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COLOR PROPERTIES OF THE CONTRAST FLASH EFFECT: MONOPTIC VS DICHOPTIC COMPARISONS

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The visibility of a brief flash of light can be greatly reduced if it is followed within a few msec by a second flash falling on an adjacent portion of the retina. This type of backward masking is widely known as "metaccontrast" (Alpern, 1952, 1953; Kahneman, 1968; Weisstein, 1972). In an influential series of psychophysical papers, Alpern (1965), Alpern and Rushton (1965, 1967), and Alpern, Rushton and Torii (1970 a,b,c,d) have used a metaccontrast version of Stiles' (1959) increment threshold technique to study spatial interactions between and within Stiles' π mechanisms. Basically, their approach has been to plot test flash threshold luminance against the luminance of a surrounding masking flash (the metaccontrast analog of Stiles' threshold vs radiance curve) and analyze the effects of stimulus parameters in terms of Stiles' displacement rules (Enoch, 1972). They call the mask a "contrast flash", and refer to the test flash threshold elevation produced by it as the "contrast flash effect". Using this approach, Alpern and Rushton (1965) showed that when the test flash is being detected by a given color mechanism π_i (e.g. π_3 for a red flash), contrast flashes of different colors produce identical threshold elevations if their intensities are adjusted to be equal according to the action spectrum for π_i . (This had already been shown for the rod mechanism π_0 by Alpern, 1965). Thus, to the extent that these psychophysically defined action spectra (i.e. Stiles' *t.v. λ* curves) are the same as those of the cones themselves (cf. Enoch, 1972; King-Smith and Webb, 1974), one can say that to be equally effective at raising threshold for a flash detected by, e.g. red cones, contrast flashes of different colors must be adjusted to produce an equal response in red cones—regardless of their effect on other receptor systems. These results have quite reasonably been interpreted as showing that the contrast flash effect is "receptor-specific; the rods of the test flash were inhibited only by rods in the surround, no matter how strongly cones were also excited; red cones of the flash were inhibited only by red cones in the surround, etc." (Rushton, 1972). This interaction presumably occurs in the retina, before the signals from different receptor systems are combined by opponent process cells. On this basis, contrast flash data have been used to infer the quantitative relationship between receptor signals and light intensity (Alpern *et al.*, 1970 a,b,c,d) and these deductions (in particular, that receptor signals are linear with light intensity over a large range) have come to be widely accepted (e.g. Brindley, 1970; Rodieck, 1973).

In all of these contrast flash experiments the test and contrast flashes have both been presented to the

same eye (monoptic presentation). However it is well established (Weisstein, 1972, p. 236) that metaccontrast masking also occurs when the test flash is delivered to one eye and the masking flash to the other (dichoptic presentation). We report here the results of experiments in which we have replicated on a small scale the essential features of the color mechanism work of Alpern and Rushton (1965) using dichoptic as well as monoptic presentation. We find, as they did, that when the test flash is red, a red contrast flash raises its threshold much more than a green contrast flash of the same luminance. However we also find that a given contrast flash is equally effective in raising test flash threshold whether presented monoptically or dichoptically. In this respect, contrast flashes act quite differently than steady backgrounds, which in our experiment, and so far as we know in all previous ones, have no effect at all dichoptically (Whittle and Challands, 1969). Our contrast flashes also differ from steady backgrounds in having what appears to be a much narrower action spectrum: the difference in effectiveness between a red light and a green one, as measured by the threshold elevation of a red test flash, is much greater when these lights are used as contrast flashes than when they are used as steady backgrounds. Thus both monoptically and dichoptically our results are incompatible with the assumption that masking takes place within a single π mechanism.

These results indicate that the contrast flash effect cannot always be reliably assumed to reflect a receptor-specific inhibitory signal acting within the retina, even when the color properties of the effect seem superficially to be consistent with such a model. Thus, one must be cautious about inferring the form of retinal signals from contrast flash data.

EXPERIMENT 1

The purpose here was to compare the color properties of monoptic and dichoptic contrast flashes. The logic of our procedure was the same as that of Alpern and Rushton (1965), except for the inclusion of dichoptic presentations. As a preliminary step, we measured the increment threshold for a 10 msec red test flash superimposed, either monoptically or dichoptically, on a steady background field. This was done for both red and green backgrounds at luminances of 0, 0.1, 1.0 and 10 cd/m². We then measured threshold for the same red test flash, superimposed on a zero background, and followed after 50 msec by a 40 msec red or green contrast flash. The spectral compositions of these red and green contrast flashes were the same as those of the corresponding steady backgrounds. Contrast flash luminance was 0.1, 1.0 or 10 cd/m².

This experiment used a Scientific Prototype 6-field binocular tachistoscope (which explains the regrettably narrow range of luminances studied here). The test flash was always a single rectangular bar, 1° in width, 3° in height, presented 2° parafoveally to the left eye for 10 msec (Fig. 1A). The contrast flash was a pair of bars, each $1^\circ \times 3^\circ$, which flanked the test flash site without overlapping it (Figs. 1B and C). Steady backgrounds were provided by illuminating the entire visual field ($8^\circ \times 10^\circ$) of the tachistoscope. White fixation lines, adjusted to be just barely visible against the prevailing steady background, were continuously presented to each eye, and fusion of these lines was maintained for all trials. The stimuli were viewed at an optical distance of 62 cm, without artificial pupils. (Natural pupil viewing was rationalized on the grounds that changes in pupil size could not affect our monoptic-dichoptic comparisons, which were the primary concern here. This shortcut admitted the possibility that our steady background *i.e.f.* curves might be somewhat distorted, which would have a definite bearing on the question of whether steady backgrounds and contrast flashes have identical action spectra. An argument given in the results section shows that the maximum distortion due to pupillary effects must have been negligibly small, but in any event this first experiment was not well adapted to provide a sharp answer to that question. After the results indicated a discrepancy between contrast flashes and steady backgrounds that was too large to be discounted as an artifact, Experiment 2 was run to provide a critical test.)

Before the start of every session in the steady background condition the subject adapted to the prevailing background light: for 10 min when the background was zero, and for 3 min for each of the higher intensities. Different sessions were devoted to red, green, monoptic and dichoptic steady backgrounds and contrast flashes. At the beginning of each session the test flash threshold for zero steady background was remeasured as a check on observer reliability.

Stimulus intensities were controlled by Kodak Wratten neutral density filters and 10-turn pots which regulated the tachistoscope lamps directly. Spectral characteristics of the lights were controlled by Kodak Wratten gelatin filters: No. 29 for red, No. 55 for green. Luminances were measured by a Pritchard Model 1980 CDB photometer.

To establish threshold at each steady background and contrast flash intensity a series of 10 trial blocks were run. These trials were controlled on line by a PDP 11/20 computer. On each trial the test flash was either presented or not, on a random basis, with probability 0.5, and the subject indicated his judgment as to its presence or absence by a key press. At the end of each 10 trial block the computer provided feedback via headphones as to the number of incorrect responses in that block. To determine threshold, test flash luminance was adjusted to the lowest level at which perfect performance could be consistently maintained. The subjects were the two authors.

Results

Figures 2A and B show the results for steady backgrounds, Figs. 2C and D the results for contrast flashes. In Figs. 2A and B it can be seen that a steady background presented dichoptically at any intensity has essentially no effect on test flash threshold. Monoptically, a red steady background is more effective than a green one of the same intensity. For both subjects this difference is on the order of 0.5 log units. (That is, the green monoptic points in Figs. 2A and B fall into alignment with the red ones if they are shifted horizontally left about 0.5 log units.) This is consistent with the assumption that the test flash was being detected by the π_5 mechanism.

Figures 2C and D show that the red contrast flash was more effective than the green one at raising threshold for the red test flash. However a given contrast flash, whatever its color and intensity, appears to be equally effective whether it is presented to the same eye as the test flash or to the opposite eye. (There are six possible comparisons for each subject: For BW the dichoptic contrast flash is equally, or more, effective than the corresponding monoptic one in 5 out of 6 cases; for JY this is true in 3 out of 6.)

Figures 2C and D also show that the difference in effectiveness between the red and green contrast flashes was much greater than for the same red and green lights when they were used as steady backgrounds. These data are too rough for precise quantitative purposes, but it appears that instead of the 0.5 log unit difference found for steady backgrounds, a horizontal leftward shift of something like 1.5 log units would be required to bring the green points in Figs. 2C and D into alignment with the red ones. Unlike the steady backgrounds, these contrast flashes apparently did not have the action spectrum of the π_5 mechanism.

This last conclusion, however, rested on questionable evidence in this experiment. First, the range of intensities involved was too small to give a good picture of either the steady background *i.e.f.* curves or their contrast flash analogs. Second, there were the complications introduced by natural pupil viewing: In the steady background condition the pupils would

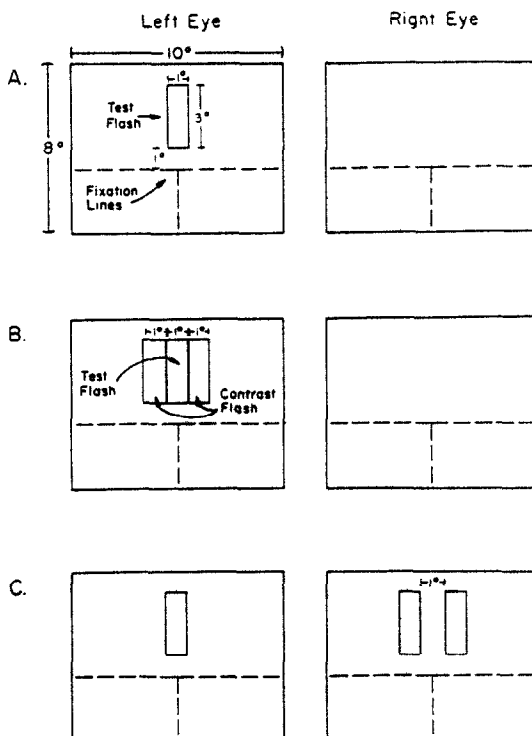


Fig. 1. Spatial arrangement of the stimuli in both experiments. Shown are the arrangements for (A) increment threshold, (B) monoptic metacontrast and (C) dichoptic metacontrast. The contrast flash fell on corresponding retinal locations in the monoptic and dichoptic viewings.

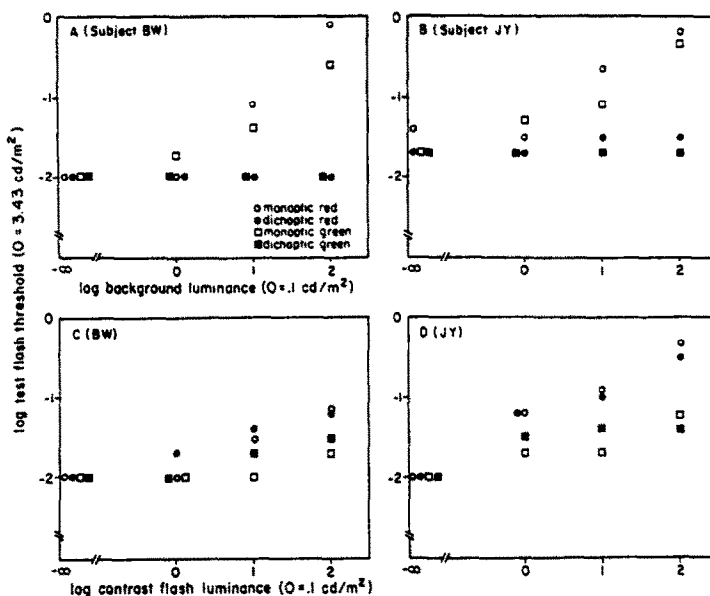


Fig. 2. Experiment 1. A and B: Increase in log threshold of the test flash as a function of log intensity of a steady background, plotted separately for each subject. In monoptic viewings the background and test flash were both presented to the left eye (open points) and in dichoptic viewings the background was presented to the right eye and test flash to the left (filled in points). Backgrounds were red (circles) or green (squares). C and D: Increase in log threshold of the test flash as a function of log intensity of a contrast flash plotted separately for each subject. Points are labelled as in A and B.

have been progressively smaller at higher luminances—perhaps somewhat more so for green backgrounds than red—whereas in the contrast flash condition pupil size would have remained constant across luminance levels. Thus it could be argued that while the contrast flash data would be expected to accurately reflect the π_3 action spectrum, the steady background data might not. This argument certainly points up a real possibility for artifact, which was eliminated in Experiment 2 by using Maxwellian view. However we do not think that controlling pupil size here would have significantly altered the results, for three reasons. First, the maximum possible distortion produced by pupillary changes in the steady background condition can be estimated, and—partly because of the Stiles–Crawford effect and partly because of the shape of the *t.v.f.* function—this proves to be negligibly small. For steady backgrounds ranging from 0 to 10 cd/m², the largest expected change in pupil diameter would be from 8 to 4 mm. If the effective retinal illuminance is corrected for the Stiles–Crawford effect (using Fig. 2 in Crawford, 1972), it follows that background luminances of 0.1, 1 and 10 cd/m² would at worst be reduced in effectiveness, relative to zero background, by the factors 0.75, 0.60 and 0.50, respectively. The same reductions would also apply to the measured increment threshold values. To correct for this in Figs. 2A and B the data points at 0.1, 1 and 10 cd/m² should be shifted downwards and to the left by at most 0.1, 0.2 and 0.3 log units respectively. If this is done, either for both red and green points, or for the green points alone, the effect is negligible, in the sense that the red and green *t.v.f.* functions still look the same, and still differ by about 0.5 log units.

Second, in actuality pupil size certainly did not

change much at all, since dichoptic steady backgrounds had essentially no effect on threshold.

Finally, in the contrast flash condition, where there was no pupillary artifact, the difference in effectiveness between red and green lights was too large to be sensibly interpreted in terms of the π_3 action spectrum. Differences as large as those shown in Figs. 2C and D (around 1.5–2 log units) would only be appropriate for monochromatic lights located at the extremes of Stiles' π_3 spectral sensitivity function (Fig. 8a in Enoch, 1972)—say at 400 and 600 nm, and it is hard to see how this much separation could be achieved with the broad band red and green lights used here.

EXPERIMENT 2

Experiment 1 showed that (a) a given contrast flash raises threshold by the same amount whether presented monoptically or dichoptically, and also suggested that (b) contrast flashes have action spectra quite different than those of Stiles' mechanisms. The evidence on the second point was, however, rather weak, because of the narrow range of intensities used, and the potential artifact introduced by natural pupil viewing. Although the latter could be largely discounted on the basis of arguments given in the last section, it was clear that these after-the-fact arguments could not be as convincing as a clean experiment. Fortunately it was possible to gain access to a Maxwellian view apparatus with which we could repeat the monoptic part of Experiment 1 on subject BW. The purpose here was simply to see whether point (b) would be confirmed in an experiment that overcame the limitations of Experiment 1. The design was the same as before, except that no dichoptic measurements were made here. As before, threshold was measured for a 10 msec red test flash superimposed on either a red or green steady background at various intensities, and then remeasured when the same

red and green lights were used as 40 msec contrast flashes. Experiment 2 used the same color filters, stimulus dimensions, and timing as Experiment 1, and differed from it only in that: (1) the stimuli were seen in Maxwellian view, which eliminated pupillary effects and allowed background intensities up to 5 log td; (2) the light source here was a Q.I. lamp instead of the gas discharge lamps used before; (3) threshold was determined here by method of adjustment: At each level of steady background and contrast flash intensity the observer adjusted test flash intensity via a neutral wedge so that the presentation with the test flash was just noticeably different than without it. Several such measurements were made, and the results are given in the form of means and confidence intervals.

Results

Figure 3 shows the results, which clearly confirm that these contrast flashes had an action spectrum quite different than that of the π_3 mechanism. The bottom panel shows test flash threshold as a function of steady background intensity (circles for red backgrounds, squares for green). The fact that the red and green points run together here means that these red and green lights had identical effects on the π_3 mechanism. However the upper panel shows that when the same lights were used as contrast flashes their effects were very different: In this case the red light was more effective than the π_3 equivalent green by a factor of 100. (That is, by an amount corresponding to a 2 log unit leftwards shift of the green points. The straight lines in the figure are least squares fits; each has a slope of 0.2.) Apparently the effectiveness of these contrast flashes was governed by an action spectrum much narrower than that of a Stiles' mechanism—as though the differences between the red and green lights had been sharpened by an opponent process.

(The stimulus intensities in Fig. 3 are specified in relative rather than absolute units because we were not equipped to make an accurately calibrated photometric measurement of our color fields and the logic of the experiment did not require one. The most accurate specification we can give is that 0 log units on the vertical scale corresponds to the retinal illuminance of a 6.2 log td Q.I. field seen through a No. 29 Wratten filter, while on the horizontal scale 0 corresponds to a 5.9 log td field seen through either a No. 29 filter (in the case of the circles) or a No. 55 (for the squares). As a rough approximation these values would correspond to something like $0 \approx 5$ log td on the vertical axis, $0 \approx 5$ log td on the horizontal axis for red points, $0 \approx 4.5$ log td on that axis for the green points. However, it should be understood that rescaling in terms of absolute intensity units would have no effect on our substantive result, since the separation between the red and green contrast flash *t.u.r.* curves would always be 2 log units greater than the separation between the corresponding steady background curves, just as in Fig. 3.)

DISCUSSION

The strikingly precise quantitative results of Alpern and Rushton (1965) provide strong evidence that under some circumstances the contrast flash effect measures a receptor-specific inhibitory interaction at the retinal level. On the other hand, our results indicate that under some circumstances such an interpretation is quite untenable. One obvious suggestion is that there are two distinct types of contrast flash effect, one retinal in origin and receptor specific, the other central and governed by spectral sensitivities appropriate to color signals that have been sharpened

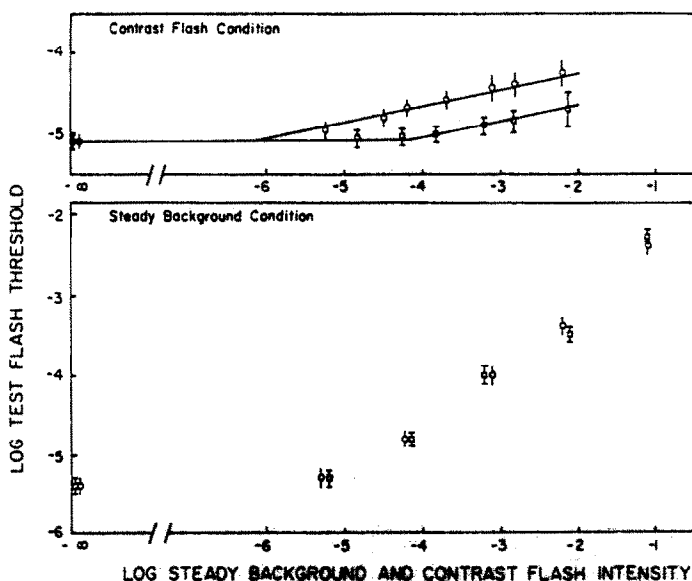


Fig. 3. Experiment 2: Test flash threshold as a function of steady background (lower panel) and contrast flash (upper panel) intensity using Maxwellian view. (Observer BW.) Circles (squares) denote means for red (green) backgrounds and contrast flashes. Error bars indicate 95% confidence intervals. Intensities on both vertical scales represent log radiance relative to the maximum radiance of the red test flash channel. Intensities on both horizontal scales represent log radiance of the steady background/contrast flash channel relative to the maximum radiance of that channel when it contained the red (circles) or green (squares) filter.

by opponent process operations. What is not obvious is what determines which kind of effect will appear. The major difference between Alpern and Rushton's (1965) experiments and ours is that their contrast flash (a 9° disc with a 1° square hole in the center) was much larger than their test flash (a 1° square) while ours were more nearly the same size. However it is not obvious why adding area to the contrast flash at regions progressively more remote from the site of the test flash should cause the effect to seem increasingly retinal. The very large contrast flashes used by Alpern and Rushton also raise the possibility that their results might not be due to lateral interaction at all, but instead to stray light scattered onto the site of the test flash. However they have considered that possibility very carefully, and ruled it out by a number of convincing experiments (Alpern and Rushton, 1967; Alpern *et al.*, 1970a).

Another possibility, of course, is that our results are simply a fluke. This seems unlikely, for two reasons. First, Fiorentini, Bayly and Maffei (1972) have also reported threshold experiments showing that "the psychophysical effects of spatial interactions between steady light stimuli are determined primarily by events occurring before binocular interaction. On the contrary, the effects of spatial interactions between time-modulated stimuli arise, at least in part, from events that take place at or beyond the site of convergence of the neural paths from the two eyes".

Second, the results reported here for objectively determined detection thresholds are in good agreement with color related brightness reduction effects that can readily be observed above threshold under metacontrast conditions. If a 10 cd/m^2 10 msec red test flash (e.g. a $1^\circ \times 3^\circ$ bar) is followed after about 70 msec by an equally intense 10 msec metacontrast mask (e.g. a pair of flanking bars) of the same color, its brightness is so dramatically reduced that naive observers will normally report that they have not seen any test flash at all. If the red mask is then replaced with a green one of the same luminance, the red test flash is greatly restored in visibility and seems to be hardly masked at all. And, most important, the effect works equally well dichoptically or monoptically.

One might propose to explain this suprathreshold effect in terms of an interaction within the Stiles mechanisms, since Whittle (1973) has shown that the effects of steady backgrounds on the brightness of suprathreshold flashes obey Stiles' displacement rules. Even the readily observable fact that this metacontrast color effect works equally well dichoptically could be accounted for (at least qualitatively) under this assumption, if one were prepared to believe that the Stiles mechanisms under these conditions somehow maintain their independence all the way to the cortex. However there is a simple subjective demonstration showing that the Stiles model cannot account for color effects in metacontrast brightness reduction. If one uses test and masking flashes of the same intensity and color (e.g. both 10 cd/m^2 red produced by No. 29 Wratten filters), and spatial and temporal arrangements like these described earlier, the test flash will appear hardly visible. Now if one removes the color filter from the light path of the masking flash, so that it appears white instead of red, the test flash becomes much more visible, despite the fact that the

white mask contains more energy at every wavelength than the colored one, and therefore must be more effective at stimulating all of the Stiles mechanisms, and producing a larger lateral inhibitory signal in all of them.

These suprathreshold demonstrations are quite robust under uniform changes in stimulus size and intensity, so long as one stays within ranges that lead to U-shaped masking functions. They indicate that for the brightness reduction phenomenon ordinarily thought of as metacontrast, a mask's effectiveness depends on its subjective color similarity to the test flash in the binocular field, rather than on the size of the responses that it elicits in peripheral receptor systems.

To summarize, the present experiments, together with the literature as a whole, reveal the following psychophysical puzzle. It appears that steady lights—whether used as backgrounds (Stiles, 1959; Whittle and Challands, 1969; Whittle, 1973) or surrounds (Westheimer, 1966; McKee and Westheimer, 1970), raise threshold and decrease brightness by way of a retinal process, as evidenced by their failure to have any effect dichoptically, and by their action spectra, which agree closely with those of the receptors. On the other hand, flashed backgrounds (Battersby and Wagman, 1962) and surrounds (Fiorentini *et al.*, 1972; Weisstein, 1972) can raise threshold and lower brightness dichoptically, and do not always share the action spectra of receptors. From this it would be natural to conclude that flashed masks always exert a central inhibitory effect as well as a possible retinal one. However under some circumstances, flashed surrounds (as in the contrast flash experiments of Alpern *et al.*) and flashed backgrounds (King-Smith and Webb, 1974) give every appearance of raising threshold entirely by way of receptor-specific inhibitory signals, presumably at the level of the retina. The open problem is to determine the circumstances under which masking flashes behave in this puzzling but particularly useful way.

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