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ROD–CONE INTERACTION IN THE AFTER-FLASH EFFECT

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Abstract—The brightness of a flash of light is reduced if it is followed a short time later by a second flash presented to a different region of the retina. Interaction between the rod and cone systems is examined in this after-flash effect for after-flash delays of from −300 to 1000 msec. The data indicate that rod–cone interaction in the effect can occur, and that in the dark-adapted eye the after-flash effect due to rod stimulation can lag behind that due to cone stimulation by about 100 msec.

Key Words—rod–cone interaction; after-flash effect; metacontrast.

INTRODUCTION

The after-flash effect, also known as metacontrast, is a visual masking phenomenon in which the brightness of a flash of light is reduced by the subsequent presentation of a second flash to a different region of the retina (Stigler, 1910; Alpern, 1953). The conditions governing this effect have been systematically investigated by Alpern (1953), who showed in his experiments that the reduction in brightness was strongest when the time-lag between the onsets of the two flashes was about 100 msec. Since the spectral compositions and intensities of the two flashes may be chosen so that different spectral classes of photoreceptor receive different levels of stimulation, it is possible to determine the extent to which the various photoreceptor systems interact in the phenomenon. In one such study, Alpern (1965) showed that the rod and cone systems acted independently in the after-flash effect when the delay between the two flashes was fixed at 50 msec. Alpern and Rushton (1965) arrived at a similar conclusion for the three types of cone mechanism, π_1, π_4 and π_5 (Stiles, 1949, 1953, 1959). Investigations of rod–cone interaction in other dynamical phenomena (MacLeod, 1972; Frumkes, Sekuler, Barris, Reiss and Chalupa, 1973) have, however, indicated that the difference in response times of the rod and cone systems is an important factor in determining the interaction. In the present study, rod–cone interaction in the after-flash effect is examined over a range of time-lags from −300 to 1000 msec.

METHODS

Stimuli

The test flash was formed by a disc of dia 0·6° and the masking flash by a concentric annulus of i.d. 0·7° and o.d. 1·1°. The stimuli were centred about a point 3·3° to the left of a small fixation target, and each presented for 25 msec. In the main experiment, the masking flash was green (499 nm) and the test flash red (>660 nm). The eye was fully dark-adapted. The luminance of the masking flash was fixed 0·6 log units above absolute threshold.

Apparatus

The stimuli were produced by a standard 4-channel Maxwellian-view optical system, similar to that described by Foster (1974). The single light source was a 12 V, 100 W quartz–iodine lamp run from a regulated power supply. One channel provided the test flash, one the masking flash, one the fixation target, and one a uniform adapting field. The last was used only in preliminary experiments on the time course of adaptation. The stimuli were viewed through a 2-mm artificial pupil. Special precautions were taken to minimize instrumental stray light. Two electromagnetic shutters, controlled by an electronic timer, interrupted the test- and masking-flash beams at intermediate foci. The duration of each flash was fixed at 25 msec in all the after-flash experiments. Rise and fall times did not exceed 2 msec. The time course of the stimulus sequence was monitored during the experiment with photodetectors and displayed on an oscilloscope. The luminance of each channel was adjusted with neutral density filters, and the luminance of the test-flash channel also controlled with a compensated neutral density wedge. A 499-nm interference filter (Balzers, type B20; peak wavelength 499 nm, half bandwidth 4 nm) was used to produce the green stimuli, and a long pass gelatin filter (Ilford, No. 609; cut-on point 660 nm) used to produce the red stimuli.

Procedure

The subject used a dental bite-bar and monocularly viewed the fixation target with his right eye.

Preliminary experiments were carried out to measure (a) the time course of adaptation for the 25-msec green annular flash and the 25-msec red disc-shaped flash and (b) the Stiles–Crawford effect for the red flash. Directional sensitivity was determined with the following matching technique. The red disc and a spatially coincident green (499 nm) disc were alternately presented to the dark-adapted eye for 200 msec each, in a 2-sec cycle. The luminance of the green stimulus was fixed 0·1 log units above absolute threshold, and then, for each pupil entry position, the luminance of the red stimulus was adjusted with the wedge so that, in brightness, it matched the green stimulus.

For the after-flash experiments, the procedure was as follows. The subject dark-adapted for half an hour and then set the luminance of the masking flash 0·6 log units above absolute threshold. For each fixed time-lag between the onsets of the test flash and masking flash, he adjusted the luminance of the test flash with the wedge so that it was just visually detectable. The final threshold setting was approached from below. Each measurement was preceded and followed by a separate determination of the test-flash threshold without the masking flash. The subject controlled the start of each presentation. For comparison purposes, the test flash could be blanked out and the annular flash presented alone. The time-lag between the onsets of the test flash and masking flash was varied progressively from 1000 msec to −300 msec, and the whole range traversed three times in each direction. The elevation of the test-flash threshold above resting level was specified as the difference between the wedge reading obtained with the masking flash and the mean of the two readings obtained without.

Subjects

There were two observers: DHF (the author) and GF. Each had normal colour vision and could accommodate the stimuli with the naked eye. GF was unaware of the purpose of the experiment.

RESULTS

Mechanism-specificity

The degree to which the stimuli are rod- or cone-specific is critical to this study. Figure 1 (a) shows the course of dark-adaptation for the red (>660 nm) disc-shaped test flash and for the green (499 nm) annular masking flash, following two minutes white-light adaptation to 5·8 log td at 2750°K. Figure 1 (b) shows for the dark-adapted eye the luminous efficiency of the red flash relative to the green disc-shaped reference flash, as the point of entry of the rays forming the stimuli is moved across the pupil. Distance r is measured from the optimal point of entry. Since the green reference flash, fixed 0·1 log units above absolute threshold, excites only rods, for which there is essentially no Stiles–Crawford effect (Crawford, 1937; Flamant and Stiles, 1948), the dependence of the relative efficiency η on distance r is attributable solely to the effect of the red stimulus. The smooth curve is defined by the formula $\eta = 10^{-0\cdot 5r^2}$ (Stiles and Crawford, 1933).

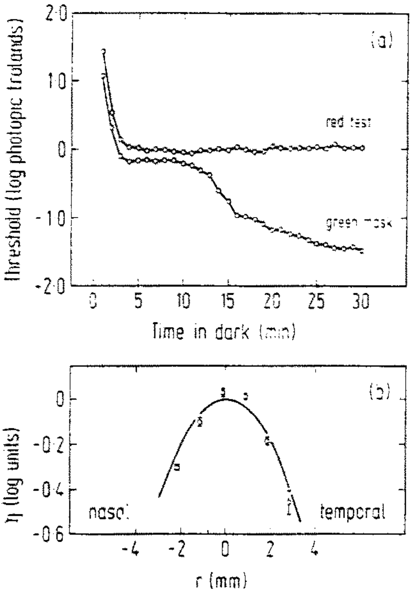

Fig. 1. (a) Dark-adaptation curves for the red (>660 nm) disc-shaped test flash and for the green (499 nm) annular masking flash. Each point represents the mean of three threshold determinations. (b) Relative luminous efficiency η of the red test flash as a function of distance r of the pupil point of entry from the optimal position. Each point represents the mean of six measurements; the vertical bars correspond to ±1 S.E. of the mean. The smooth curve is defined by the formula $\eta = 10^{-0\cdot 5r^2}$. The observer was DHF.

The red test-flash curve in Fig. 1 (a) is flat after 5 min. This, in conjunction with the evidence of the Stiles-Crawford effect of Fig. 1 (b) (see Flamant and Stiles, 1948), implies that there is no effective rod involvement in the detection of the test flash. The green masking flash curve in Fig. 1 (a) divides into the expected rod and cone branches, with the eventual rod-mediated threshold lying about 1·3 log units below the cone plateau. Since the masking flash in the main experiment is set 0·6 log units above absolute threshold, it is, at 499 nm, unlikely to produce any effective cone excitation.

After-flash effect

The main experiment concerns the effect of the green annular masking flash on the threshold of the red disc-shaped test flash at various masking-flash delay times. Figures 2 (a) and (b) show the results. Elevation of test-flash threshold above resting level is expressed as a function of the time-lag in the stimulus onsets, with negative values indicating that the masking flash preceded the test flash. For both subjects, there is a clear after-flash effect, significant at the 0·01 significance level. The magnitude of the elevation is similar for DHF and GF, and reaches about 0·25 log units at 100 msec and about 0·15 log units at 0 msec. (Recall that the magnitude of the masking flash is 0·6 log units above absolute threshold.) This after-flash effect is not due to poor fixation, since it was obtainable under conditions in which involuntary eye movements (measured with an i.r. corneal-reflection device) did not exceed 0·1°. The magnitude of the effect was furthermore found to be reduced when the disc and annulus were decentred by 0·25°.

In addition to the metacontrast, there is evidence in Figs. 2 (a) and (b) of some paracontrast (Stigler, 1910), i.e. a rise in test-flash threshold when the masking flash precedes the test flash. The effect, significant at the 0·01 level, is of magnitude about 0·2 log units at −300 msec for DHF and about 0·15 log units at −300 msec for GF. The possibility that at −100 msec the test-flash threshold is actually reduced by the annular flash, i.e. that facilitation rather than inhibition occurs, is examined later.

It does not follow immediately from the data of Figs. 2 (a) and (b) that the rod and cone systems can interact in the after-flash effect. Two other possible causes for the rise in test-flash threshold are (i) the failure of the masking flash to be sufficiently rod-specific, and (ii) the presence in the test region of scattered light from the masking flash. Note that the elevations in test-flash threshold shown in Figs. 2 (a) and (b) cannot be attributed to rod–rod interaction since in relation to the red test flash the cone system

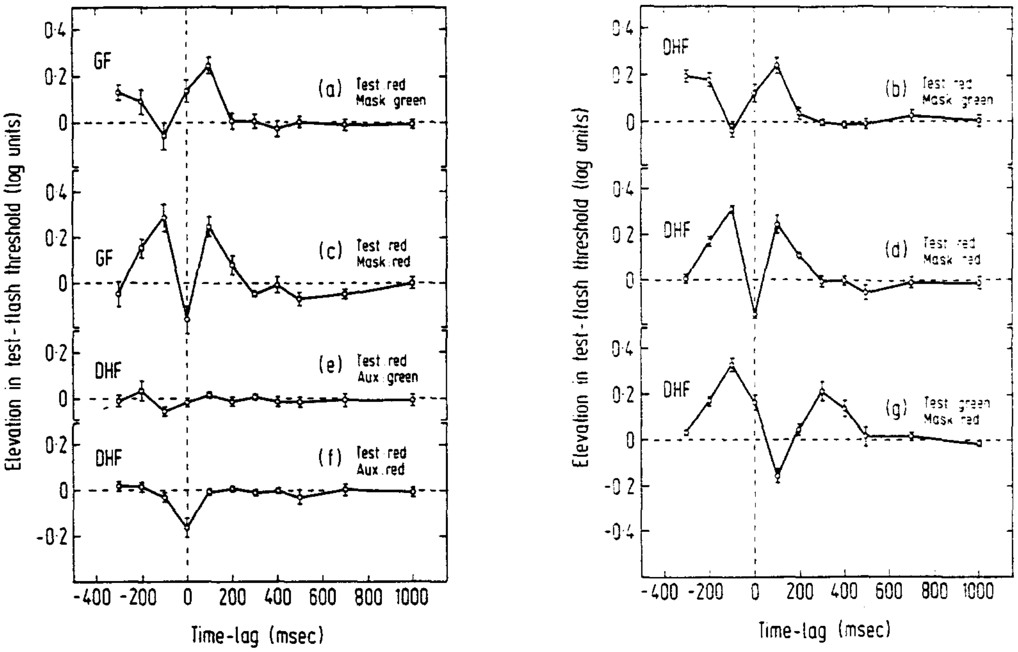

Fig. 2. (a)–(d) and (g) Elevation in test-flash threshold as a function of delay in presentation of the masking flash (e) and (f) Elevation in test-flash threshold as a function of delay in presentation of the auxiliary flash. All flash durations were 25 msec. The stimulus combination (red >660 nm, green 499 nm) and observer (GF, DHF) is indicated in each case. Each point represents in (a)–(f) the mean of six determinations and in (g) the mean of eight determinations. The vertical bars correspond to ±1 S.E.M.

is more sensitive than the rod system (by at least 0·4 log units, Fig. 1 (b)).

The hypothesis that the green masking flash achieves its effect by excitation of the red-sensitive cone system, despite the flash being 0·7 log units below the nearest cone threshold (Fig. 1 (a)), was tested in the following way. The preceding experiment was repeated with the masking flash changed from green to red (same filter as for the test), but all other parameters, including the relative luminance of the masking flash (0·6 log units above absolute threshold) kept the same. If the hypothesis is correct, a much greater rise in test-flash threshold should then be obtained corresponding to the much greater stimulation of the red-sensitive cone system (Alpern, 1953). The results of this experiment, plotted for each subject in Figs. 2 (c) and (d), show that this is not so. As with the green masking flash, the test-flash threshold is raised by the presentation of the red masking flash at both positive and negative onset delays. The maximum magnitude of the after-flash effect, however, is about 0·25 log units, and is not significantly greater than the maximum value for the green after-flash, even at the 0·1 significance level. The curves of Figs. 2 (a) and (b) may thus be concluded to reflect a genuine rod–cone interaction. The shift to the right by the red masking flash data in relation to the green masking flash data is discussed later.

Frumkes *et al.* (1973) have shown that excitation of rods by a spatially superimposed conditioning flash can lower the test-flash threshold when that is determined by cones. In the present study, it seemed likely that light from the annular masking flash scattering into the test region caused the marked fall in test-flash threshold at 0 msec delay, in the case of the red masking flash (Figs. 2 (c) and (d)), and the slight fall in test-flash threshold at −100 msec delay, in the case of the green masking flash (Figs. 2 (a) and (b)). The hypothesis that this scattered light is also responsible for the elevations in test-flash threshold, i.e. the metacontrast and paracontrast, was tested in the following way. The previous two experiments were repeated, but with the annular masking flash replaced by a scattered-light equivalent, consisting of a red or green auxiliary disc-shaped flash which had the same size as the test flash and the same duration as the masking flash. The luminance of the green auxiliary was adjusted to such a value that at −100 msec delay, the test-flash threshold was reduced by, on average, 0·05 log units (Fig. 2 (b)); the luminance of the red auxiliary was adjusted to such a value that at 0 msec delay, the test-flash threshold was reduced by, on average, 0·15 log units (Fig. 2 (d)). If the scattered-light hypothesis is correct, then exactly the same variations in test-flash threshold should be obtained with these auxiliary flashes as with the corresponding annular flashes.

Figures 2 (e) and (f) show, respectively, the elevation in the red test-flash threshold above resting level as a function of the delay in presentation of the green and red auxiliary flashes. Results are for one observer only (DHF). In neither case is there any significant inhibition of the test flash, even at the 0·1 significance level. The only effect of the auxiliary is facilitatory, the maximum depression in test-flash threshold occurring at the expected time-lags of −100 msec for the green auxiliary and at 0 msec for the red auxiliary. The hypothesis that the elevations in test-flash threshold and in particular the rod–cone after-flash effect are here caused by scattered light is accordingly rejected.

It thus appears that there is a genuine after-flash interaction between the rod and cone systems and that under the present experimental conditions the effect of a rod after-flash can lag behind the effect of a mainly cone after-flash by about 100 msec (compare, in Fig. 2, (a) with (c) and (b) with (d)). McDougall (1904) and Frumkes *et al.* (1973) have given estimates of the difference in rod and cone response latencies that are of this order. If the overall shift to the left in the time course of the heterochromatic interaction with respect to that of the homochromatic interaction shown in Figs. 2 (a)–(d) is indeed due to latency differences, then reversing the colours of the test flash and after-flash in the heterochromatic case should reverse the direction of the shift. Accordingly, the effect of a red masking flash upon the threshold of a green test flash was determined in the same way as before. Figure 2(g) shows the results. Elevation in test-flash threshold above resting level is plotted against masking flash delay. The displacement of the time course to the right in relation to the homochromatic case (Fig. 2(d)) is evident. The time-lag at which the maximum after-flash effect occurs has increased to about 300 msec. The implied latency difference for the test flashes is thus about 200 msec, which is considerably longer than that for the after flashes. Some increase in the latency difference is, however, to be expected, in view of the different luminance levels involved (Arden and Weale, 1954; Frumkes *et al.*, 1973; Roufs, 1974).

GENERAL DISCUSSION

It has been shown here that the rod and cone systems can interact in the after-flash effect. Frumkes *et al.* (1972) have suggested that Alpern's (1965) result showing rod–cone independence may have arisen from his failure to take latency differences between rod and cone signals into consideration. If the latency differences in Alpern's experiments were similar to the values found here, then the 50 msec time-lag he introduced between the test flash that stimulated rods and the after-flash that stimulated both rods and cones would certainly have been too short to reveal a rod–cone effect. He worked with a range of adaptation levels, however, and relative latencies would have been much smaller at the higher levels. Other factors accounting for his negative result cannot therefore be ruled out.

It is not immediately clear whether the present results affect the conclusions of Alpern, Rushton and Torii (1970) concerning the linearity of rod signals. In their experiments, the authors compared the effect of two configurations of red after-flash on the threshold of a blue test-flash. Data were obtained for a wide range of after-flash luminances. Alpern *et al.* (1970) assumed complete independence of rod and cone action in the effect and attributed the rise in test-flash threshold, when rod-mediated, to the activity in the surround of rods alone. Since the after-flash they used lasted 100 msec and lagged behind the test flash by 100 msec, it is possible that there was, at some levels, a significant cone component in the after-flash inhibition of the test flash.

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