion of steady luminances often (though not always) obey the same rules as flicker perception for luminances flashed sequentially over time. For dark spots, both binocular and flickering stimuli produced a winner-take-all response. For light spots, both binocular and flickering stimuli showed analogues of Fechner's paradox and Levelt's contour effect. Subtractive adaptation may tell us about the appearance of a single spot on a surround, but it has nothing to say about these combinations of dichoptic luminances.

The strong asymmetry between increments and decrements is puzzling. Whereas increments averaged linearly (fusion) or quadratically (flicker), decrements always followed a winner-take-all function. Thus decrements showed a stronger overweighting of the higher contrast than increments did. Where does this asymmetry come from? There are at least two possibilities.

1. It might be that a fixed white surround will hold the visual gain control constant, so that spatial decrements seen on a white surround would reveal the characteristics of the gain control with a fixed operating point. For spatial increments on a black surround the gain control would be set by the local spot luminance, so gain control would be different for each spot. The problem with this story is that our spatial decrement results showed a highly nonlinear winner-take-all function for the supposedly fixed gain control, which would then become somewhat linearised for spatial increments when the gain floated with the local spot luminance. This nonlinear gain control does not sound very plausible.
2. Looking back at the Heinemann curves in Fig. 2, Figs 3 and 7, notice the strongly asymmetrical effect of lateral inhibition from a surround, which subjectively darkens spatial increments but has virtually no effect upon spatial decrements. Spots that are darker than the surround (decrements) on the right of Fig. 7 are subjectively darkened by a light surround, but spots that are lighter than the surround (increments) on the left of Fig. 7 are barely affected. Thus, it might be that the decremental spots in Fig. 9(c, d) are subjectively darkened by the white surround first, before being averaged binocularly or over time. (It is well known that lateral inhibition operates before the point of binocular fusion, since a white surround in one eye has zero effect upon the subjective lightness of a spot seen in the other eye.) The overweighting of contrast in the winner-take-all curves of Fig. 9(c, d) may indicate the increase in subjective contrast (that is, the subjective darkening) induced into the monocular spots before binocular averaging or time-averaging, rather than being a property of the averaging itself.

In summary, we have demonstrated a number of phenomena in which a pair of congruent spots are presented sequentially in flicker perception or simultaneously in binocular fusion. All the phenomena share the common property that the visual system greatly overweights the stimulus that has the higher contrast. Since it is important to any organism to see objects as clearly as possible, it makes sense teleologically for the visual system to accept the "best" view of any object and reject any visually inferior images.

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