INTERACTIONS BETWEEN BLUE- AND RED-SENSITIVE COLOUR MECHANISMS IN METACONTRAST MASKING[1]

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Abstract—In metacontrast masking the apparent brightness of a brief flash of light is reduced by the subsequent presentation of a second flash in an adjacent but non-overlapping region of the visual field. This study is concerned with interactions between blue- and red-sensitive colour mechanisms (Stiles' π_1 and π_5 mechanisms respectively) in this effect. By suitable choice of the spectral compositions and intensities of the stimulus flashes and conditioning fields, the first (test) flash and second (masking) flash are arranged so that each effectively stimulates just one of these two colour mechanisms. Elevation in test-flash threshold is measured as a function of the delay in presentation of the masking flash. It is shown that metacontrast can be obtained with each combination of test- and masking-flash stimulus and that the temporal characteristics of the effect vary with the particular combination of π mechanisms involved. It is argued that the conclusions also hold for the signals generated by the short- and long-wavelength-sensitive cones subserving the two mechanisms.

1. INTRODUCTION

Metacontrast is a visual masking phenomenon in which the apparent brightness of a brief flash of light (the test flash) is reduced by the subsequent presentation of a second flash (the masking flash) in an adjacent but non-overlapping region of the visual field (Stigler, 1910; Alpern, 1953; Kahneman, 1968; Weisstein, 1972; Lefton, 1973). It is sometimes referred to as the after-flash effect (Alpern, 1965; Alpern and Rushton, 1965) or the contrast-flash effect (Yellott and Wandell, 1976; Barris and Frumkes, 1978).[2] Its spatial and temporal characteristics have been investigated by, amongst others, Alpern (1953), Kolers (1962), Weisstein and Growney (1969), Growney (1976) and Saunders (1977) (for additional references see Lefton, 1973).[3] The present study is concerned with metacontrast in which the test flash selectively stimulates one colour mechanism and the masking flash selectively stimulates another colour mechanism.

Two previous investigations concerned with metacontrast interactions between colour mechanisms are those by Alpern and Rushton (1965) and Yellott and

Wandell (1976). Alpern and Rushton (1965) determined metacontrast analogues of Stiles' *threshold-vs-radiance* (tvr) curves (Stiles, 1939, 1949, 1953, 1959); thus, for a fixed time-lag of 50 msec between the onsets of the test flash and masking flash, increment threshold of the test flash was measured as a function of masking-flash intensity with various combinations of wavelengths for the stimuli. Alpern and Rushton showed that the three Stiles' mechanisms, blue-sensitive π_1, green-sensitive π_4, and red-sensitive π_5 acted independently of one another in the masking effect. In a small-scale replication of this study, however, Yellott and Wandell (1976) demonstrated that with a red test flash, the action spectrum of the masking flash was not that of π_5. They concluded that the masking does not necessarily take place within a single π mechanism.

The approach adopted in the present work differs from that of the above studies in that our technique (Foster, 1976; Foster and Mason, 1977) is not to fix the temporal relationship of the stimuli and then deduce mechanism independence or interaction from the metacontrast action spectra, but to choose the spectral compositions and intensities of the test and masking flashes so that each is effectively specific to a particular colour mechanism, and then to measure the temporal dependence of any masking effect that is obtained. The advantages of this procedure are that the outcome indicating independence or otherwise does not depend upon the choice of a certain interval between the stimulus onsets (Foster, 1976; Barris and Frumkes, 1978), and that if an interaction is revealed its temporal characteristics, measured here by elevation in test-flash threshold vs masking-flash delay, are immediately evident. Central to this method is the assumption that the metacontrast obtained with a particular combination of stimuli is due to interaction between the chosen π mechanisms. This is established

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[1] The results of experiment (1) of this study have already been reported (Foster, 1978).

[2] Strictly, the term metacontrast is used to describe this masking only when the test flash precedes the masking flash; the term paracontrast being used when the test flash follows the masking flash (Stigler, 1910). In practice, however, "metacontrast" is often applied to any visual masking with spatially non-overlapping stimuli, independent of the temporal order of the stimuli (Kahneman, 1968; Weisstein, 1972).

[3] The form of the dependence of metacontrast on spatial configuration of the stimuli implies that it is not a simple consequence of some general interference with visual sensitivity, equivalent, for example, to that produced by a "distracting stimulus"; neither is it due to poor fixation (Foster, 1976).

by two procedures. First, for each set of stimuli, tvr curves and field spectral sensitivities are determined for the test flash alone and for the masking flash alone. These data, though not necessarily verifying the specificity of the stimuli in the metacontrast measurements, do provide evidence of the selectivity of the flashes for the chosen mechanisms. Second, to confirm that the observed masking effects in a meta-contrast experiment are indeed the result of the action of one chosen mechanism upon another, control experiments are performed with substitute stimuli to show that there is no masking activity by the remaining mechanisms.

The colour mechanisms of interest here are the blue-sensitive mechanism π_1 and the red-sensitive mechanism π_5. We consider in turn the temporal dependence of the metacontrast action of π_5 on π_1, π_5 on π_5, π_1 on π_5 and π_1 on π_1. It is argued subsequently that, because of the levels of mechanism-isolation employed, the results also apply to the signals generated by the short- and long-wave-length-sensitive cones subserving the two types of π mechanism.

2. METHODS

2.1. Stimuli

The test flash was disc-shaped, dia. 0.6°, and was presented on a steady disc-shaped conditioning field, dia. 0.7°; the masking flash was annular, i.dia. 0.8°, o.dia. 1.2°, and was presented on a steady annular conditioning field, i.dia. 0.7°, o.dia. 11.0°. The stimuli were all concentric and appeared central about a point 1.0° to the left of a small bright fixation spot. [The choice of stimulus location was determined principally by the requirement that the density of blue cones should be maximal (Marc and Sperling, 1977; Wald, 1969) and the density of rods minimal.] The durations of the test flash and masking flash were each 25 msec.

Table 1 shows the spectral compositions of the test flash and masking flash and those of the corresponding conditioning fields chosen for the selective stimulation of π_1 and of π_5. Wavelengths were chosen with reference to data by Wyszecki and Stiles (1967, Table 7.6) and Stiles (1953). The intensities of the conditioning fields were set according to tvr data (see Section 3.1), and values for one of the subjects (DHF) are shown in parentheses in Table 1. The intensity of the masking flash was fixed 0.6 log units above increment threshold. (Typical values of the masking-flash intensity are, respectively, 8.6 and 8.9 log quanta.sec^{-1}.deg^{-2} at 421 and 664 nm; typical values of the test-flash intensity are 8.4 log quanta.sec^{-1}.deg^{-2} at 421 and the same at 664 nm.)

2.2. Apparatus

A standard 5-channel Maxwellian-view optical system, similar to that used in previous studies (Foster, 1976; Foster and Mason, 1977), was used to produce the stimuli. The single light source was a 24 V 150 W tungsten–halogen

lamp run from a stabilized power supply. Light output was continuously monitored with a silicon photodiode connected to a digital voltmeter. One channel was used for the test flash, one for the masking flash, one for the 465 nm conditioning field, and two were used for the combination 576–620 nm conditioning field. Photographically produced masks were inserted in these channels to obtain the appropriate arrangement of stimulus geometry and wavelengths. 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; rise and fall times were less than 2 msec. The time course of the flash sequence was monitored with photodiodes connected to an oscilloscope.

The spectral compositions of the channels were controlled with Balzers B40 interference filters with half bandwidths each less than 12 nm. The peak-transmission wavelengths of these filters ranged from 401 nm to 702 nm. For the preliminary field spectral sensitivity measurements, a violet gelatin filter, Ilford No. 621, was added to the short-wavelength filters to reduce unwanted long-wavelength transmission when these filters were used to provide variable-intensity conditioning fields. The intensities of the stimuli were controlled with neutral density filters and compensated neutral density wedges. The stimuli were viewed through a 2 mm artificial pupil and stability of head position was maintained with the aid of a dental bite-bar.

2.3 Procedure

At the beginning of each session, the positions of the stimulus masks were adjusted so that they were seen by the subject to be concentric and in sharp focus. For the tvr determinations, the subject dark-adapted for 30 min, but for the metacontrast measurements this period was reduced to 10 min. The stimuli were viewed monocularly, with the right eye.

Threshold-vs-radiance curves and field spectral sensitivities. Stimuli were presented exactly as in the main metacontrast experiment, except that when measurements were made with the disc-shaped flash, the annular flash and its conditioning field were occluded, and vice versa. For later reference, note that the wavelength of the test flash (disc or annulus) is denoted by λ and the wavelength of the corresponding variable conditioning field by μ.

For tvr measurements with either the disc-shaped or annular flash at 664 nm the procedure was straightforward: stimulus threshold was determined as a function of the intensity of the corresponding 465 nm conditioning field. With the 421 nm stimulus flashes, however, the possibility of rod-intrusion had to be taken into account. The 576 nm component of the mixed conditioning field was therefore set so that rod threshold at 421 nm was raised above that of the most sensitive cone mechanism. This value of the 576 nm component (6.1 log quanta.sec^{-1}.deg^{-2}) was determined by preliminary tvr measurements. The threshold of the 421 nm flash was then measured as a function of the intensity of its corresponding 620 nm conditioning field in the same way as for the 664 nm flash.

For the field spectral sensitivity determinations, the stimulus flash was set 0.3 log units above increment threshold on the corresponding conditioning field, which with intensity fixed as in Table 1 acted as the *auxiliary field*

Table 1

Mechanism selectively stimulated	Wavelength of flash	Wavelength composition of conditioning field
π_1	421 nm	576 nm (8.4 log quanta.sec^{-1}.deg^{-2}) and 620 nm (8.5 log quanta.sec^{-1}.deg^{-2})
π_5	664 nm	465 nm (8.6 log quanta.sec^{-1}.deg^{-2})

of Stiles. (To avoid confusion in the following, the fixed-intensity conditioning fields will continue to be referred to as auxiliary conditioning fields.) A concentric 10° disc-shaped conditioning field of wavelength μ was then introduced and the intensity of this field adjusted to bring the stimulus flash to threshold. Measurements were made with increasing and decreasing values of μ. Particular care was taken to avoid changes in the 10° conditioning-field intensity which could give rise to transient adaptation effects (Mollon and Polden, 1977, p. 225). Four field spectral sensitivities were obtained, one for each combination of stimulus shape and wavelength.

Metacontrast masking characteristics. The procedure for the determination of the metacontrast masking effect as a function of masking-flash delay was the same as that followed in earlier studies (Foster, 1976; Foster and Mason, 1977). At the beginning of each session, the subject dark-adapted for 10 min and then set the intensity of the masking flash 0.6 log units above increment threshold. (The auxiliary conditioning fields of both test and masking flash were always present.) For each selected time-lag between the onsets of the test flash and masking flash, the subject adjusted the intensity of the test flash by means of a neutral density wedge until the test flash was just detectable. The final threshold setting was approached from subthreshold values. For comparison purposes, the test flash could be occluded and the masking flash presented alone. The subject controlled the start of each presentation sequence; but, to prevent one presentation interfering with another (Kolers and Rosner, 1960), stimulus

sequences could not be initiated more rapidly than about once every 2 sec. Each measurement was preceded and followed by a separate measurement of the test-flash threshold without the masking flash. Elevation in test-flash threshold due to the masking flash was expressed as the difference between the threshold setting (in log units) obtained with the masking flash and mean of the two settings obtained without. The time-lag between the onsets of the test and masking flashes was varied progressively over both positive and negative values, within the limits of -300 and $+300$ msec, and the whole range traversed either three or four times in each direction. Thus either six or eight determinations were made at each masking-flash delay.

2.4 Subjects

There were two principal observers: FMF and DHF (the author). A third observer IEB confirmed the main result of experiment (1). All had some myopia and appropriate correcting lenses were inserted behind the eyepiece. All had normal colour vision and were familiar with the experimental method. FMF was unaware of the purpose of the experiment.

3. RESULTS

3.1 Mechanism-selectivity

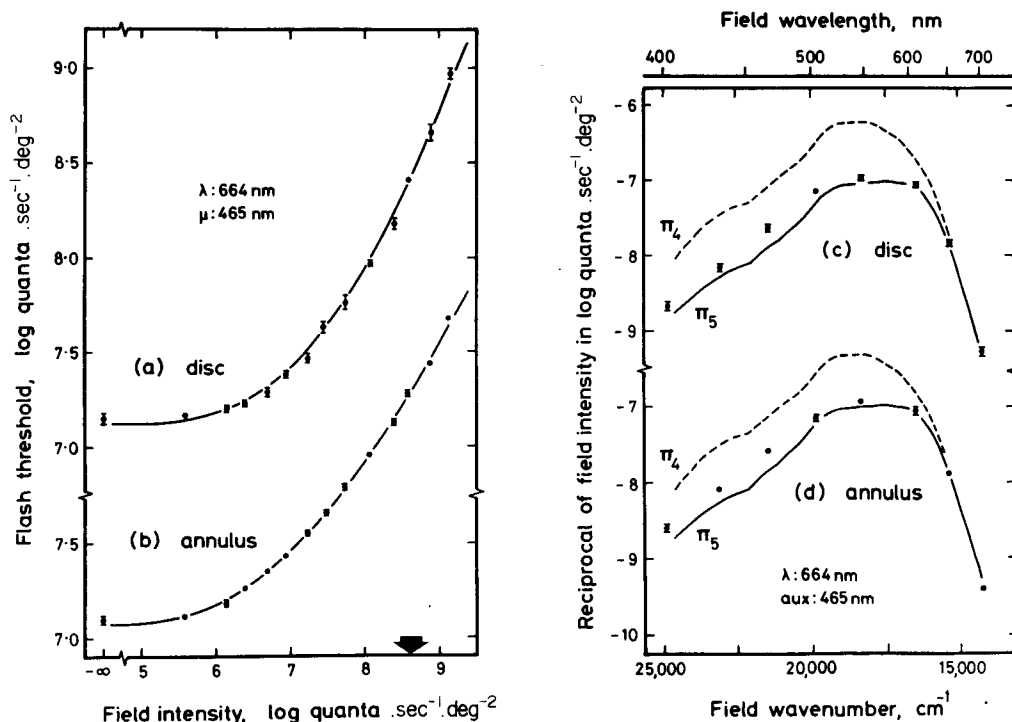The results of the threshold-vs-radiance measurements and field spectral sensitivities for the disc-

Fig. 1. Mechanism-selectivity. (a) and (b) Threshold of the 664 nm disc-shaped flash (a) and annular flash (b) as a function of the intensity of the corresponding 465 nm disc-shaped and annular conditioning field. Each point is the mean of four readings. The smooth curves are Stiles' function $\zeta(x)$ (Wyszecki and Stiles, 1967, Table 7.5) scaled linearly. The value of each conditioning field intensity used in the metacontrast experiment is indicated by the arrow. (c) and (d) Field spectral sensitivity curves for the 664 nm disc-shaped flash (c) and annular flash (d) on the corresponding 465 nm auxiliary conditioning fields. The reciprocal of the intensity of the additional 10° conditioning field necessary to raise the threshold of each stimulus flash 0.3 log units above its value on the auxiliary conditioning field is plotted against the wavenumber of the 10° field. Each point is the mean of six readings. The continuous and broken curves are for Stiles' π_5 and π_4 mechanisms respectively (from Wyszecki and Stiles, 1967, Table 7.6) shifted vertically to give best fit to the data at long wavelengths. In all cases, the vertical bars show ± 1 S.E.M., where this is sufficiently large. Observer: DHF.

shaped flash and for the annular flash, each at 421 nm and 664 nm, are given below. Note that the configurations and durations of these flashes are precisely as in the main metacontrast experiments. Data presented in this section are for DHF; those for FMF are similar.

Tvr's and field spectral sensitivities

π_5 Mechanism. In Figs 1(a) and (b) respectively the threshold of the 664 nm disc-shaped flash and of the 664 nm annular flash is plotted as a function of the intensity of the corresponding 465 nm disc-shaped and annular conditioning field. Each point is the mean of four consecutive settings and the vertical bars show ± 1 S.E.M., where this is large enough to be displayed. The smooth curves fitted to the experimental data are Stiles' function $\zeta(x)$ (Wyszecki and Stiles, 1967, Table 7.5) scaled such that the linear part of the curve gives the correct gradient (see Barlow, 1958). The conditioning field intensity used in the metacontrast experiment is indicated by the arrow.

Figures 1(c) and (d) show respectively field spectral sensitivities for the 664 nm disc-shaped flash and for the 664 nm annular flash on the corresponding auxiliary conditioning fields (see Table 1). The reciprocal

of the intensity of the additional 10° conditioning field necessary to raise the threshold of the stimulus flash 0.3 log units above its value on the auxiliary conditioning field is plotted as a function of the wavenumber of the 10° field. Each point is the mean of six readings and the vertical bars show ± 1 S.E.M., where this is sufficiently large. The continuous curve is for Stiles' π_5 mechanism and, for comparison, the broken curve is for Stiles' π_4 mechanism (from Wyszecki and Stiles, 1967, Table 7.6). The curves are shifted vertically to give best fit to the data at long wavelengths, where inter-subject differences in lens transmission and macular pigment absorption are least. Although for both disc-shaped and annular stimuli there are deviations from the Stiles' curve below 500 nm, these deviations are not large enough to be attributable to the detection of either flash by π_4. It follows that at threshold the 664-nm disc-shaped flash and 664 nm annular flash are each detected by π_5 alone.

π_1 Mechanism. In Figs 2(a) and (b) respectively the threshold of the 421 nm disc-shaped flash and of the 421 nm annular flash is plotted as a function of the intensity of the corresponding 620 nm component of
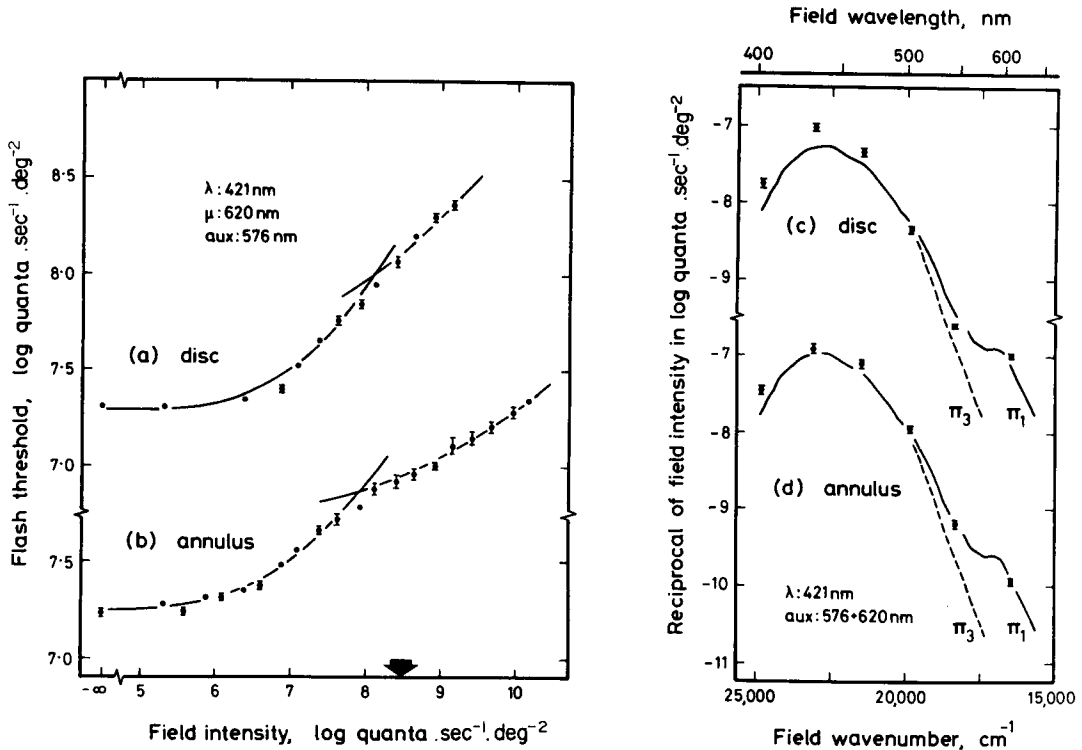

Fig. 2. Mechanism-selectivity. (a) and (b) Threshold of the 421 nm disc-shaped flash (a) and annular flash (b) as a function of the intensity of the corresponding 620 nm component of the disc-shaped and annular conditioning field. The 576 nm component of each conditioning field was fixed at 6.1 log quanta.sec^{-1}.deg^{-2}. Each point is the mean of four readings. The smooth curves are Stiles' function $\zeta(x)$ (Wyszecki and Stiles, 1967, Table 7.5) scaled linearly. The value of the intensity of the 620 nm component of each conditioning field used in the metacontrast experiment is indicated by the arrow. (c) and (d) Field spectral sensitivity curves for the 421 nm disc-shaped flash (c) and annular flash (d) on the corresponding 576–620 nm auxiliary conditioning fields. The reciprocal of the intensity of the additional 10° conditioning field necessary to raise the threshold of each stimulus flash 0.3 log units above its value on the auxiliary conditioning field is plotted against the wavenumber of the 10° field. Each point is the mean of six readings. The continuous and broken curves are for Stiles' π_1 and π_3 mechanisms respectively (from Wyszecki and Stiles, 1967, Table 7.6). In all cases, the vertical bars show ± 1 S.E.M., where this is sufficiently large. Observer: DHF.

the disc-shaped and annular conditioning field. The 576 nm component of each conditioning field was fixed at 6.1 log quanta.sec^{-1}. deg^{-2} which raised the threshold of the rod system in the region of the test stimuli above that of the cone mechanism used to detect the flashes. Each point is the mean of four readings and the vertical bars show ± 1 S.E.M., where this is sufficiently large. The continuous curves are obtained, as before, from Stiles $\zeta(x)$ function scaled linearly to fit the data. On the basis of Stiles' (1953) analysis, the lower section of each curve in (a) and (b) is identified with the blue-sensitive mechanism π_2 and the upper section with π_1. In the metacontrast experiment, the intensity of the 620 nm component of the conditioning field was fixed at the level shown by the arrow. The intensity of the 576 nm component was fixed at 8.4 log quanta.sec^{-1}.deg^{-2} to secure adequate suppression of π_4. Because of the different spectral sensitivies of π_1 and π_4, the effect on the 421 nm threshold of the increase in intensity of the 576 nm component above that used to obtain the tvr data was small: the threshold of the disc-shaped flash was raised by less than 0.3 log units and the annular flash by less than 0.1 log units. (Note the difference in gradients in Figs 2(a) and (b); see Barlow (1958) for discussion of the effect of stimulus size on tvr shape.)

Figures 2(c) and (d) show respectively field spectral sensitivities for the 421 nm disc-shaped flash and for the 421 nm annular flash on the corresponding auxiliary conditioning fields (see Table 1). The reciprocal of the intensity of the additional 10° conditioning field necessary to raise increment threshold by 0.3 log units is plotted as a function of the wavenumber of the 10 field. Each point is the mean of six readings and the vertical bars show ± 1 S.E.M., where sufficiently large. The continuous curve is for Stiles' π_1 mechanism and, for comparison, the broken curve is for the other blue-sensitive mechanism π_3 (from Wyszecki and Stiles, 1967, Table 7.6). The small but significant elevations in the experimental data at 605 nm confirm that the 421 nm disc-shaped flash and the 421 nm annular flash are, at threshold, detected by π_1 alone.

Note. It might be hypothesized that the threshold specificity of the 664 nm and 421 nm stimuli for π_5 and π_1 respectively is upset when the conditioning fields of the flash stimuli are made contiguous as in the metacontrast experiment. For example, the 465 nm annular auxiliary conditioning field might reduce the efficacy of the combined 576–620 nm disc-shaped auxiliary conditioning field in isolating π_1 with respect to the 421 nm disc-shaped test flash. This effect could arise either through the direct action of scattered light from the surround field or by lateral interaction. An obvious estimate of the disturbance is given by the change in test-flash threshold: with the introduction of the 465 nm surround field, the 421 nm test-flash threshold was raised less than 0.15 log units; for the 576–620 nm surround field, there was no elevation in the 664 nm test-flash threshold. Similar results were obtained for the action of the disc-shaped conditioning field on the threshold of the annular flash. That under these conditions the stimuli actually retain their specificity, at threshold, for the selected π mechanisms and that this specificity is preserved at suprathreshold levels is verified by the control experiments described later. It is recalled that in all the metacontrast experiments the 421 nm and 664 nm flash stimuli are always presented on their respective auxiliary conditioning fields.

3.2 *Experiment* 1: *Masking Action of* π_5 *on* π_1

The effect of the 664 nm masking flash on the threshold of the 421 nm test flash is shown in Figs 3(a) and (b) for subjects FMF and DHF respectively. Elevation in test-flash threshold above resting level is plotted as a function of the time-lag between the stimulus onsets (the masking-flash delay or *stimulus onset asynchrony*). Positive delay values indicate that the masking flash follows the test flash and negative values that it precedes it. Each data point is in (a) the mean of eight determinations and in (b) the mean of six determinations. The vertical bars show ± 1 S.E.M. As can be seen, there is a pronounced masking effect, which for FMF reaches 0.21 log units at 100 msec and for DHF 0.26 log units at 100 msec; there is, in addition, a smaller effect of 0.17 log units for FMF at -50 msec and 0.21 log units for DHF at -100 msec. Each of these threshold elevations is statistically highly significant ($P < 0.001$) and is of the same order of magnitude as the masking flash (0.6 log units above increment threshold) used to induce them. The bimodal nature of the masking dependence, reported in previous studies (Kolers and Rosner, 1960; Foster, 1976; Foster and Mason, 1977), is discussed later.

Given that the 421 nm test flash is, at threshold, specific to π_1 (Section 3.1), and therefore that any increase in test-flash threshold entails an increase of at least that magnitude in the threshold of π_1, it might be hypothesized that it is residual direct excitation of π_1 in the *surround* by the 664 nm suprathreshold annulus that underlies the masking effects shown in Figs 3(a) and (b). To test this hypothesis of direct π_1-π_1 masking, the above experiment was repeated, but with the 664 nm annular flash replaced by a 429 nm annular flash that had the same effect on π_1 in the surround as the original 664 nm flash. All other conditions including test-flash wavelength remained the same. (This π_1-equivalent 429 nm annular flash was subliminal for both observers by about 2 log units.) Figures 3(c) and (d) show the results of this replication for each subject. Threshold elevation is plotted against masking-flash delay and each point is the mean of six determinations. Clearly, there is no significant masking effect at any onset delay, except possibly for DHF at 150 msec ($0.1 > P > 0.05$), but the magnitude of this elevation (0.05 log units) is negligible in comparison with the elevations produced by the 664 nm flash (Fig. 3(b)).

Although it is thus not direct excitation of π_1 in the surround by the 664 nm masking flash which gives the elevations in test-flash threshold shown in Figs 3(a) and (b), it might be argued that there is an important contribution to the masking from direct excitation of π_4 in the surround. This hypothesis was tested precisely as in the previous case except that the 664 nm annular flash was replaced by a 431 nm annular flash which had the same effect on π_4 in the surround as the 664 nm flash. (This 431 nm π_4-equivalent was found by both observers to be close to threshold.) Figures 3(e) and (f) show the elevation in the 421 nm test-flash threshold as a function of the 431 nm-masking-flash delay for each subject. Each point is the mean of six determinations. At no onset delay is there a significant elevation in test-flash
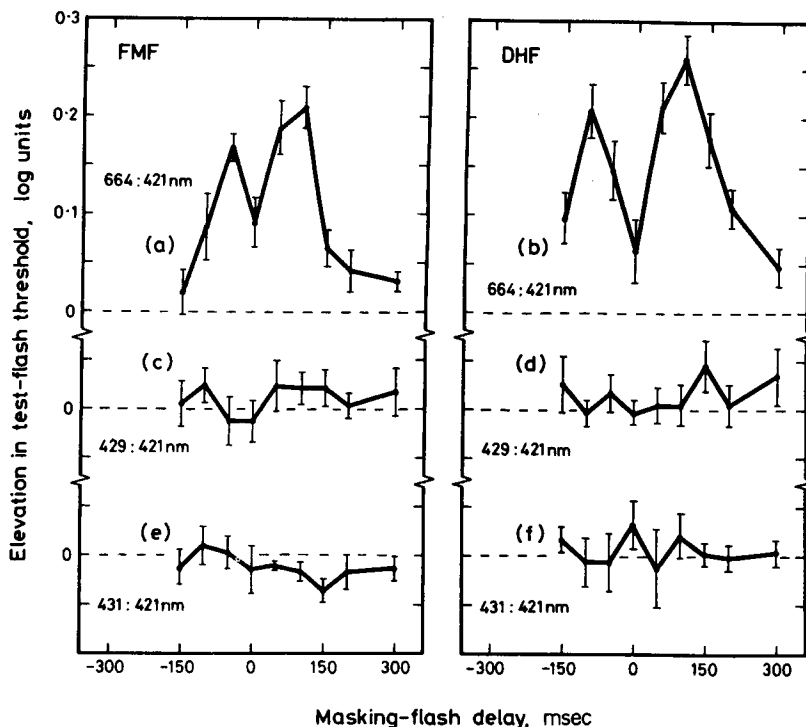
Fig. 3. Metacontrast masking (experiment 1). Elevation in test-flash threshold above resting level is shown as a function of delay in presentation of the masking flash. Negative delays indicate that the masking flash precedes the test flash. Data in (a) and (b) are for the 421 nm test flash and a 664 nm masking flash; data in (c) and (d) are for a 421 nm test flash and a 429 nm masking flash equivalent to the 664 nm masking flash with respect to π_1 in the surround; data in (e) and (f) are for a 421 nm test flash and a 431 nm masking flash equivalent to the 664 nm masking flash with respect to π_4 in the surround. All flash durations were 25 msec. Each point in (a) represents the mean of eight determinations and in (b) to (f) the mean of six determinations. The vertical bars denote ±1 S.E.M. Observers: FMF and DHF.

threshold for either observer ($P > 0.1$). There is a depression in threshold for FMF at 150 msec which is significant ($P < 0.05$) but its magnitude (0.04 log units) is negligible relative to the effect of the 664 nm flash. This and the preceding control experiment confirm that the masking effects shown in Figs 3(a) and (b) are a consequence of the direct excitation of π_5 in the surround by the masking flash. (The possibility that with other stimulus wavelengths and intensities π_4 can give rise to masking of π_1 is of course not precluded by these control measurements.)

When the 421 nm test-flash is presented at threshold on just the 576–620 nm combined auxiliary conditioning field, it is certainly specific to π_1 (Section 3.1). That this specificity is preserved in the presence of the contiguous 465 nm annular auxiliary conditioning field was verified by replacing the 421 nm threshold test flash first by a 516 nm flash equivalent to the 421 nm flash with respect to π_4 and then by a 653 nm flash equivalent to the 421 nm flash with respect to π_5. In both cases, these replacement flashes were found to be subthreshold by at least 0.4 log units. Since π_1 is thus at least 0.4 log units more sensitive to the 421 nm test flash than either π_4 or π_5, any elevation in the 421 nm test-flash threshold must involve an elevation of at least the same magnitude in the threshold of π_1, independent of any additional threshold shifts in π_4 and π_5. The elevations in test

flash threshold shown in Figs 3(a) and (b) thus reflect a real masking action of π_5 on π_1.

3.3 Experiment 2: Masking Action of π_5 on π_5

Figures 4(a) and (b) show the effect of the 664 nm masking flash on the threshold of a 664 nm test flash for each subject. The auxiliary conditioning field was a spatially uniform 465 nm 11° disc, intensity 8.6 log quanta.sec^{-1}.deg^{-2} (Table 1). Elevation in test-flash threshold above resting level is plotted against masking flash delay and each point is the mean of six determinations. As before, negative delays indicate that the masking flash precedes the test flash. In contrast with the data of Figs 3(a) and (b), the masking characteristics are unimodal. Threshold elevation reaches 0.23 log units for FMF at 50 msec onset delay and 0.27 log units for DHF at 50 msec onset delay; each elevation is highly significant ($P < 0.001$).

From the tvr and field-spectral sensitivity measurements described in Section 3.1 and from the control experiments described in experiment (1), it follows that the data in Figs 4(a) and (b) represent the direct metacontrast masking action of π_5 on π_5. There is evidence of some masking at negative masking flash delays for DHF; the elevation of 0.05 log units at −100 msec is statistically significant ($P < 0.05$) but negligible relative to that at 50 msec.
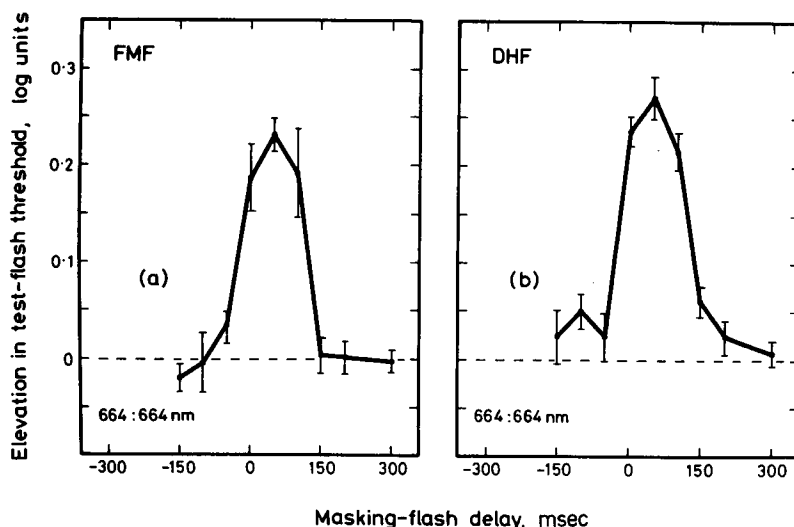
Fig. 4. Metacontrast masking (experiment 2). Elevation in test-flash threshold above resting level is shown as a function of delay in presentation of the masking flash. Data are for a 664 nm test flash and 664 nm masking flash. All flash durations were 25 msec. Each point represents the mean of six determinations and the vertical bars denote ± 1 S.E.M. Observers: FMF and DHF.

3.4 Experiment 3: Masking Action of π_1 on π_5

The effect of the 421 nm masking flash on the threshold of the 664 nm test flash is shown for each subject in Figs 5(a) and (b). Each point is the mean of six determinations and, as usual, negative masking flash delays indicate that the masking flash precedes the test flash. Elevation in test flash threshold is maximum at 0 msec onset delay for both subjects and has values 0.18 log units for FMF and 0.24 log units for DHF. These values are both highly significant $(P < 0.001)$. The temporal dependence is unimodal for both subjects, although for DHF there is again evidence of a small subsidiary maximum at -250 msec, which is significant $(P < 0.05)$.

As in experiment (1), control experiments were performed to establish that the masking effects shown in Figs 5(a) and (b) were not the result of direct excitation in the surround of either π_5 or π_4 by the 421 nm annular flash. The 421 nm masking flash was first replaced by a 653 nm masking flash of intensity such that its effect on π_5 in the surround was the same as that of the 421 nm masking flash and then by a 516 nm masking flash of intensity such that its effect on π_4 in the surround was the same as that of the 421 nm masking flash. (For both subjects, the π_5-equivalent masking flash was found to be subliminal; the π_4-equivalent masking flash was found on some occasions to be close to threshold.) Figures 5(c) and (d) show elevation in the 664 nm test-flash threshold as a function of onset delay for the π_5- and π_4-equivalent masking flashes respectively. Each point is the mean of six determinations. Data for FMF only are shown; data for DHF are similar. There is no significant elevation in test-flash threshold for either masking flash at any onset delay $(P > 0.1)$.

Additional control measurements to test the specificity of the 664 nm test flash were also performed. The 664 nm test flash, at increment threshold, was replaced first by a 429 nm test flash equivalent to the 664 nm flash with respect to π_1 and then by a 431 nm test flash equivalent to the 664 nm flash with respect to π_4. Both substitute flashes were subthreshold by at least 0.3 log units. Since π_5 is thus at least 0.3 log units more sensitive to the 664 nm test flash than either π_1 or π_4, the elevations in the threshold of this flash shown in Figs 5(a) and (b) must be the result of elevations in the threshold of π_5. The preceding control experiments (Figs 5(c) and (d)) show that this elevation is not due to any excitation of π_5 or π_4 in the surround. It follows that the data in (a) and (b) manifest a real masking action of π_1 on π_5.

3.5. Experiment 4: Masking Action of π_1 on π_1

Figures 6(a) and (b) show the effect of the 421 nm annular masking flash on the threshold of the 421 nm test flash for each subject. The auxiliary conditioning field was a spatially uniform $11°$ 620–576 nm disc (Table 1). Each point is the mean of six determinations and negative masking-flash delays indicate that the masking flash precedes the test flash. Both curves are unimodal and the elevations in test-flash threshold have maxima of 0.36 log units at 50 msec onset delay for FMF and 0.37 log units at 50 msec onset delay for DHF. These elevations are each highly significant $(P < 0.001)$.

To confirm that these large metacontrast effects are indeed due solely to the action of π_1 on π_1, control experiments similar to those used in experiment (3) were performed. The 421 nm annular flash was replaced first by a 516 nm annular flash which had the same effect on π_4 in the surround as the 421 nm annular flash, and then by a 653 nm annular flash which had the same effect on π_5 in the surround as the 421 nm annular flash. (The π_5- equivalent flash was subliminal; the π_4-equivalent flash was on some occasions close to threshold.) These experiments were performed on DHF only. Figures 5(e) and (f) show elevation in the 421 nm test-flash threshold as a function
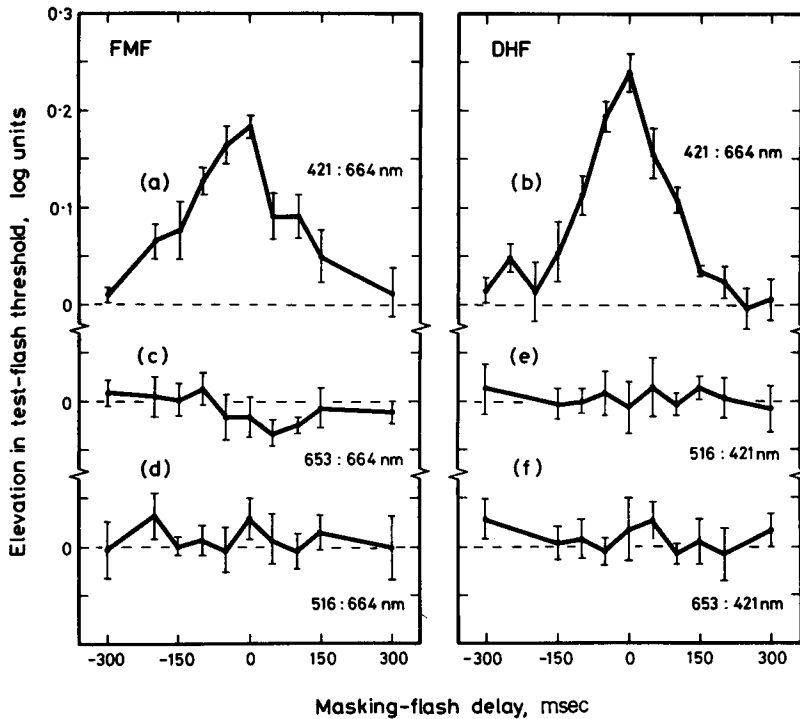
Fig. 5. Metacontrast masking (experiment 3). Elevation in test-flash threshold above resting level is shown as a function of delay in presentation of the masking flash. Data in (a) and (b) are for a 664 nm test flash and a 421 nm masking flash; data in (c) are for a 664 nm test flash and a 653 nm masking flash equivalent to the 421 nm masking flash with respect to π_5 in the surround; data in (d) are for a 664 nm test flash and a 516 nm masking flash equivalent to the 421 nm masking flash with respect to π_4 in the surround. (e) and (f) relate to experiment (4): data in (e) are for a 421 nm test flash and a 516 nm masking flash equivalent to the 421 nm masking flash with respect to π_4 in the surround; data in (f) are for a 421 nm test flash and a 653 nm masking flash equivalent to the 421 nm masking flash with respect to π_5 in the surround. All flash durations were 25 msec. Each point is the mean of six determinations and the vertical bars denote ± 1 S.E.M. Observers: FMF and DHF.
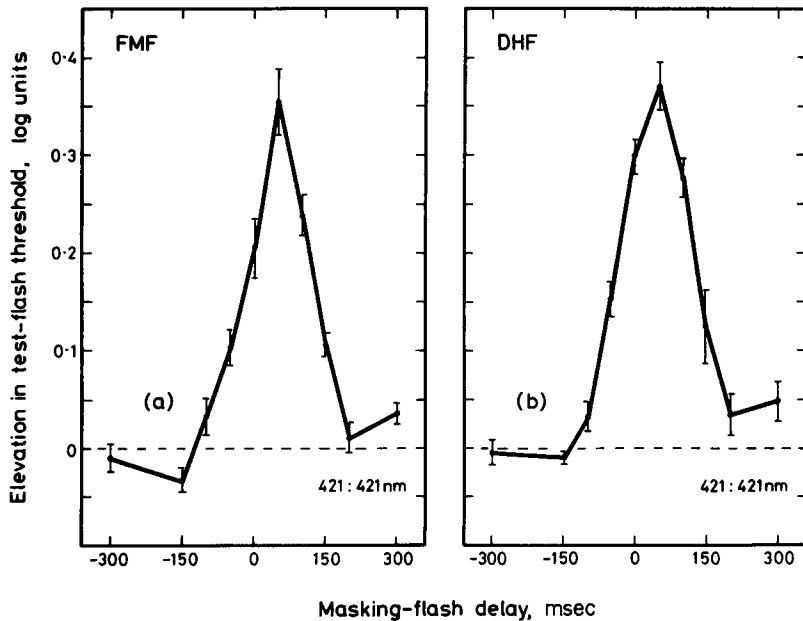

Fig. 6. Metacontrast masking (experiment 4). Elevation in test-flash threshold above resting level is shown as a function of delay in presentation of the masking flash. Data are for a 421 nm test flash and a 421 nm masking flash. All flash durations were 25 msec. Each point represents the mean of six determinations and the vertical bars denote ± 1 S.E.M. Observers: FMF and DHF.

of onset delay for these π_4- and π_5-equivalent masking flashes respectively. Each point is the mean of six determinations. There is no significant masking effect at any onset delay ($P > 0.1$). These results and the demonstration (in experiment 1) that π_1 is at least 0.4 log units more sensitive to the 421 nm test flash than either π_4 or π_5 imply that the data of Figs 6(a) and (b) represent a direct metacontrast masking action of π_1 on π_1.

4. DISCUSSION

The results of the present investigation show that metacontrast masking can be obtained by interactions between each possible combination of the blue- and red-sensitive mechanisms π_1 and π_5. Yellott and Wandell (1976) in discussion of their own data indicating a metacontrast interaction of π_5 with some other colour mechanism suggest that the discrepancy between their results and those of Alpern and Rushton (1965) showing no interaction might be reconciled if there were two kinds of metacontrast: the one retinal and receptor-specific, which Alpern and Rushton studied, and the other central and governed by opponent-process operations. Such an explanation might be appropriate here, although, as Yellott and Wandell (1976) point out, it is not obvious what conditions determine which kind of effect will appear.

In what follows, we (i) examine the dependence of the masking effect on the combination of π mechanisms stimulated, (ii) consider some implications of the data in relation to the processing of luminance and chromaticity information, and (iii) show that the conclusions reached here concerning the properties of metacontrast interactions between π_1 and π_5 apply also to the signals generated by the underlying short- and long-wavelength-sensitive cones.

4.1 Temporal dependence

The masking-flash delays at which the metacontrast effect is maximum (Figs 3a, b; 4a, b; 5a, b; 6a, b) are listed below:

      (i) π_5 on π_1 : 100 msec,

    (ii) π_5 on π_5 : 50 msec,

   (iii) π_1 on π_1 : 50 msec,

   (iv) π_1 on π_5 : 0 msec.

As with the temporal characteristics of rod–cone metacontrast (Foster, 1976; Foster and Mason, 1977; Barris and Frumkes, 1978), the variation in the value of the onset delay for peak effect may be attributed to differential latencies in the responses of the π mechanisms to the various arrangements of test- and masking-flash stimuli. It is known that π_1 has a response latency greater than that of the longer-wavelength mechanisms and Mollon and Krauskopf (1973) have suggested that the latency difference may be as much as 50 msec measured in reaction-time experiments. If such a relative delay were to occur here, before the site of the metacontrast interaction, then the onset delay for peak effect at the site of the interaction would be reduced by 50 msec for the action of π_5 on π_1, remain the same for π_5 on π_5 and for π_1 on π_1, and be increased by 50 msec for π_1 on π_5. In each

case, the optimum onset delay at the site of the interaction would be 50 msec (see Alpern, 1953).

The dependence of the shape of the metacontrast masking characteristics on the combination of mechanisms involved is less easy to interpret. For the action of π_5 on π_1, the characteristics are bimodal (Fig. 3a, b), whereas for all other combinations the characteristics are essentially unimodal (Figs 4a, b; 5a, b; 6a, b). One explanation might be that the variation in shape is merely a reflection of the different temporal processing which occurs in the π_1 and π_5 pathways (Kelly, 1974; Idris, 1974; see also Boynton and Baron, 1975). Several authors (Alpern, 1953; Kolers and Rosner, 1960; Weisstein, 1972) have shown that metacontrast characteristics depend on the durations of the test and masking flashes, and although the waveforms and durations of the flashes are identical here, there are likely to be considerable differences between the corresponding signals after transmission along the different pathways. From the present experiments, however, it is not possible to distinguish between this interpretation of the differences in metacontrast masking characteristics and one which supposes distinct sites and modes of interaction for each of the pairs of π mechanisms involved.

4.2 Luminance and chromaticity encoding

In view of the earlier remark concerning the possible opponent-process origin of the interactions measured here, it may be useful to consider the masking data in relation to theories of luminance and chromaticity encoding (Hurvich and Jameson, 1957; Guth and Lodge, 1973; King-Smith and Carden, 1976). Various authors (Guth et al., 1968; Mollon and Krauskopf, 1973; Smith and Pokorny, 1975) have proposed that signals from blue cones (or π_1) do not have access to the luminosity channel (see also Whittle, 1973, and Marks, 1974). It has also been argued by Bowen et al. (1977) in a study of the roles of hue and luminance in metacontrast that for metacontrast to occur the masking stimulus must provide a change in luminance. But the present experiments have demonstrated that metacontrast masking can be obtained solely through activity of the blue-sensitive π_1 mechanism. In fact, it is when π_1 alone is involved that masking is here found to be greatest (Fig. 6a, b). Clearly, the preceding hypotheses cannot be simultaneously true under all conditions: either signals from π_1 can have access to the luminosity channel or metacontrast can be obtained without changes in masking-flash luminance. For the present results, the latter explanation seems the more plausible for the following reason. The metacontrast action of π_5 on π_5 gives rise to a maximum threshold elevation of about 0.25 log units (Fig. 4a, b), whereas for π_1 on π_1 the maximum threshold elevation is about 0.35 log units (Fig. 6a, b). If the π_1–π_1 masking were the result of action solely within the luminance system, then the magnitude of the effect should be lower than that for π_5–π_5 masking, since it is the latter which is more likely to be determined by activity in the luminance channel. If π_1–π_1 masking does in fact take place at the level of chromaticity and luminance encoding, then it would appear that the activity within the chromaticity channel is mainly responsible.

4.3 Relation of π mechanism masking data to fundamental colour mechanisms

It seems unlikely that the action spectrum of π_1 (defined in the field) can be identified with that of the short-wavelength fundamental spectral mechanism which in conjunction with the medium- and long-wavelength fundamental mechanisms determine trichromacy. First, if it is assumed that trichromacy is determined by three distinct photopigments, then π_1 can probably be rejected as a fundamental mechanism since the shoulder on the long-wavelength side of its spectral sensitivity curve (Fig. 2c, d) is atypical of a single photopigment (Brindley, 1970). Second, Pugh (1976) has shown that π_1 does not exhibit additivity for combinations of long-wavelength ($\geqslant 550$ nm) and short-wavelength ($\leqslant 500$ nm) fields; π_1 thus does not satisfy the principle of univariance (Naka and Rushton, 1966). In contrast, the π_5 and π_4 mechanisms probably can be identified with the long- and medium-wavelength fundamental mechanisms (Estévez and Cavonius, 1977; Pugh and Sigel, 1978; Bowmaker et al., 1978).

The results of the present work showing that π_1 and π_5 can interact in metacontrast might therefore be argued to be artifacts of activity taking place solely within a single fundamental mechanism, namely the long-wavelength fundamental mechanism. This hypothesis may, however, be rejected by applying an argument similar to that used by Pugh (1976) in his analysis of π_1 sensitivity. Consider the action of the 664 nm masking flash on the threshold of the 421 nm test flash (experiment 1). The control experiment in which the test flash was replaced by a long-wavelength stimulus equivalent with respect to π_5 showed that the disc-shaped auxiliary conditioning field raised the threshold at 421 nm for π_5 more than 0.8 log units above that for π_1. Since any putative contribution by the long-wavelength fundamental mechanism to detection by π_1 is certainly smaller than the contribution to detection by π_5, it follows that the long-wavelength fundamental mechanism provides a negligible contribution to the signal for the detection of the 421 nm test flash. Note that the assertion that the signal for the detection of the 421 nm test flash is generated solely by the short-wavelength-sensitive cones is not inconsistent with the existence of the secondary mode on the action spectrum of π_1 (Fig. 2c, d) since this mode describes one of the *adaptational* sites of π_1. A similar argument may be applied to the case in which the 421 nm masking flash is used with the 664 nm test flash (experiment 3). The yellow annular auxiliary conditioning field raised the threshold for π_5 more than 1.0 log units above that for π_1. The annular masking flash, set 0.6 log units above increment threshold, was thus 0.4 log units below the threshold of π_5.

It follows from these arguments and from the results of the other control experiments that in experiment (1) the 421 nm test flash is detected solely by short-wavelength-sensitive cones and the 664 nm masking flash effectively stimulates only long-wavelength-sensitive cones; similarly, in experiment (3), the 664 nm test flash is detected solely by long-wavelength-sensitive cones and the 421 nm masking flash effectively stimulates only short-wavelength-sensitive cones. The observed metacontrast effects are thus the result of interactions between signals which are separately generated by these two cone types.

It·is not clear whether these interactions involve the same transient inhibitory processes as considered by Augenstein and Pugh (1977) and Mollon and Polden (1977) in their investigations of the effect of signals from long- or medium-wavelength-sensitive cones on visual sensitivity to signals from short-wavelength-sensitive cones. In experiment (1), the 664 nm masking flash excites long-wavelength-sensitive cones in the surround and signals from these might well act by such a transient inhibitory process to attenuate the signals from the short-wavelength-sensitive cones detecting the 421 nm test flash. Such a process would, of course, have to be able to act laterally. This interpretation does not, however, explain the results of experiment (3) in which the opposite occurs, that is, signals from short-wavelength-sensitive cones attenuate signals from long-wavelength-sensitive cones.

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