THE INDEPENDENCE OF THE TEMPORAL INTEGRATION PROPERTIES OF INDIVIDUAL CHROMATIC MECHANISMS IN THE HUMAN EYE

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SUMMARY

1. Since it has been shown by Stiles that the adaptive states of the primary chromatic (π) mechanisms of the human eye vary independently and since recent theories of visual function have postulated an intimate relation between sensitivity and the temporal characteristics of the retinal response, it is asked whether the temporal integration properties of the eye depend upon the state of adaptation of the retina as a whole or vary independently for each of the chromatic mechanisms.

2. It is found that the critical duration, or limit of time-intensity reciprocity, for the detection of monochromatic increments presented on monochromatic background fields depends only upon the adaptive state of the individual π mechanism mediating the detection. Our results support the hypothesis that each chromatic mechanism has its own automatic gain control.

3. At both dark-adapted and asymptotic levels the critical durations for the short wave-length mechanisms appear to be greater than those for π_4 and π_5.

4. When 500 nm test flashes are presented on 600 nm adaptation fields, critical durations increase at high background intensities. This anomaly adds further support to the hypothesis that the critical durations of different chromatic mechanisms vary independently, since 500 nm flashes are probably detected by π_1, rather than by π_4, when presented on long wave-length adaptation fields of high energy.

5. Our findings provide partial support for the suggestion that the Fechner–Benham subjective colours are due to differences in the time constants of the different colour mechanisms.

6. It is concluded that the critical duration is principally determined at a very distal stage in the visual system before interactions occur between chromatic mechanisms.

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INTRODUCTION

Stiles (1939, 1953, 1959) has used the increment threshold procedure to deduce the spectral sensitivities of individual chromatic mechanisms in the human eye. A fundamental assumption of his method of analysis is that the sensitivity of each π mechanism is independent of the adaptive states of the remaining mechanisms. His results suggest that this assumption is substantially correct.

Many indices of the rapidity of visual processes are known to vary with the level of adaptation. Critical flicker frequencies increase with test field intensity and the peaks of temporal modulation transfer functions are shifted towards higher stimulus frequencies (de Lange, 1958); the critical duration, or limit of time-intensity reciprocity, for the detection of stimulus increments decreases as a function of background energy (Herrick, 1956; Barlow, 1958); and similar relations have been reported for sensory latency (Alpern, 1968) and for the persistence of the primary visual image (Allport, 1968). The inverse relation between the rapidity of visual processes and sensitivity has been of central significance in several recent models of visual function (Fuortes & Hodgkin, 1964; Matin, 1968; Sperling & Sondhi, 1968). Since temporal integration is gained at the expense of temporal resolution it may be biologically appropriate that summation intervals are long when illumination levels are low and are reduced by an increase in light adaptation.

Since the sensitivities of individual chromatic mechanisms may be controlled independently and since the acceleration of visual processes seems intimately linked to a reduction in sensitivity, it may be asked whether the temporal characteristics of the visual response vary independently for the separate π mechanisms. The experiments described in this paper were intended to determine whether each chromatic mechanism enjoys its own critical duration and whether variations in the critical duration for an isolated π mechanism depend upon the state of adaptation of that mechanism alone. Such independence would not be predicted by models, such as that of Shallice (1964), in which the critical duration depends upon the state of adaptation of the retina as a whole or is determined more centrally.

THEORY

The principle of the experiments was to isolate an individual chromatic mechanism, manipulate its adaptive state by means of background wave-lengths to which it was differentially sensitive, and then determine whether the critical duration for the detection of increment flashes varied only with the adaptive state of the particular mechanism involved.

On the basis of Stiles's data and theory (Wyszecki & Stiles, 1967), combinations of

test and adaptation wave-lengths were chosen such that detection of the target flash was probably mediated by a single mechanism. Where one mechanism is considerably more sensitive than the others, the analysis is not complicated by the possible inter-actions that may occur when mechanisms are nearly equal in sensitivity (Boynton, Ikeda & Stiles, 1964). For example, a threshold flash of 650 nm presented on adapta-tion fields of either 500 or 600 nm is normally detected only by the red (π_5) mechan-ism. This is true for the case of zero background and for all background intensities except the very highest (where π_5' may be involved).

According to Stiles's model, the elevation of the increment threshold with increase in background energy is related only to the number of quanta absorbed from the background by the mechanism mediating the detection. In those parts of the spec-trum where the comparison can be made, the empirical field sensitivity of each mechanism, derived by manipulating adaptation wave-length (μ), is found to co-incide closely with the test sensitivity, derived by manipulating test wave-length (λ). Thus, when the threshold for a 650 nm test flash is raised equally by backgrounds of 500 and 600 nm, the sensitivity of π_5 is assumed to be reduced equally in the two cases, even though, by any conventional measure, the 500 nm background is more luminous and even though the sensitivities of the other chromatic mechanisms are not reduced equally in the two cases. If a single mechanism has been successfully isolated, and if the variation of temporal response characteristics is controlled within the chromatic mechanisms, then changes in these characteristics should be related only to changes in sensitivity and should be independent of the adaptation wave-length used to induce these changes. Cases in which a change occurs in the mechanism mediating detection as background energy is increased, cases, that is, in which the increment threshold function has two distinct branches, have a special interest of their own and such conditions will be discussed below.

Derivation of t_c. The present experiment required estimates of the critical duration, t_c, for several combinations of test and background wave-lengths and for a series of adaptation levels. An economical measure of temporal integration was therefore needed. The general procedure was to estimate t_c from foveal increment thresholds for short (10 msec) and long (1000 msec) monochromatic flashes presented on mono-chromatic adapting fields of varying energy. The estimation of t_c from two threshold measurements is illustrated by the idealized plot of log threshold *vs.* log duration shown in Fig. 1. If one target duration is brief enough for its threshold to lie on the segment of the function having a slope of -1 and if the other is long enough for its threshold to lie on the segment of zero slope, then log t_c can be derived from the difference between the second threshold and the first. The equation

$$\frac{\text{Log } I_\text{S} - \log I_\text{L}}{\text{Log } t_s - \log t_c} = -1 \tag{1}$$

holds for the first segment of the function and thus

$$\text{Log } t_c = \log I_\text{S} - \log I_\text{L} + \log t_s \tag{2}$$

The log duration, t_s, of the short flash enters only as a scaling factor.

This estimate might differ in its significance according to different theories of temporal integration, but, since the present experiments were primarily concerned with the equivalence of estimates made under different conditions, the difference between thresholds for short and long flashes provides a satisfactory measure of temporal summation.

METHODS

Apparatus. Light from two ribbon-filament lamps wired in series with a constant-current d.c. supply was delivered to the observer's right eye through a two-channel Maxwellian-view system. A small digital computer (Varian 620/*i*) controlled the wave-length, intensity and duration of the stimuli. Since these parameters could be changed very rapidly, the experiments could be conducted at rates limited only by the observer's capacity and the specific temporal requirements of the experiment.

In the figure:

$$\frac{\log I_S - \log I_L}{\log t_s - \log t_c} = -1$$

$$\log t_c = \log I_S - \log I_L + \log t_s$$

Axis labels: log threshold intensity (vertical), log duration (horizontal), with markers I_S, I_L, $\log I_s - \log I_L$, $\log t_s - \log t_c$, t_s, t_c, t_L.
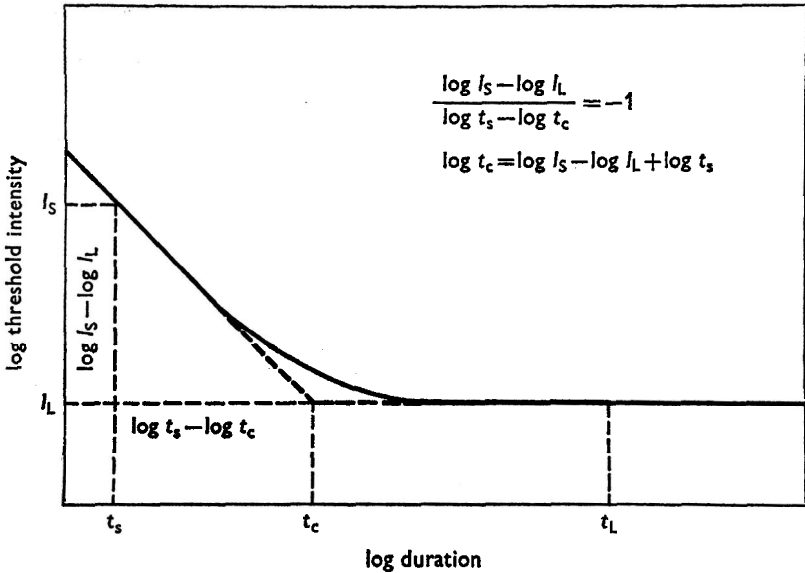
Fig. 1. Idealized relation between log intensity and log duration at threshold (continuous line), illustrating the derivation of the critical duration (t_a) from the difference between the log threshold energy for very brief flashes (I_S) and that for long flashes (I_L).

The spectral distribution in each channel was regulated by a servo-controlled interference wedge. The resulting stimuli had full band-widths at half power of approximately 12 nm.

Stimulus energy was controlled by a series of neutral density filters mounted on vanes driven by rotary solenoids. The nominal filter densities were 0·1, 0·2, 0·4, 0·8, 1·6 and 3·2, this being the minimum set of filters needed to regulate light energy over a range of 6·4 log units. This arrangement was particularly well adapted to computer control, since each filter was set in a natural way by a bit in the word specifying log stimulus energy.

Stimulus duration was controlled by shutters of a double-vane type driven by rotary solenoids. Measured flash duration was accurate to less than 0·1 msec.

The final filament images fell on a plate located about 1 cm from the observer's cornea. A 2 mm aperture in this plate served as an artificial pupil. A 1 in.-thick beam splitter combined the light from the two channels and thus the filament image arising

from reflexion at the second surface of the beam-splitter fell far to one side of the artificial pupil.

The artificial pupil was attached to the observer's side of a phoropter, which was adjusted to correct for the observer's refractive error. A lens that compensated for the chromatic aberration of the eye was added between the phoropter lenses and the artificial pupil. Plastic dental impressions were used to control head position; and before each experimental session the observer's eye was lined up with the beam by adjusting cross-slides to which the bite-board was attached.

The areas of the test and background stimuli were defined by stops placed 1 m from the eye. The test flash was a disk subtending 1 deg of visual angle. The adaptation field was a concentric disk subtending 3 deg. Under dark-adapted conditions and at low background intensities fixation was guided by a diamond array of four red light-emitting diodes placed 1 m from the eye in the test-stimulus channel and centred on the target aperture. The vertical and horizontal separation of the fixation lights was 2 deg. At high adaptation-intensities the fixation lights were replaced by a corresponding array of opaque dots in the background channel.

The duration and sequence of all experimental events were regulated by a binary clock in the computer system. The observer requested stimuli, and responded, by means of a set of push-buttons linked to the computer. The program generated tone signals to mark improper responses, the end of adaptation intervals and the end of the experimental session.

The neutral density filters and the interference wedge were separately calibrated with the aid of a recording spectrophotometer. With the neutral density filters removed, the final spectral energy-distribution of each channel was measured by means of a silicon photodiode placed in the position of the observer's eye.

Procedure. Increment thresholds were measured for 1 deg foveal targets of wave-lengths 430, 500 and 650 nm. The wave-length of the adaptation field was either 500 nm or 600 nm. Each experimental session was devoted to a single combination of test and background wave-lengths and each combination was tested in two separate sessions. The order of experimental conditions was randomized and was different for each subject.

A session began with a dark-adaptation period lasting at least 2 min. Thresholds for first 10 msec. and then 1000 msec target-flashes were determined for the dark-adapted condition and these measurements were then repeated for ten backgrounds of increasing energy. For the 500 nm adaptation field the lowest energy level was approximately $-4\cdot8$ log erg/deg^2.sec; for the 600 nm field it was $-4\cdot4$ log erg/deg^2.sec; both fields were increased in steps of $0\cdot5$ log units. At each new background level the threshold measurements were preceded by an adaptation interval of 1 min.

Each threshold was measured by a staircase procedure. In six preliminary trials, which corresponded to the six bits of the computer word controlling stimulus energy, the approximate threshold value was determined by successive bisection of the energy range. This estimated level, and the energy levels $0\cdot1$ log units above and below it, were taken as the starting points for three randomly interleaved staircases. Each staircase was followed through twelve reversal cycles and the final threshold was derived by taking the average of the peaks and troughs of the stimulus series.

The computer system was able to prepare stimuli and conduct the psychophysical procedure fast enough for observers to work on a demand basis. When he was prepared, the observer pressed one button to secure a flash and pressed one of two others to signal his response. An experimental session lasted approximately 50 min.

RESULTS

Fig. 2 shows the increment threshold functions for one observer when test flashes of 650 nm are presented on 500 nm backgrounds. For both test durations the curves exhibit the typical unbranched form to be
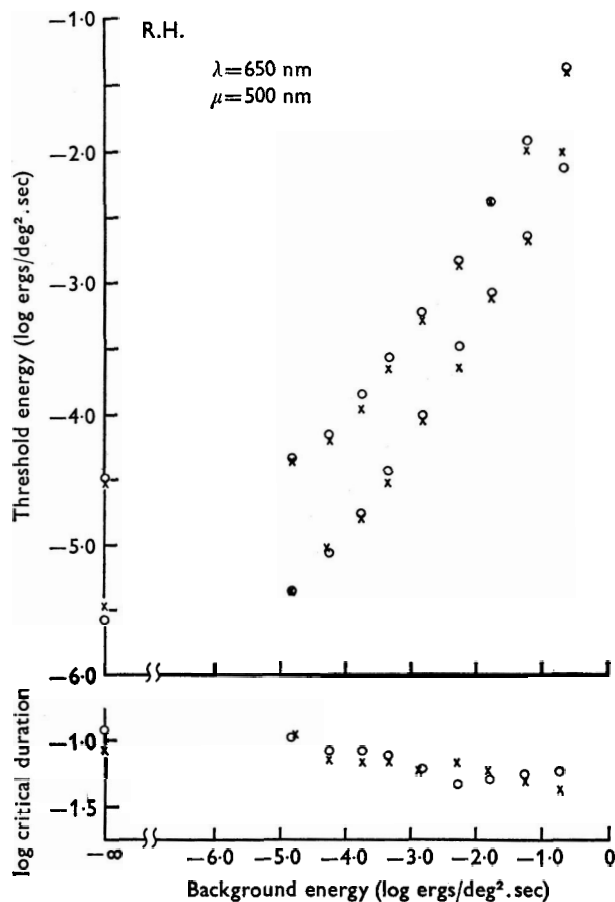

Fig. 2. Upper panel: increment thresholds when $\lambda = 650$ nm and $\mu = 500$ nm. The upper points correspond to 10 msec flashes, the lower to 1000 msec flashes. Results from two different experimental sessions are presented to illustrate variability. Observer: R.H. Lower panel: differences in threshold plotted according to Formula (2) to yield estimates of critical duration.

expected from these conditions. The 1000 msec threshold, however, increases more with increasing background energy than does the 10 msec threshold. The difference between the two thresholds is plotted at the bottom of the Figure and reflects the typical decrease in critical duration

as background energy is increased. Fig. 3 shows the relation of mean log t_c to log background luminance under each condition. It can be seen from this Figure that both under dark-adapted conditions and at asymptotic levels the critical durations for 430 nm flashes are higher than those for 500 and 650 nm targets. However, although this type of plot may be useful for certain purposes, it does not present a simple structure.
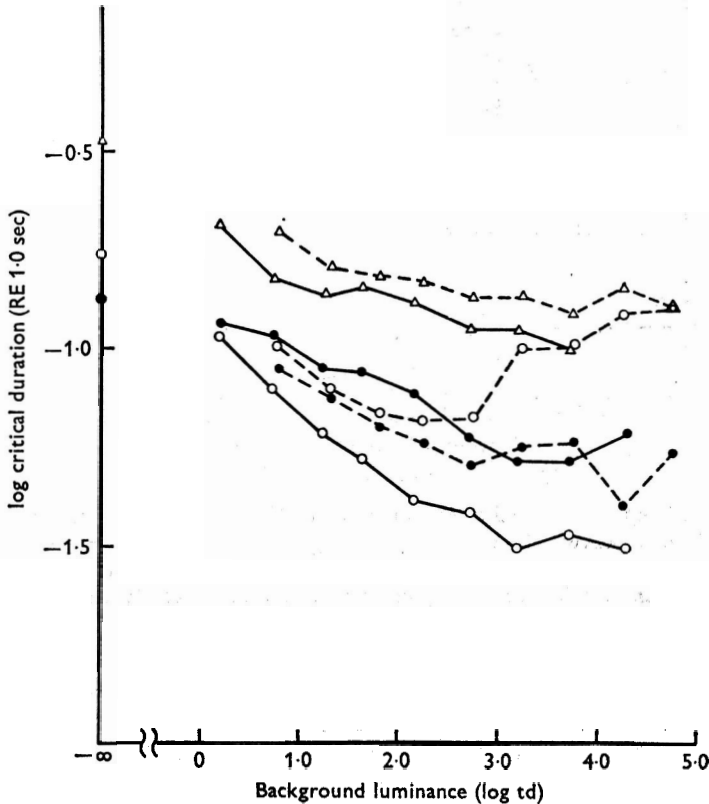

Fig. 3. Mean critical duration as a function of log luminance of backgrounds. Test wave-lengths: 430 nm △, 500 nm ○, 650 nm ●. Background wave-lengths: 500 nm continuous line; 600 nm dashed line. The results are the means for three observers.

Since the models proposed by Fuortes & Hodgkin and by Sperling & Sondhi predict a simple relation between critical duration and sensitivity, the results were re-plotted to reflect this relation. Fig. 4 shows for all three observers the relation of mean log t_c to log sensitivity. Log sensitivity is defined as the difference between the log absolute threshold for the 10 msec target and the log threshold energy for this target at each background level

(note that log sensitivity decreases to the right in Fig. 4). In each panel of the Figure results are plotted separately for the two adaptation wavelengths.
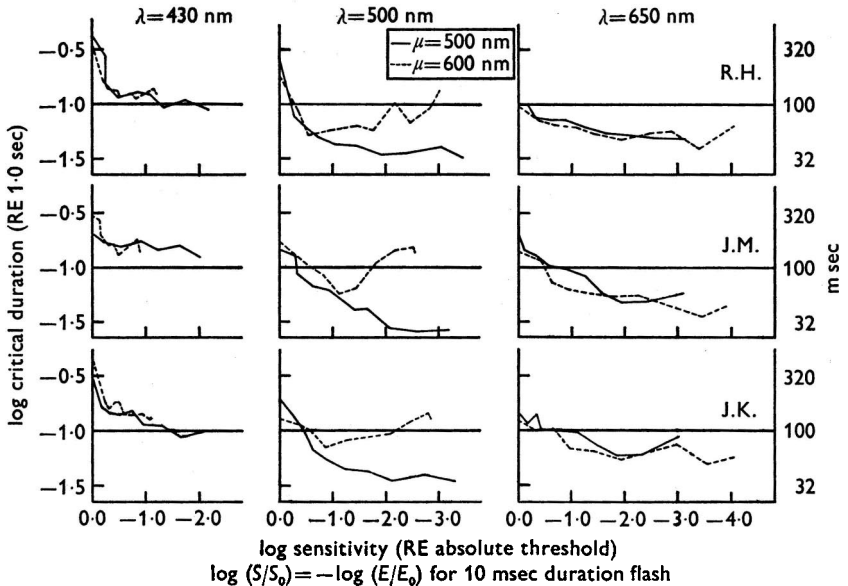

Fig. 4. Mean log critical duration as a function of log sensitivity. Results for three observers, three test wave-lengths and two background wavelengths. Results for $\mu = 500$ nm are shown by continuous lines; those for $\mu = 600$ nm by dashed lines (note sensitivity decreases to the right).

DISCUSSION

Plotted as in Fig. 4 the results display a high degree of order and there is good agreement between observers in the form of the curves. For the 430 and 650 nm test flashes the functions are all of the general form predicted by Sperling & Sondhi and the coincidence of each pair of functions when plotted against sensitivity supports the hypothesis that the critical duration is principally determined at a very distal stage of the visual system by processes within the primary chromatic mechanisms. Our findings lend further support to the proposal of Du Croz & Rushton (1966) that each cone mechanism has its own automatic gain control.

The results for the 650 nm test flashes can be wholly attributed to the red mechanism (π_5), but the interpretation of the data for 430 nm flashes must be more complex. Stiles (1953) found that when short wave-length flashes were presented on long wave-length backgrounds the increment threshold functions showed two, and often three, branches, corresponding

to the mechanisms named π_1, π_2, and π_3. Fig. 5 shows the 10 msec and 1000 msec increment threshold functions for one of our observers when the target wave-length (λ) was 430 nm and adaptation wave-length (μ) was 600 nm. All three observers showed similar branches. The lowest branch, attributed by Stiles to π_2, is especially marked for the 1000 msec flashes. This result suggests that π_2 may have a particularly long critical duration, a feature that might be exploited in the further study of this little understood mechanism.
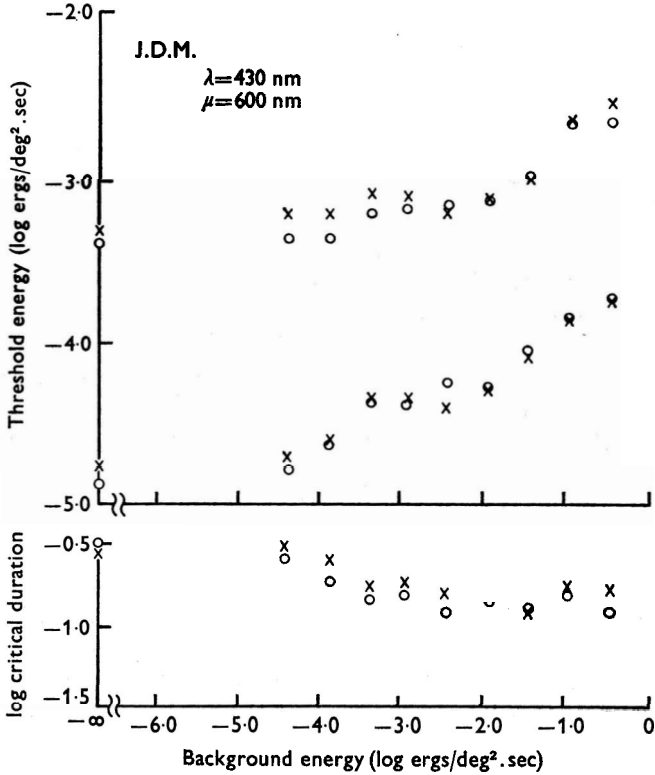

Fig. 5. Increment threshold functions for 10 and 1000 msec flashes when $\lambda = 430$ nm and $\mu = 600$ nm. Observer: J. D. M.

The results for 500 nm test flashes might appear *prima facie* to contradict the hypothesis that t_c is dependent only on the adaptive state of the individual chromatic mechanism. For not only is the variation of critical duration dependent on the adaptation wave-length, but in the case of the 600 nm background t_c actually increases with decreasing sensitivity. However, this apparent discrepancy is predicted by Stiles's theory and in

fact provides additional support for the hypothesis that the time con-
stants of individual mechanisms vary independently. Stiles suggests that
targets of 500 nm presented on an adaptation field of 600 nm are detected
by the green mechanism (π_4) only at relatively low background intensities.
When the background is more energetic, detection is mediated by π_1, and
ultimately by π_3 (Stiles, 1953). The beginning of the π_1 branch can be seen
in our own data and it is interesting to note that all observers reported
that the 500 nm flashes appeared distinctly blue or violet at the two highest
background levels (cf. Stiles, 1949a). π_1 is relatively insensitive to 600 nm
backgrounds and thus when it begins to mediate the detection of 500 nm
flashes its adaptive state will be very different to that of π_4 and its critical
duration will be relatively little reduced from its dark-adapted value.
Moreover, our results for 430 nm targets suggest that there is a primary
difference between the critical durations of π_1 and π_4 even when their
sensitivities are similar. Thus the increase in t_c shown by all observers when
500 nm targets are presented on high-intensity 600 nm backgrounds pro-
vides additional confirmation of the hypothesis that the critical durations
of the π mechanisms vary independently. The increase in t_c is gradual
rather than sudden, but this might be expected: there will necessarily be
a transitional range of background intensities at which the 500 nm test
flashes may be detected by either π_1 or π_4 and, as mentioned earlier, the
rules that govern detection when two mechanisms have similar thresholds
remain uncertain. The very difference between the critical durations of
π_1 and π_4 will cause the 1000 msec flashes to be detected by π_1 at back-
ground levels at which short flashes are detected by π_4 (cf. Ikeda & Boynton,
1962).

If critical durations were determined by the general adaptive state of the
retina we should expect that the critical duration functions for each test
wave-length would be superimposed when plotted against photopic
luminance; the systematic lateral shifts apparent in Fig. 3 rule out this
alternative hypothesis. The agreement of the curves in Fig. 4 is clearly
better.

Relation to earlier work. The present experiments confirm and extend the
results of Krauskopf (1969), who used 510 and 650 nm test stimuli sub-
tending 1·3 min and concluded that changes in the critical durations of
π_4 and π_5 depended only upon changes in their individual sensitivities. It
is of interest, however, that the 1 deg targets used in the present experi-
ments yield critical duration estimates for π_4 and π_5 that are systematically
lower than the corresponding values reported earlier by Krauskopf. Since
the experimental conditions were otherwise very similar, this difference
probably reveals an effect of stimulus area upon temporal summation
(cf. Barlow, 1958).

Our finding of absolute differences in the critical durations of different chromatic mechanisms lends some support to the recurrent suggestion that the subjective colours generated by intermittent, achromatic stimuli, such as Benham's top, are due to differences in the time constants of the different colour responses of the eye (Piéron, 1922; Cohen & Gordon, 1949). Brindley, Du Croz & Rushton (1966) reported that the maximum flicker fusion frequency is about three times lower for π_1 than for the long wave-length mechanisms, although Green (1969), finding that the de Lange characteristic for the blue mechanisms is not shifted towards lower stimulus frequencies, has suggested that the depressed CFF of these mechanisms is only secondary to their elevated Weber fractions. Earlier studies of the critical duration for monochromatic stimuli have generally produced negative results. Stiles (1949b) himself reported a preliminary failure to find differences in the temporal integration properties of the π mechanisms. He gives no details of his experiment and the discrepancy between his finding and ours must remain unexplained. Other failures to find effects of wave-length upon critical duration may be attributed to failure to isolate the individual π mechanisms. Rouse (1952) presented 1 min targets of 665, 538 and 470 nm to the dark-adapted central fovea and found no differences in summation times, but his blue test flashes would be of too long a wave-length to be detected only by π_1 or π_2 and their size and position would additionally favour detection by π_4 (Stiles, 1949a; Brindley, 1954). Sperling & Joliffe (1965) found no difference in critical duration for 650 and 450 nm foveal targets subtending 4·5 min, but when target diameter was 45 min the deviation from full reciprocity occurred later for the 450 nm stimuli and partial summation continued for at least 1 sec. Sperling & Joliffe associate their finding directly with the greater receptive-field size of the blue cone mechanisms; but the relation is probably indirect, for it is almost certain that their small 450 nm targets would be detected by π_4, rather than by π_1 or π_2, and thus the explicit relation between integration time and receptive-field size must remain an open question.

Form of the increment threshold function. Since the critical duration does appear to be greater for π_1 than for the long wave-length mechanisms, no absolute significance can be placed upon the differences that Stiles (1953) notes in the shapes of the increment threshold functions for different mechanisms. The form of the functions will depend upon interactions between the temporal and spatial parameters of the test stimuli and the corresponding integrative properties of individual mechanisms. The standard curves given by Stiles are for 200 msec flashes subtending 1 deg: at absolute threshold the stimulus duration would be shorter than the critical duration of π_1 and at high background levels it would be longer. It is interesting to note, however, that if the 'displacement rules' (Stiles,

1959) do hold exactly for large 200 msec targets when a single π mechanism is isolated, if in particular the manipulation of μ displaces the increment threshold function along the abscissa without distortion, then the changes in the extent of temporal, and also spatial, integration that occur with variation of background energy must necessarily depend only upon changes in the adaptive state of the individual mechanism.

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