CHROMATIC DETERMINANTS OF THE MONOCULAR AND HAPLOSCOPIC INCREMENT THRESHOLD

by

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CHAPTER I

INTRODUCTION

Exposure to light reduces visual sensitivity (this phenomenon termed light adaptation), but the time course of this effect varies with experimental conditions. Historically, two approaches to studying light adaptation have been used. One, the recovery method, obtains a measure of the initial phase of dark adaptation (the recovery of visual sensitivity); and from this measure extrapolates the level of light adaptation which existed immediately preceding termination of the adapting light. The values obtained via this paradigm depend on the temporal interval between termination of the adapting stimulus and measurement of the threshold. Piper (1903) found that 15 min of adaptation to daylight reduced visual sensitivity about 3500 times. The paucity of this effect compared with that more commonly obtained under such intense and prolonged adapting conditions was due to the long time (1-2 min) required to obtain the first threshold reading. Lohmann (1906-1907) used a 10 sec dark interval and varied the luminance and exposure time of the adapting stimulus. He found that the rate of sensitivity loss and

the final, asymptotic, value depended on the luminance of the adapting stimulus, with moderate levels requiring more than 30 min for complete adaptation.

Geldard (1928) and Wright (1934) used a technique that employed a brightness match that was obtained between two fields presented haploscopically so as to fall on adjacent retinal loci in the fused binocular field. Before obtaining this match, one eye was exposed to an adapting luminance. The eye so exposed was found to require a brighter matching field than the other, unadapted, eye in order to appear subjectively equivalent. With this method, the early stages of dark adaptation were sufficiently linear to allow extrapolation of the initial sensitivity. With parametric variation of the adapting field luminance, a light adaptation curve could be obtained.

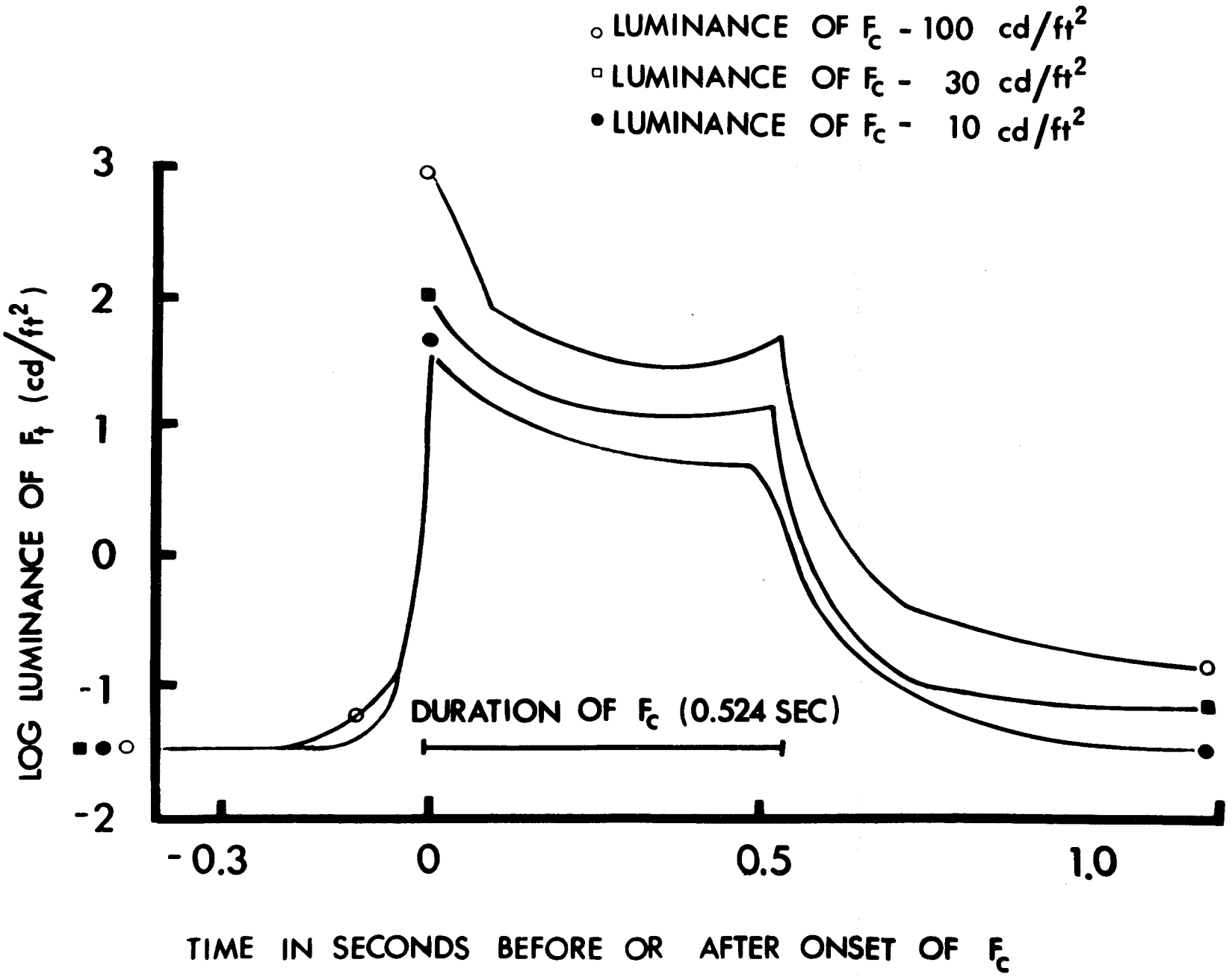
The Increment Threshold Technique

The measurement of the early phases of light adaptation while such processes were ongoing (thus constituting a kinetic measure) was accomplished when Crawford (1947) obtained the brightness increment threshold (dL) for a small test flash of light (F_t) superimposed at varying intervals from the onset of another supraliminal conditioning (adapting) flash (F_c). The results showed that the threshold rose before F_c onset, reaching a maximum

increment of 3 to 4 log units about the 0 ms F_c-F_t interval. The threshold then declined to a relatively asymptotic value and, finally, rose again to a smaller secondary maximum near the end of F_c (see Figure 1).

The data obtained prior to the use of the increment threshold technique had supported the then widely held theory that light and dark adaptation were mediated solely by the breakdown and regeneration of photochemical subtances (Hecht, 1937). Crawford pointed out that the initial rise of F_t threshold at negative F_c-F_t intervals as well as the fall of F_r threshold during exposure to F_c could not be explained on a photochemical basis since there is no way that a chemical event can anticipate changes in stimulating conditions, nor does the Hecht theory allow for an increase in visual sensitivity during exposure to light. In order to account for these events, Crawford hypothesized that neural mechanisms such as different rates of conduction of the intense F_c and the weaker F_t, or some more complicated cerebral perception mechanism allowed neural stimulus effects to interact despite small temporal differences in initial stimulation change. The F_c-F_t interaction was based on a signal (F_c) to noise (F_t) model. In this approach, activity engendered by F_c rendered a further increment due to F_t difficult to detect. It is, however, possible that the neural effects of F_c actively inhibit

Figure 1. Time course of the F_t threshold under the influence of F_c presented for 524 ms. The threshold (F_t) luminance is plotted on the ordinate in log cd/ft^2. The abcissa represents time in seconds before or after the onset of F_c. Open circles are for F_c luminance of 100 cd/ft^2, squares for F_c luminance of 30 cd/ft^2, and filled circles for F_c luminance of 10 cd/ft^2. Duration of F_c is depicted by a line parallel to the abcissa. (After Crawford, 1947)


○ LUMINANCE OF F_c - 100 cd/ft²
□ LUMINANCE OF F_c - 30 cd/ft²
● LUMINANCE OF F_c - 10 cd/ft²
LOG LUMINANCE OF F_t (cd/ft²)
3
2
1
0
-1
-2
DURATION OF F_c (0.524 SEC)
-0.3
0
0.5
1.0
TIME IN SECONDS BEFORE OR AFTER ONSET OF F_c

the transmission of F_t effects. Thus, the increment threshold data may reveal a visual phenomenon analogous to that termed "backward masking" which has been found in earlier audition studies (Stevens and Davis, 1938; Raab, 1963), where response to a transient event can be inhibited by the subsequent presentation of a second stimulus.

The Crawford masking effect has been obtained in a variety of situations involving similar paradigms, some emphasizing the increase in F_t threshold which occurs about F_c onset referred to as the "on" effect (Boynton, Bush, and Enoch, 1954; Boynton, 1956; Boynton and Kendel, 1957; Boynton, 1958; and Baker, Doran, and Miller, 1959); others emphasizing the increase in F_t threshold which occurs about the termination of F_c and subsequent early dark adaptation, termed the "off" effect (Baker, 1963; Battersby and Wagman, 1959, 1962, 1964; and Battersby, Oesterreich, and Sturr, 1964). In general a variety of spatial and intensitive parameters have been investigated showing that changes in visual sensitivity occurring as a function of transient, post-photochemical, stimulus effects are themselves complexly determined by integrative neural processes.

Initial Light Adaptation Studied in Relation to Chromatic Variables

The Crawford technique has had only limited application to studies of color vision despite the fact that it forms a logical extension of the method used over many years by Stiles, and others, in attempts to delineate the spectral sensitivity functions of the mechanisms that mediate color vision (Stiles and Crawford, 1933; Stiles, 1946, 1959; Auerbach and Wald, 1955; Wald, 1964; Hecht and Hsia, 1945; Boynton, 1956; and Boynton, Scheibner and Yates, 1965).

The Stiles method is based on how the adaptive effect of a (continuous) F_c upon a superimposed (brief) F_t varies as a function of their respective wavelength. That is, the curve relating F_t increment threshold as a function of F_c radiance is experimentally generated. The spectral sensitivity of a given color mechanism is then measured by observing how the threshold vs. radiance (TVR) curve is affected by changes in F_c or F_t wavelength. There are two equivalent ways in which this can be done. In one, the F_c wavelength can be varied parametrically. As it is assumed (and supported by Stiles' data) that a mechanism always responds in the same way to the same number of quanta absorbed, a change in F_c wavelength is equivalent, in terms of its action on the mechanism determining the F_t increment

threshold (by altering the number of quanta absorbed), to a change in its energy. This change will cause a conventionally plotted (threshold on ordinate, radiance on abcissa) TVR curve to assume different positions on the abcissa as a function of the F_c wavelength. The resulting series of TVR curves can be inspected for the values of F_c radiance which yield the same F_t threshold at each F_c wavelength. The number of acting (absorbed) quanta of F_c is assumed to be directly related to the proximity of the F_c wavelength to the peak sensitivity of the mechanism responding to F_t. Thus, a plot of the radiance of F_c required to raise the F_t increment threshold by some constant amount (usually 1 log unit above absolute threshold) as a function of F_c wavelength will reveal, within certain limitations, the spectral sensitivity of the mechanism responding to F_t. Alternatively, F_c may be held constant, the wavelength of F_t varied, and the resulting series of TVR curves (now displaced along the ordinate) inspected for the values of F_t radiance required for a fixed increment threshold. In either case the results and interpretation are equivalent. Furthermore, by appropriate selection of F_c and F_t parameters, the sensitivity of one mechanism can be selectively depressed (adapted) by the action of F_c so as to allow the delineation of the spectral

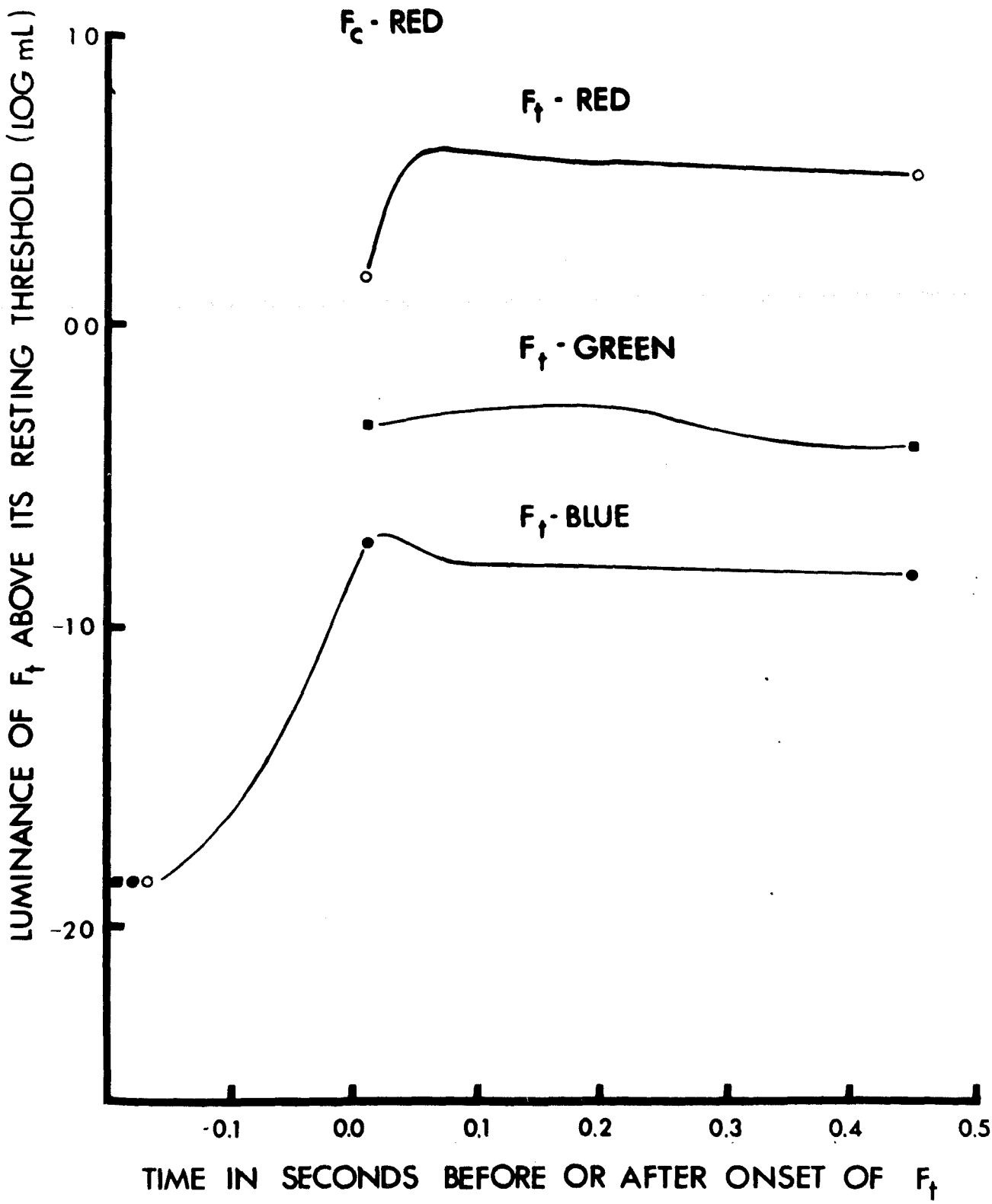
sensitivity of a mechanism not normally the most sensitive at the F_t wavelength. In this instance the TVR curves show a double brance or scallop similar in form to, but the mirror image of, the human dark adaptation curve. The initial, lower, section depicts the sensitivity of a mechanism which because it is less sensitive to F_c begins to respond to F_t.

The present study is based on the assumption of the Stiles method that the adaptive effect of a F_c of one wavelength upon a mechanism responding to a F_t of another wavelength varies inversely as the F_c-F_t spectral separation. In this study the Crawford technique was used to extend the increment threshold method so as to include transient (kinetic) as well as steady-state processes. These thresholds are primarily limited by the burst of neural activity caused by F_c onset, rather than by photochemical availability as in steady-state adaptation. This interpretation suggests that the transient adaptive effect of F_c onset upon the machanism responding to F_t will depend largely upon the degree to which both the same receptor and the same neural pathways are shared by both stimuli. Homochromatic F_c-F_t combinations would yield the maximum increment of F_t threshold as it would be difficult for F_t to cause a perceptible increment in an already high level of activity along a given pathway.

This relationship would also apply to negative F_c-F_t intervals assuming either that F_c neural effects overtake F_t neural effects, or that they were given some brief interval in which to interact. Conversely, in heterochromatic F_c-F_t combinations, F_t reception and transmission should involve receptors and pathways relatively unaffected by F_c and thereby reduce the adaptive effect of F_c upon F_t. This reduction would be determined by two related factors: the extent of the spectral sensitivity of the specific mechanisms involved; and the degree to which the particular heterochromatic F_c-F_t combinations chosen resulted in the stimulation of separate mechanisms.

Bush (1955) has shown that when the relative wavelength of F_c and F_t are varied in the Crawford paradigm (using foveal stimulation) the magnitude of the adaptation effects are inversely related to the F_c-F_t wavelength difference (see Figure 2). It is significant to note that Bush employed only combinations of red, green, and blue stimuli in his design. This choice of F_c wavelength seems to imply an <u>a priori</u> commitment to a three-mechanism receptor system with sensitivity peaks in the red, green, and blue spectral regions. Trichromatic theory is not the only possibility either logically, historically, or empirically. As will be discussed below, other wavelengths of F_c and F_t may have led to results markedly different from those obtained by Bush.

Figure 2. Representative data from the experiment by Bush (1955). F_c is 658 nm (red). Open circles are for F_t at 658 nm, squares are for F_t at 524 nm (green), and filled circles represent F_t at 452 nm (blue). The ordinate shows the elevation of F_t above its resting threshold in log mL. The abcissa shows time in seconds before or after the onset of F_c. F_c termination occurred at 0.56 sec and had no apparent effect on F_t threshold.


F_c - RED
F_t - RED
F_t - GREEN
F_t - BLUE
10
00
-10
-20
LUMINANCE OF F_t ABOVE ITS RESTING THRESHOLD (LOG mL)
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
TIME IN SECONDS BEFORE OR AFTER ONSET OF F_t

Boynton (1956) used the Crawford technique for the special case where F_t follows F_c onset by 50 ms (near the point of maximum elevation of the F_t threshold and obtained the F_t increment threshold luminance for F_t wavelengths from 420 to 700 nm (at 10 nm intervals), under conditions of red, green, yellow, and blue F_c (equated for luminance at approximately 16 mL). The resulting series of spectral sensitivity curves were then used to generate theoretical spectral sensitivity curves. The results of this transformation showed a marked sharpening of the response curves possibly caused by the strong selective adapting effect of F_c obtained in the Crawford paradigm. More importantly, however, the sensitivity data could be converted into theoretical spectral response curves only when at least four underlying mechanisms were postulated with peak sensitivities in the red, yellow, green, and blue regions.

Limitations of the Chromatic Initial Light Adaptation Studies

Two important aspects of wavelength-related neural effects have not been adequately investigated prior to the present study. First, no studies have evaluated, through the selection of appropriate parameters, the relative effectiveness of theories assuming trichromatic color

mechanisms as compared with those employing more than three receptor or transmission mechanisms. Second, there has been no research bearing upon the degree to which central and peripheral mechanisms may contribute to the total initial light adaptation phenomenon when it is studied in relation to chromatic variables.

Determining the Loci of Neural Mechanisms Responsible for the Crawford Effect

It is generally agreed that the Crawford effect is partially due to neural mechanisms. In this view much of the adaptive effect of F_c is produced by a burst of neural activity accompanying rapid changes of F_c intensity (onset and termination), which renders additional activation by F_t possible only when F_t intensity is made quite large. Thus, it is reasonable to assume that the transient aspects of the Crawford phenomenon will only obtain where both F_c and F_t share common neural pathways, wherein such an interaction of their effects is possible. The term pathway should be taken to include any nervous system location where mutual interaction can occur, and therefore, includes both peripheral afferent tracts and their central (cortical) projections.

Boynton and Triedman (1953) have shown the Crawford effect in the b-wave of the electroretinogram where the

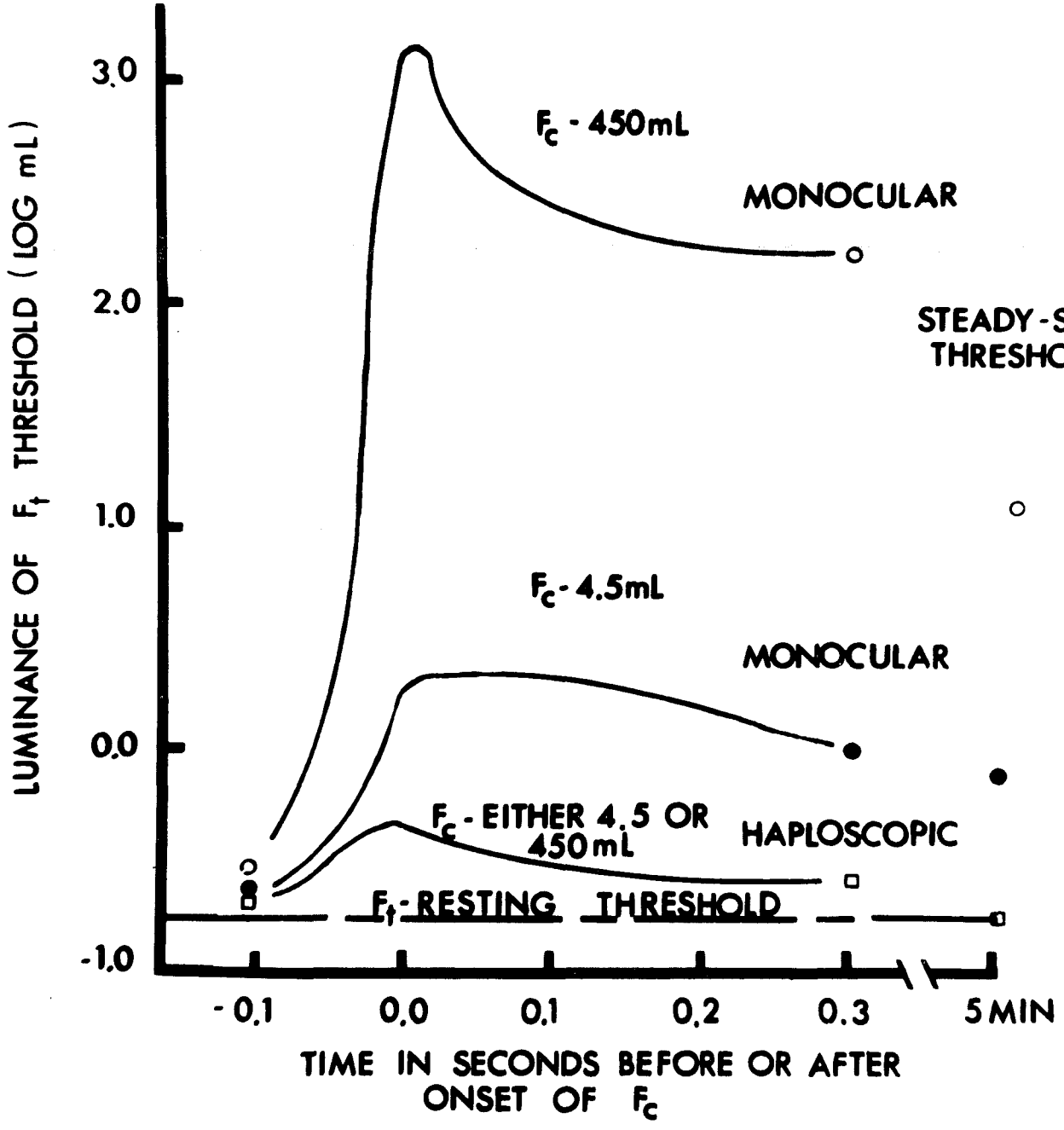
presence of F_c often renders detection of F_t as a separate graphic event virtually impossible. This led Boynton and Triedman to assume that the location of such effects was at least partically retinal. The classic work of Riggs and Graham (1940) on the eye of Limulus lends additional support to the Boynton and Triedman position. These researchers found that the onset of a stimulus produced a transient peak of neural activity during which a further increment was difficult to obtain (presumably the equivalent of the highly elevated "on" effect increment threshold). This finding indicated that initial adaptation effects depend heavily on processes in the retina. Rushton (1963) has also shown that the neural mechanisms responsible for the transient aspects of the Crawford effect probably lie between the receptor and ganglion cell levels.

Another approach to determining the loci of neural interaction was taken by Bouman (1955), Kandel (1959), and by Battersby and his collaborators (Wagman and Battersby, 1959; Battersby and Wagman, 1962; and Battersby, Oesterreich, and Sturr, 1964) who each employed haploscopic presentation of the adapting and test stimuli. These conditions, where only retrochiasmal interaction was possible (presumably this interaction occurs in visual cortex), yielded a relatively small (compared to the

monocular data) but significant effect, the magnitude of which was found to depend on the spatial arrangement of the stimuli. Figure 3 depicts the general form of the data obtained haploscopically compared to monocular results. Note that F_c intensity is not a significant variable in determining the haploscopic threshold.

Bush (1955), as discussed above, assumed that the (at least partial) independence of the peripheral color mechanisms was responsible for the direct relationship he obtained between the spectral proximity of F_c to F_t and the adaptive effect of F_c. In view of the well-known facts of color mixing and of visual physiology, no recent theory of color vision assumes that each discriminable wavelength reaches cortex via separate neural pathways. Instead, color responses are said to be based on a synthesis of the relative activity levels in several peripheral color mechanisms. This synthesis results in a specific neural condition which allows the color discrimination to occur. Such a synthesis of separate color mechanisms would probably result in a reduction of the system's capacity to resolve changes in activity level in each specific mechanism distal to the point of synthesis. Evidence will be presented below that integrative transformations of peripherally coded color recptor information occur in the neuroretina and in the lateral geniculate.

Figure 3. Representative data from Kandel (1959). The open circles are for a monocular presentation of F_c and F_t where F_c luminance is 450 mL. The filled circles are for a monocular F_c at 4.5 mL. The squares are the approximate values for haploscopic presentation of either a 450 mL or 4.5 mL F_c. The ordinate shows the luminance of F_t in log mL. The abcissa represents time in sec before or after the onset of F_c. Steady-state values are given at the far right at a F_c-F_t interval of 5 min.


3.0
2.0
1.0
0.0
-1.0
LUMINANCE OF F_t THRESHOLD (LOG mL)
F_c - 450mL
MONOCULAR
STEADY-STATE THRESHOLDS
F_c - 4.5mL
MONOCULAR
F_c - EITHER 4.5 OR 450mL
HAPLOSCOPIC
F_t - RESTING THRESHOLD
-0.1
0.0
0.1
0.2
0.3
5 MIN
TIME IN SECONDS BEFORE OR AFTER ONSET OF F_c

These transformed ("coded") signals may still project centrally along several independent pathways, to be fused or transformed again in cortex. This possibility is also suggested by the phenomenon of haploscopic color fusion (Hecht, 1928) which indicates that central processes are responsible for at least part of the synthesis of color receptor information into neural states that account for the psychophysical response to various wavelengths of light.

If central color mechanisms are structured in such a way as to allow mutual interaction, then they may be more spectrally broad-band than their peripheral counterparts. That is, they may respond to stimulation by light of spectrally disparate wavelengths rather than a single "primary" of limited spectral extent. Thus, if the Bush paradigm were to be applied haploscopically, the data might reveal that that magnitude of the neural "on" (or "off") effect is largely independent of the spectral characteristics of the test and adapting stimuli. One purpose of the present experiment was to test the assumption that wavelength is not a determining factor of the haploscopic increment threshold.

Theories of Color Vision and Chromatic Initial Light Adaptation

There are two major alternative views on how wavelength is allocated to afferent neural pathways: trichromatic and opponent-process theory. The trichromatic theory originated in the writings of Thomas Young (1802). As elaborated by Helmholtz (1866) and Hecht (1930), this approach postulates three peripheral mechanisms with different peak, but broadly overlapping, spectral sensitivities. Each mechanism projects centrally via separate neural pathways rendering the phenomenological qualities of red, green, and blue. These "colors" are then synthesized into intermediate hues. More recent forms of trichromatic theory, however, have tended to avoid implying limits as to type of receptor or specific nervous pathways (Brindley, 1957). There has been substantial confirmation of the (at least partial) validity of the trichromatic system through the identification of three distinct foveal pigments in man, functionally corresponding to the red, green, and blue primaries. This confirmation has been accomplished in a variety of ways. Rushton (1962, 1964) isolated two cone pigments with maximum absorption in the yellow and in the green spectral regions (erythrolabe and chlorolabe, respectively) via retinal densitometry. Wald (1964) has

shown the presence of three pigments corresponding to peak wavelengths of yellow, green, and blue (cyanolabe) by selective bleaching, and this finding has been confirmed by MacNichol and others (MacNichol, 1964; Marks, Dobelle, and MacNichol, 1964) using microspectrophotometry. These data agree with the isolation of three main foveal response curves (out of five or possibly even seven) by Stiles (1959). The so-called "red" mechanism in all of the foregoing studies has peak sensitivity in the yellow wavelengths, but a spectral bandwidth sufficient to allow it to respond to the red wavelengths with greater sensitivity than the "green" mechanism. This ability is sufficient in terms of trichromatic theory to consider it the "red" receptor.

One assumption which remains basic to the many variants of trichromatic theory is that the relative sensitivity of each color mechanism decreases as the stimulus wavelength differs from the peak spectral sensitivity of that mechanism. If the basic assumptions of the trichromatic theory are correct for the increment threshold situation, then the magnitude of the Crawford effect should be proportioned to the F_c-F_t wavelength difference regardless of the specific wavelengths used. Bush (1955) partially confirmed this conclusion, but he did not test for the case where F_c or F_t was yellow,

and did not look for central effects. Boynton (1956), who included a yellow F_c together with F_t spaced at 10 nm intervals along the visual spectrum but only at one F_c-F_t interval did not obtain results that supported the assumptions of trichromatic theory, but rather of a minimally tetrachromatic theory of color vision.

The opponent-process theory (which is tetrachromatic) is an alternative to the trichromatic approach and was initiated by Hering about 1872. Hering's original theory postulated three receptor mechanisms, each capable of taking positive and negative values corresponding to the pairs of sensations white-black, red-green, and yellow-blue. Catabolysis and anabolysis of receptor substance was supposed to determine which type of sensation each receptor mechanism yielded.

Recent variations of opponent-process theory have attempted to accomplish a rapprochement of the two systems. Such an attempt is the theory proposed by Hurvich and Jameson (1957) based primarily on color neutralization experiments. This theory avoids the receptor chemistry issue by providing a purely analytic demonstration of how a Young or Hecht type trivariant receptor mechanism can be organized in such a way as to generate opposing functional states in the nervous system. Empirical support for the combined Young-Hering system of Hurvich

and Jameson has been supplied by the research of numerous investigators (De Valois, Smith, Kitai, and Karoly, 1957; De Valois, Jacobs, and Abramov, 1964; Hubel and Wiesel, 1962; Jacobs and De Valois, 1965; MacNichol and Svaetichin, 1958; Tomita, 1965; Wagner, MacNichol, and Wolbarsht, 1960; and Wiesel and Hubel, 1966). In general, the position supported by these experiments is that if there are three independent primary color receptors (cones) then their activity becomes integrated, at both the neuroretinal and geniculate levels, into two or more opponent neural processes (as measured from single cells). For example, one typical response pattern obtained from a geniculate cell might be: excitation by onset of a red light or termination of a green light; inhibition by red termination and green onset. Often, within the receptive field of single units such action interacts with spatial variables so that adjacent retinal loci have opponent chromatic effect (e.g., "red-on" center, "green-off" periphery, etc.). These electrophysiological findings are commensurate with a Hering-type theory and demonstrate that retinal color information is transmitted to cortex via the modulation, by excitation and inhibition, of ambient unit activity.

The trichromatic theory of color vision has been mainly substantiated by numerous investigations of

receptor chemistry and of psychophysical response, whereas opponent-process theory appears primarily supported by electrophysiological data concerning the retino-cortical transmission pathways. The Crawford effect depends on events occurring within these same neural pathways and thus constitutes a means of studying their nature. This assumption is particularly applicable where the wavelength of F_c and F_t are varied. A monotonic function inversely related to the F_c-F_t wavelength difference would be predicted for the case of a trichromatic system where the three color-receptor information channels maintain independence to their cortical projections. A monotonic function would not be predicted from opponent-process theory. This is because opponent colors such as red and green do not follow separate pathways as in trichromatic theory, but are mediated by mutually exclusive states of the same pathway. This position leads to several possible outcomes, all of which imply an irregularity in the curve relating the magnitude of the increment threshold as a function of the F_c-F_t wavelength difference for the case of opponent wavelengths. In this regard De Valois has discussed the possible temporal interactions of opponent stimuli in the folowing way:

> If one thinks of the "red-on", "green-off" cell as signaling red by an increase in firing rate and green by a decrease in firing rate,

> the response of this cell to a single pulse of monochromatic light can be seen to exhibit the characteristics of successive color contrast.
>
> Thus in a psychophysical experiment a pulse of "red" light induces "green" as an aftereffect, and this cell is inhibited ("green") at the termination of a "red" light. Correspondingly, it is excited ("red") at the termination of stimulation with "green" light. It is perhaps more convincing to observe its response when stimulation by one wavelength is followed by a light stimulus of the complementary wavelength. A "red" light seen after inspecting a "green" light for a time is redder than if it had not been preceded by the "green" light. (De Valois, 1960).

This finding, explained by the "on" response to red light summing with the "off" response to the green light, concurs with Jameson and Hurvich's (1956) conclusion that adaptation by one opponent-color reduces the threshold of the complementary opponent color. Accordingly, in the present study one would predict that the increment threshold for opponent F_c-F_t wavelengths will depend on whether it is obtained at negative or positive intervals; being higher for one F_c-F_t temporal order than for the reversed temporal order depending on the F_c and F_t wavelength. Furthermore, the presence of such an interaction, be it facilitation or inhibition, caused by the same pathways being followed by F_c and F_t, would only occur for opponent colors. Thus, in general, increment thresholds for opponent colors should not fall in line with the increment threshold function predicted

on the basis of absolute F_c-F_t wavelength difference.

The purposes of the present research were, therefore, twofold. The first purpose was to determine the contributions of peripheral and central mechanisms in determining the increment threshold when studied in realtion to chromatic variables. The second purpose was to examine in detail the magnitude of the increment threshold as a function of both temporal order and relative wavelength of the conditioning and test flashes. From this examination it may be inferred whether trichromatic or opponent-process mechanisms predominate in determining the increment threshold.

CHAPTER II

APPARATUS

The stimuli were presented via a 4-channel Maxwellian view optial bench which has been described in detail by Battersby, et al. (1964).

Optical System

Main Channels (F_c and F_t)

Two of the four channels were individually focused upon electronically activated shutters consisting of a vane attached to the shaft of a d-c oscillograph coil. Accurate control of luminance was provided by then passing the beam through circular wedges and balancing filters having a density range of 4-log-units. The wedges had neutral spectral transmission characteristics over the visual spectrum. The light was then recollimated. Neutral density filters for gross luminance control and color filters were interposed at this point. The beams were then passed through individual target plates, each independently movable in two planes by means of micromanipulators to allow placement of the

stimuli in the field of view. The two main channels were then independently focused through beam splitters together with the adapting fields (see below), upon two apertures either one of which could be opened by means of an electrically operated controlling vane. In this way, a main channel was mixed with an adapting channel and both could then be presented independently to either, or both, eyes. To accomplish the presentation, the mixed beams were recollimated, passed through rotatable rhomboid prisms to permit interpupillary adjustment, and finally focused upon the nodal points of the eyes; the size of the final filament image was of 0.5 x 2 mm. This was found to be smaller than the Os' pupil diameter under all experimental conditions.

Adaptation Fields

Two other light channels, without shutters or wedges, were derived from the same light source by passing a single collimated beam through a filter rack where neutral density filters adjusted the adapting field luminance to 0.0 log mL, and then through a beam-splitter. The two beams thus derived proceeded through clear slides containing central fixation spots and then they were mixed with the projection system of the test 2 conditioning channels (described above).

Observer Fixation

The observer's head position was established and stabilized by means of a Bausch and Lomb chin-and-head rest. This rest was mounted on a table itself adjustable for orthogonal motion in three planes plus rotation about the vertical axis. The optical projection system provided for interpupillary adjustment and there was a diopter adjustment for each final eye lens.

Stimulus Size and Retinal Position

Spatial parameters were determined by precision-drilled holes in a metal plate placed in a collimated portion of each main-channel beam as specified above. An aperture of 1 mm at this location provided d target field size of $1^{\circ}\ 20'$. This relationship was used to specify the dimensions of the actual stimuli as well as their displacement from the center of the field.

Light Source

The light source was a GE projection lamp No. PH-18-AT-10P having a helical tungsten filament that was operated at approximately 17.5 amperes. This current corresponded to a voltage of approximately 6 VDC supplied by an Electro Products d-c power supply. Voltage input to the power supply was regulated by a Sola constant

voltage transformer (that was used for all electrical components of the bench) and adjusted by means of a series connected variable autotransformer. Current and voltage were continuously monitored by appropriate moving-coil meters. Luminous flux was constantly monitored (indirectly) by means of an RCA 929 phototube that received light input directly from the tungsten source. The power supply to the lamp was regulated such that the cathode current of the phototube amplifier was constant at 0.8 mA. A single pre-aged lamp was used throughout the entire experiment.

Luminance Calibration

The luminance calibration procedure employed has been described in detail by Battersby and Wagman (1959). In essence, the procedure was to closely estimate by using several observers to match the luminance of each main channel with that of a known luminance in a bipartite field. The luminance of the adapting fields was obtained by similar photometric matches with the previously calibrated test fields. Relative luminance of the main channels was calibrated with a Photovolt photometer so that the percent transmission was plotted as a function of wedge reading. From such measures the luminance corresponding to any given wedge reading could be derived.

Duration Control

The duration of F_c and F_t was controlled by vane-type shutters, placed at the nodal point of the focused beam, driven by galvanometer movements modified from use in a Grass EEG apparatus. These were driven by specially constructed d-c amplifiers which received input from Tektronix 161 pulse generators.

The temporal characteristics of the system were determined as follows. A Tektronix 162 waveform (sawtooth) generator was used both as a time base to determine the recycling rate and to trigger a second 162 waveform generator. This generator, in turn, triggered both the two pulse generators controlling the shutter system, and the sweep of a Tektronix 360 indicator oscilloscope. The controls of these pulse generators served two functions: they allowed variation of the onset of the two main-channel stimuli by setting the point along the sawtooth output of the waveform generator when they would trigger, and they established the duration that the shutters remained open. The accuracy of such settings were determined and monitored by diverging some light from each of the main beams to independent RCA 929 phototubes via microscope slide cover glasses used as partially reflecting surfaces. The cathode-follower output of

the phototube amplifiers were fed into the y-axis input of the 360 oscilloscope where the flash duration and the F_c-F_t interval were continuously displayed. The rise and fall time for both F_c and F_t were approximately 1.25 ms.

Luminance Control

The E could adjust the circular wedges by hand, where O employed a telephone-type spring-return lever switch capable of motion in opposite directions from a neutral point. This switch controlled a solenoid-operated stepping motor that moved the wedge. Momentary deflection of the switch in one direction (right) increased the luminance by 0.01 log unit, while motion in the opposite direction reduced luminance by an equal amount.

Blanking Controls and Auditory Ready Signal

Miniature momentary-contact push-buttons mounted on the wedge control-switch box permitted O to independently interrupt the power amplifier input circuits to F_c and F_t. When the push-buttons were depressed for the duration of an F_c or F_t interval, the blanked stimulus (or both stimuli) would not occur. An auditory pulse was produced by amplifying the trigger pulse

coincident with the onset of the second waveform generator sawtooth and feeding it to a loudspeaker. This resulted in a "click" that served as an auditory ready signal for O, just prior to the onset of the stimulus or paired stimuli appropriate for a given trial.

CHAPTER III

PROCEDURE

Observers

Two observers (O), both with uncorrected 20/20 vision and normal color vision as indicated by the Ishihara Pseudo-isochromatic Plates, were used in this study. KAG (Female, 26 years of age) had little previous experience in psychophysical observation. A training program was established and reliability of judgments was obtained for this O in a few hours of practice. JCS (Male, 27 years of age, the author) was the other observer and had considerable previous experience in making psychophysical judgments.

Fixation

Head position was stabilized by a Bausch and Lomb chin-and-head rest described in the previous section. Central fixation was obtained by a crosshair superimposed on a small annulus, both targets were viewed against an adapting background. The crosshair was black except where it fell upon the annulus, where it was

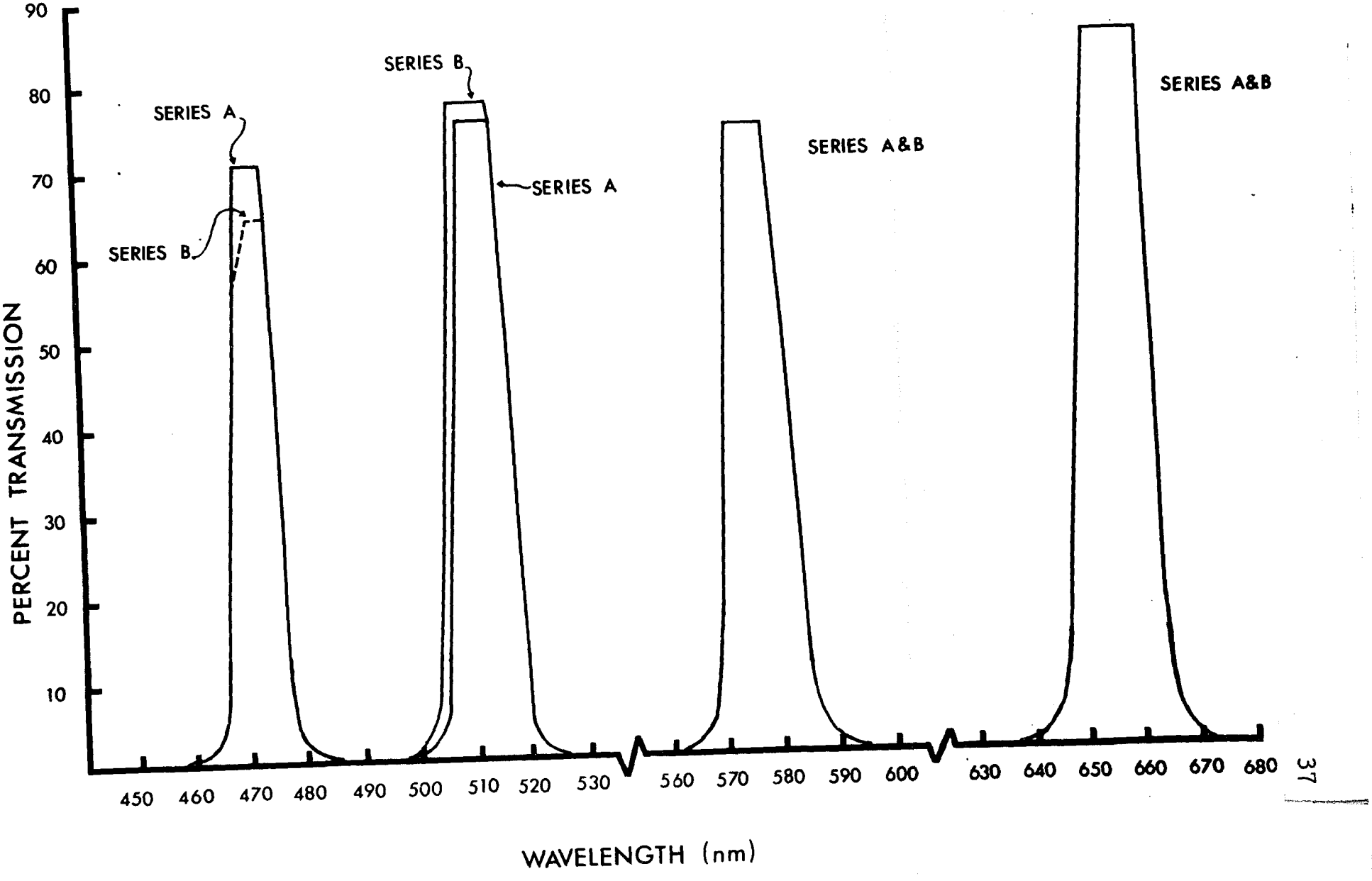
"white", i.e., at the same luminance as the adapting background.

Experimental Design and Independent Variables

Excitability functions (incremental threshold functions over time) were determined by presenting F_c and F_t to O under the following temporal separations (negative values indicating F_t preceding F_c onset, positive values indicating F_c onset preceding F_t): -100, -50, -25, 0, 25, 50, 100, 175, 250 ms. In addition a "steady-state" condition was used where F_c was 3250 ms in duration and F_t was presented at 3000 ms. Pilot data had shown that adaptation to F_c was virtually complete at 3000 ms and that there was no indication of an "off" effect where F_t preceded F_c termination by 250 ms.

F_t was a circular disc of light, 5 ms in duration and 1° in diameter, either red (655 nm), yellow (576 nm), green (512 nm), or blue (472 nm) obtained through the use of Baird Atomic Model B-2 interference filters.[1] The 1 percent transmission bandwidth of these filters was less than 30 nm in all cases and the values listed above represent the peak transmission points. The complete spectral transmission curves for the filters used in this experiment are shown in Figure 4.

Figure 4. Spectral transmission curves of the interference filters. Percent transmission (on the ordinate) is plotted as a function of wavelength (on the abcissa). Series A filters were used for F_t; Series B filters (472 and 655 nm) were used for F_c. Differences in transmission were compensated for in the luminance matching procedure.


90
80
70
60
50
40
30
20
10
PERCENT TRANSMISSION
SERIES A
SERIES B
SERIES B
SERIES A
SERIES A&B
SERIES A&B
450 460 470 480 490 500 510 520 530 560 570 580 590 600 630 640 650 660 670 680
WAVELENGTH (nm)

In the all conditions F_c was presented at $6^o40'$ along the horizontal meridian of the temporal field of the right eye (OD). In the monocular mode F_t was concentric to F_c in OD. In the haploscopic mode F_t was presented at $6^o40'$ in the horizontal meridian of the nasal field of the left eye (OS, this was the homotopic locus). F_c was a concentric disc of light $1^o20'$ in diameter and 250 ms in duration, except for the "steady-state" condition where it was 3250 ms. The F_c was either red (655 nm) or blue (472 nm) and these values were also obtained by using Baird Atomic B-2 filters (see Figure 4). Since the two F_c differed in wavelength, it was necessary to equate them for intensity in some way. Stimulus intensity, however, can be equated in terms of three alternative criteria: equal energy, equal brightness, or equal threshold effects. In the present study, it was decided to define the equal intensity state by means of a threshold match. This condition was operationally specified by setting F_c intensity 1.4 log units above its threshold as measured against the 0.0 log mL adapting background. Preliminary data had indicated that this level was the highest F_c value that would allow determination of the F_t threshold under all experimental conditions.[2]

Experimental Procedure

The O made two types of threshold discrimination, threshold of F_c and F_t presented alone rise against 0.0 log mL adapting background and the "two-flash" increment threshold of F_t when paired with F_c, in all cases the same procedure was used for all measurements. E randomly set the appropriate wedge at some point clearly above the required threshold (with a typical range 0.1 to 0.4 log units above threshold), and then O reduced the flash luminance in small steps (multiples of 0.01 log units up to about 0.1 log unit per presentation). Typically, the size of the flash-luminance decrement made decreased as the threshold was approached. After the initial occasion on which a flash could not be seen, the O did not alter flash luminance unless the flash was detected within two additional consecutive presentations. If this event occurred, reduction of flash luminance was continued in small steps, as before, until detection no longer occurred for three consecutive presentations. In order to facilitate the discrimination at near-threshold values, the O could "blank" or inhibit a flash presentation to provide a no-stimulus standard. O could also choose not to reduce flash luminance after a suprathreshold occasion in order to provide a more

definite stimulus criterion. The 0's task constituted a form of the method of adjustment, with descending series only.

Although the procedure for obtaining a given reading was the same for both Os, certain considerations resulted in different orders of experimental conditions being used in the case of each O.

For JCS the sequence of data collection was as follows: Step 1) an F_c-F_t interval was chosen randomly from among the ten transient values (-100, -50, -25, 0, 25, 50, 75, 250 ms). All data within this condition were then collected over a series of experimental sessions. Step 2) an F_c-F_t wavelength combination was randomly chosen from the eight possible combinations (red-red, red-yellow, red-green, red-blue, blue-red, blue-yellow, blue-green, blue-blue). Step 3) the order of the stimulating mode (monocular or haploscopic) was counterbalanced in an ABBA order over consecutive determinations of the increment threshold for each combination of Step 1 and 2 conditions. Step 4) the F_c threshold was established as the average of five readings of the F_c threshold, with the level of F_c then raised to 1.4 log units above this value.[3] Step 5) the resting threshold of F_t was then identically established. Step 6) the threshold of F_t paired with F_c (the increment threshold) was then

taken in the same way. Step 7) steps 4, 5, and 6 were then repeated for the stimulating mode as specified by step 3. The sequence then returned to step 2 and continued to cycle through steps 2 to 7 until all wavelength combinations had been used, whereupon the cycle returned to step 1. The complete series was then repeated for the next F_c-F_t interval, and so on until all data for this O was collected.[4]

The sequence of data collection for KAG was as follows. Step 1) all data within the monocular mode was collected over the initial experimental sessions. Step 2) a F_c-F_t wavelength combination was chosen randomly and all data within that (monocular) condition collected in a single session. Step 3) all ten transient F_c-F_t intervals were used, resulting in a complete excitability cycle, in a different random order each time this step was repeated. Step 4) the level of F_c was set as in JCS step 4 above. Step 5) three readings of the F_t resting threshold were taken. Step 6) increment threshold readings for the first five randomly selected F_c-F_t intervals were obtained, each defined as the average of five settings of F_t. Step 7) three additional settings of the F_t resting threshold were obtained and averaged with those in step 5, with the mean used to derive the increment threshold of F_t. Step 8) because steps 1 to 7

required one hour to conduct, it was necessary to re-establish the F_c threshold in order to maintain equivalent adapting effect. (Preliminary data had indicated that the F_c threshold would rise from 0.1 to 0.2 log units in a two-hour period of observation.) F_c was then reset to 1.4 log units above this value. Step 9) steps 5, 6, and 7 were repeated for the last five F_c-F_t intervals. A fifteen minute rest period intervened between steps 7 and 8. Step 10) steps 2 through 9 were repeated in the haploscopic mode.[5]

The "steady-state" data were obtained in an identical manner for both observers. Step 1) the mean F_c threshold was calculated for each O, based on all readings of this value obtained during the transient-conditions data collection described above. The level of F_c was then set at 1.4 log units above this value. Step 2) the resting threshold of F_t was obtained as the mean of five settings as in the transient conditions. Step 3) the increment thresholds of F_t superimposed upon F_c, under the conditions where F_c was 3250 ms in duration and F_t (5 ms) occurred at 3000 ms, were taken also as above.[6] As effects obtained in the haploscopic mode reflect primarily neural processes, the "steady-state" conditions were not expected to affect the increment threshold when measured haploscopically. Preliminary data confirmed this

prediction and data were collected in the monocular mode only.

Finally, initial data collection revealed that the data obtained in the haploscopic mode appeared to be independent of the F_c-F_t wavelength difference. It was decided to add a condition in which both F_c and F_t were "white" (as defined by the spectral distribution of the Tungsten source at approximately 2600° K derived from known emission spectra for the Tungsten filament operated at 17.5 A without color filters) in both monocular and haploscopic modes in order to ascertain the degree such a condition would be representative of an "average" of results over specific F_c-F_t wavelength combinations. These data were collected from both Os at the completion of the previously described procedures, in the manner for a given F_c-F_t wavelength combination in the case of KAG. This was done for the conditions where F_c had 250 ms duration only.

FOOTNOTES

[1]The selection of the particular filter values used, except for the red (655 nm) filter, was based on color naming data (Judd, 1932; Beare, 1963). These values are generally representative of the many theoretical alternatives suggested by the literature, and their use avoided the arbitrary adoption of any of the diverse values used in prior studies related to the present experiment. The red (655 nm) filter was chosen so as to be as far towards the end of the visual spectrum as could be allowed while still maintaining adequate brightness.

[2]Since the F_c were set at near threshold values, it was assumed that a threshold match should result in comparable stimulus effects at the suprathreshold values used. In the present study, the low level of F_c and the difficulty of using the apparatus for flicker photometry led to the use of the threshold technique. In this regard, Blackwell (1963) has emphasized the appropriateness of matching techniques predicated on observer-determined effects (e.g. brightness) rather than energy or other purely physical parameter. Some investigators, however, (e.g., Bush, 1955) have chosen to equate F_c intensity via flicker photometry rather than threshold

matching. It should be noted that Sperling and Lewis (1959) found that threshold luminance matches of different wavelengths yield comparable results to suprathreshold (e.g., flicker photometric) matches, indicating that results of studies using flicker matches should be comparable to data obtained in the present experiment.

[3]If the variability of the obtained thresholds had a range of greater than 0.15 log units, additional readings were taken until a consecutive series of five readings were obtained with a variability less than this value. The mean of these five readings were then considered the threshold.

[4]The rationale for this procedure was based on the necessity for JCS to be his own E, thus limiting the number of readings that could be taken as the O had to briefly readapt to the background luminance after recording each reading. It should also be noted that when shifting from one stimulating mode to another, step 4 had to be repeated because F_c was presented to the contralateral eye to that previously used to set the F_c threshold, and also fell in the alternative visual field (nasal vs. temporal). Step 5 was repeated because it was impossible to present the adapting background to OS in the monocular mode, resulting in slightly different levels of F_t threshold in OD. Steps

4, 5, 6, and 7 constituted a session and required approximately one hour to complete, including initial adaptation.

[5]In the case of KAG, the greater efficiency of E being able to test O for long blocks of time resulted in the use of this different procedure. The use of separate procedures for the two Os reduces the possibility of a given experimental procedure producing artifacts.

[6]Preliminary data showed that for the intensities that were used, the three seconds of exposure to F_c conservatively exceeded the time required to approach complete adaptation. It is generally agreed upon that the neural "off" effect does not operate at or near 250 ms prior to F_c offset, thus the thresholds obtained represent approximations to the limiting "steady-state" or "photochemical" threshold of F_t. These data were of value in determining the magnitude of any "off" effect present in the transient-condition results (see Results section below). Because of the extended F_c duration, it was necessary to use a recycling interval of 6.2 sec. Step 3 was repeated for the eight F_c-F_t wavelength combinations in random order within a single session.

CHAPTER IV

RESULTS

Figures 5 to 13 depict the raw data plotted as threshold vs. time interval, or excitability, functions. More specifically, the ordinates show the log ratio of the F_t increment threshold to its own resting threshold (log F_t/RT) in relative units, obcissae read in msec of the F_c-F_t temporal interval, negative intervals indicate that F_t precedes F_c in time.[1] Figure 5 shows the data obtained under achromatic stimulation. These data are generally similar to the data of Crawford (1947) and later workers, in indicating that F_t threshold rises before F_c onset, reaches a maximum at about the point of F_c onset, and then returns to an elevated but constant level, rising again at the termination of F_c. The haploscopic functions of Figure 5 also reveal the characteristic attenuation of effects obtained in previous haploscopic studies.

Figures 6 to 13 depict the data obtained with chromatic stimulation and show that these chromatic functions are similar in shape to functions obtained in previous achromatic studies. Figures 6, 7, 8, and 9

(Text continued on page 58)

Figure 5. Excitability functions obtained with achromatic stimuli. Data from both observers plotted on the same axis, and taken under both monocular and haploscopic stimulation. The log ratio of the F_t increment threshold to its resting threshold (log F_t/RT) in relative units (on the ordinate) vs. the F_c-F_t temporal interval in ms (on the abcissa).

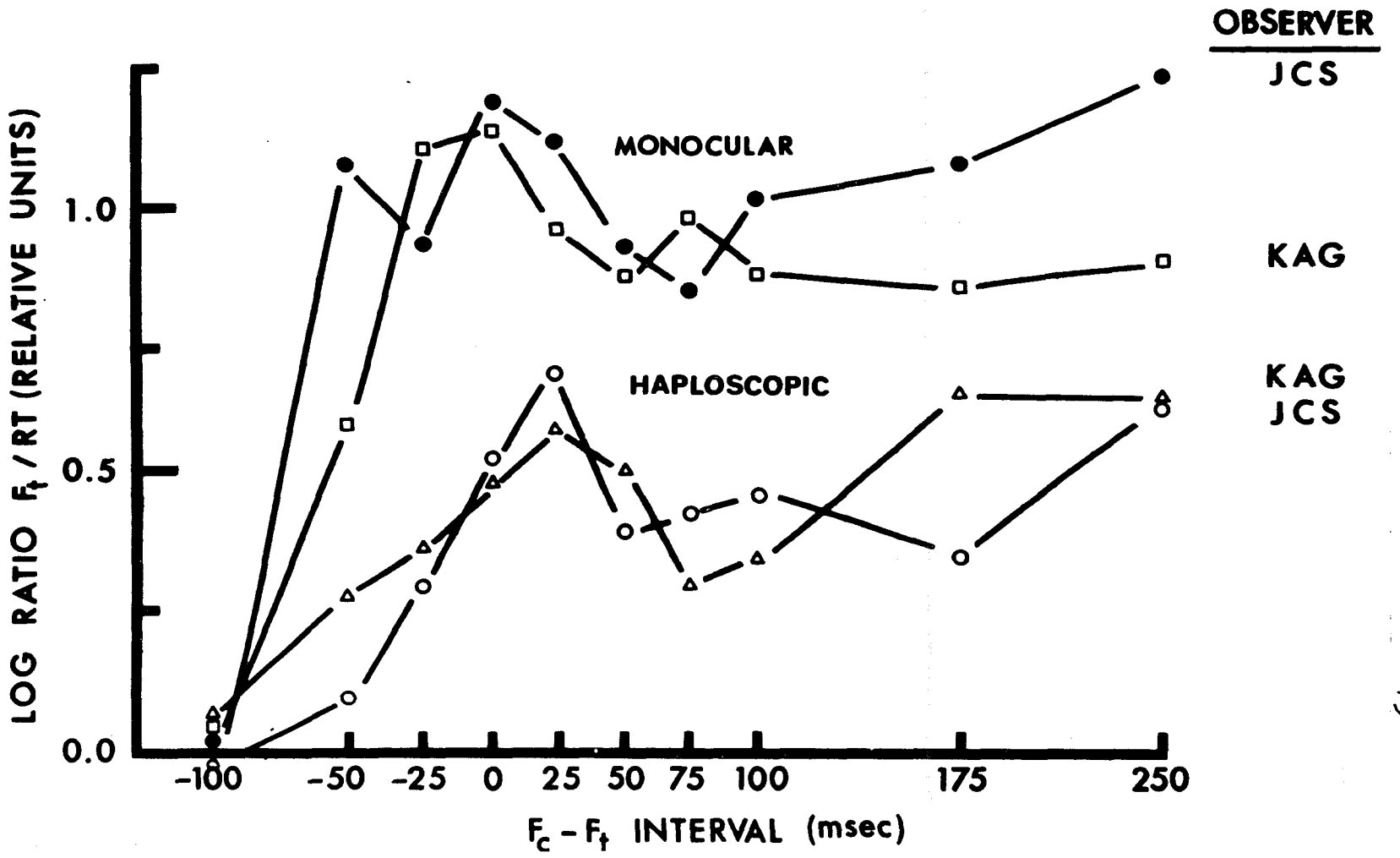

ACHROMATIC STIMULATION
OBSERVER
JCS
KAG
KAG
JCS
MONOCULAR
HAPLOSCOPIC
LOG RATIO F_t / RT (RELATIVE UNITS)
1.0
0.5
0.0
-100
-50
-25
0
25
50
75
100
175
250
$F_c - F_t$ INTERVAL (msec)

Figure 6. Excitability functions obtained with monocular stimulation. F_c wavelength: 655 nm (red). Observer: JCS.

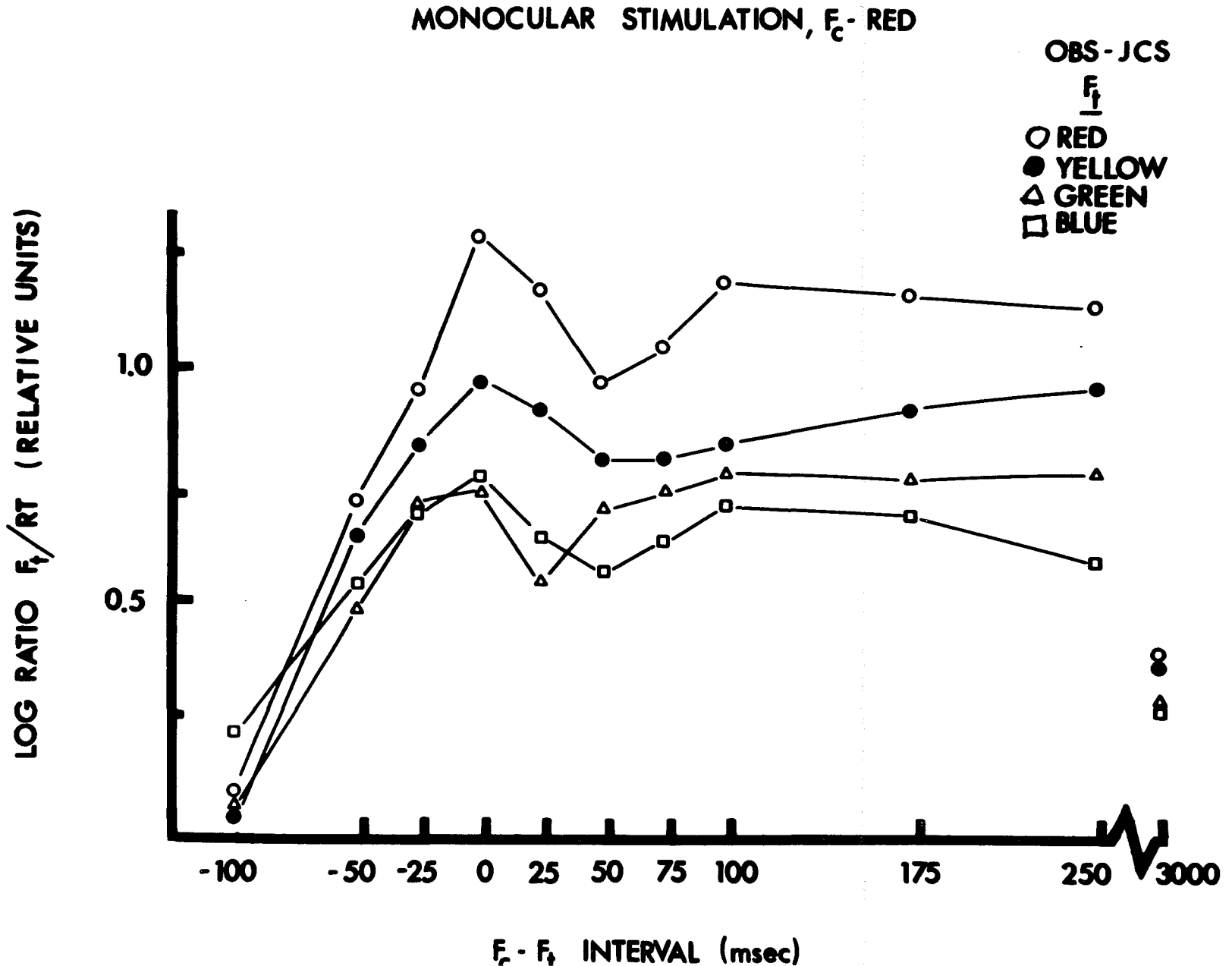

MONOCULAR STIMULATION, F_c - RED
OBS - JCS
F_t
RED
YELLOW
GREEN
BLUE
LOG RATIO F_t/RT (RELATIVE UNITS)
1.0
0.5
-100
-50
-25
0
25
50
75
100
175
250
3000
F_c - F_t INTERVAL (msec)

Figure 7. Excitability functions obtained with monocular stimulation. F_c wavelength: 655 nm (red). Observer: KAG.

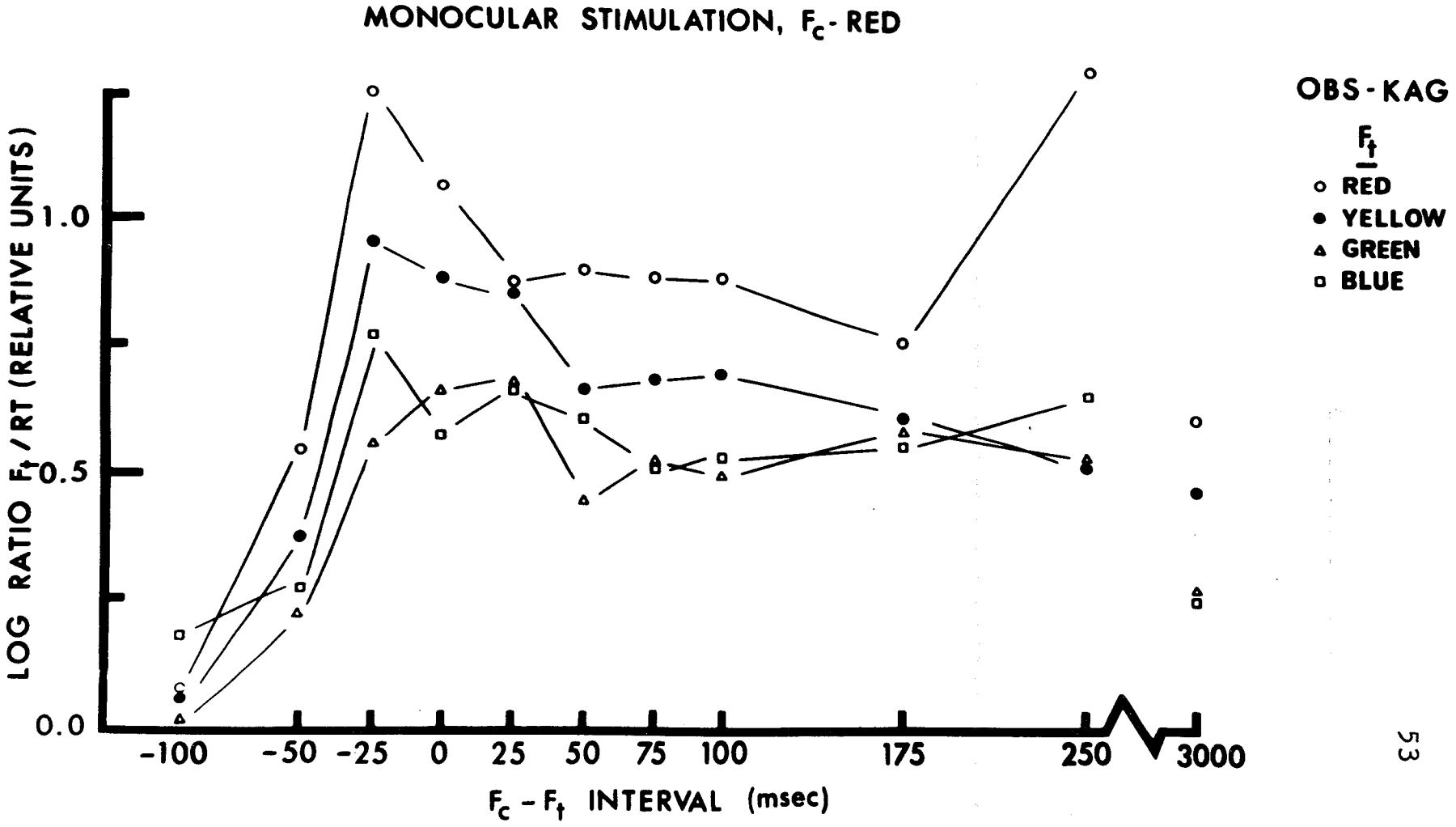

MONOCULAR STIMULATION, F_c - RED
OBS - KAG
F_t
RED
YELLOW
GREEN
BLUE
LOG RATIO F_t / RT (RELATIVE UNITS)
1.0
0.5
0.0
-100
-50
-25
0
25
50
75
100
175
250
3000
$F_c - F_t$ INTERVAL (msec)

Figure 8. Excitability functions obtained with monocular stimulation. F_c wavelength 472 nm (blue). Observer: JCS.

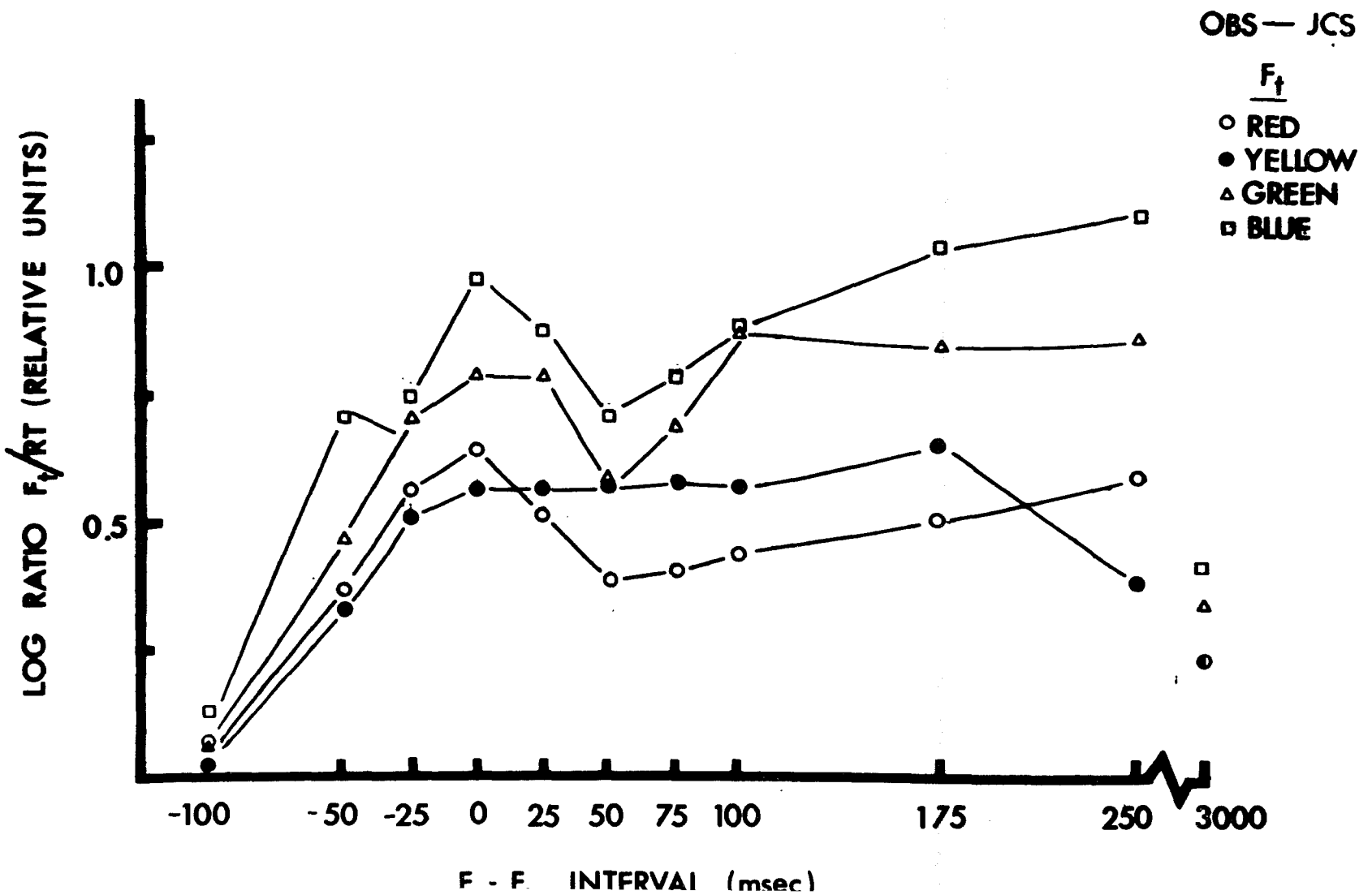
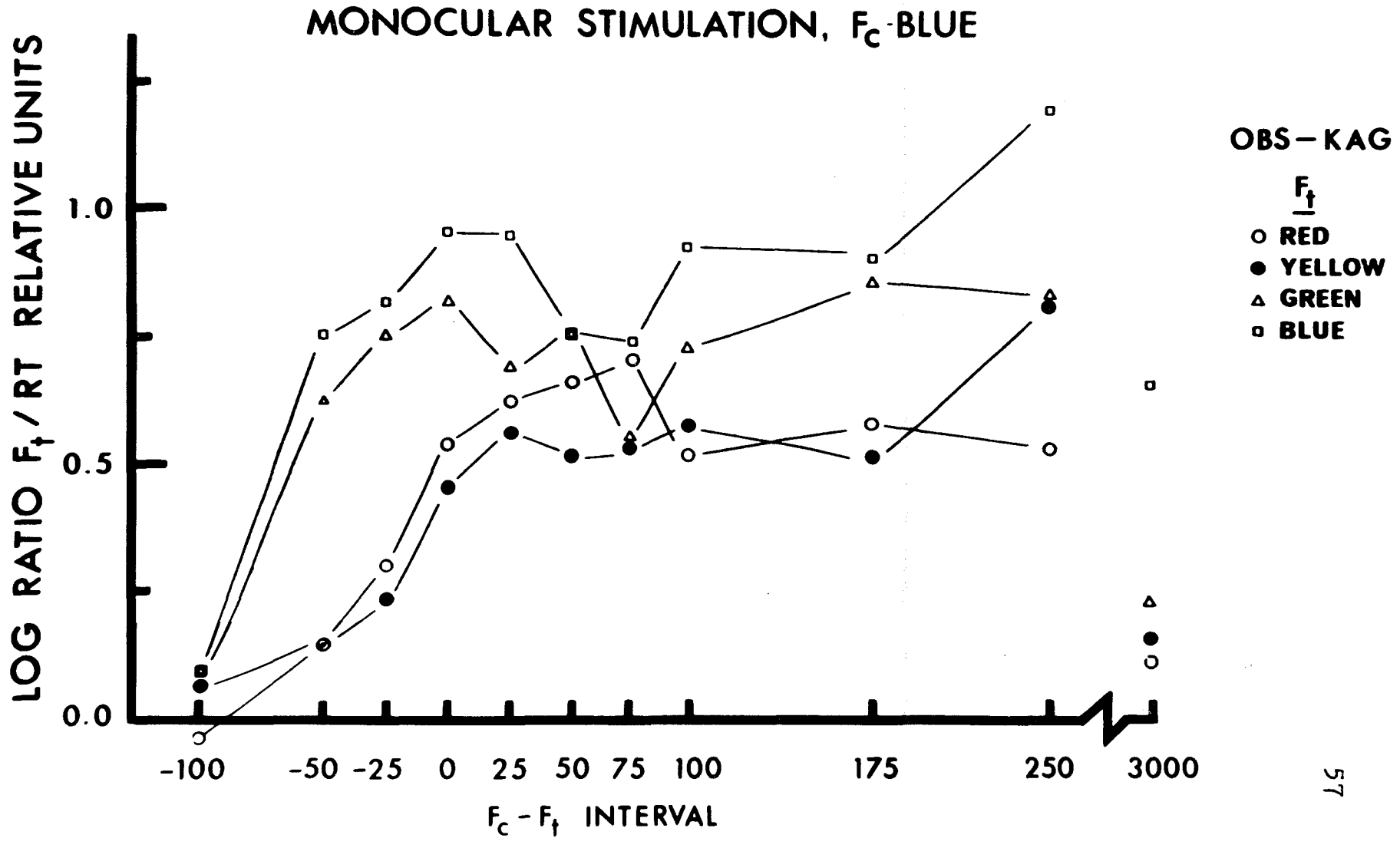

MONOCULAR STIMULATION, F_c -BLUE
OBS — JCS
F_t
RED
YELLOW
GREEN
BLUE
LOG RATIO F_t/RT (RELATIVE UNITS)
1.0
0.5
-100
-50
-25
0
25
50
75
100
175
250
3000
F - F INTERVAL (msec)

Figure 9. Excitability functions obtained with monocular stimulation. F_c wavelength 472 nm (blue). Observer: KAG.


MONOCULAR STIMULATION, F_c -BLUE
LOG RATIO F_t / RT RELATIVE UNITS
1.0
0.5
0.0
-100
-50
-25
0
25
50
75
100
175
250
3000
$F_c - F_t$ INTERVAL
OBS – KAG
F_t
RED
YELLOW
GREEN
BLUE

represent the monocular data only and show the four excitability functions (for the four F_t wavelengths) obtained with red and blue F_c for both Os. Confirming the work of Bush (1955), these data show functions similar to those obtained with white light, although somewhat smaller in magnitude and more variable in terms of the latency of maximum F_t increment. In addition, they show the intensity of F_t necessary for its detection varies inversely with the spectral separation of F_c and F_t. For both the 472 and 655 nm F_c, however, there was negligible difference between the increment thresholds obtained when these F_c were paired with either of the two spectrally most-distant F_ts (e.g., F_c = 472 nm with F_t = 576 and 655 nm). This result is treated further below.

Figures 10 to 13 show the data obtained in the haploscopic mode of observation. The form and height of the haploscopic functions are in agreement with previous investigations using white light (Kandel, 1961; Battersby and Wagman, 1962; and Battersby, Oesterreich and Sturr, 1964) in that they are attenuated when compared with corresponding monocular functions. Systematic variation of the F_c wavelength appear to have no consistent effect on the increment thresholds within any set of haploscopic excitability functions

except JCS, F_c = 472 nm (Figure 8).[2]

The results presented in Figures 6 through 13 can be summarized as follows: the F_t threshold rises well above its resting threshold for at least 50 ms prior to F_c onset and remains elevated for the duration of F_c, in some instances rising again preceding F_c termination. In order to more clearly depict the presence of this secondary increase about the termination of F_c, Figure 14 has been prepared. This figure is a histogram representing frequency of F_t maxima as a function of the F_c-F_t interval. The bimodal distribution indicated that the F_t increment threshold reaches its peak values about the onset and termination of F_c, thus demonstrating the presence of "on" and "off" effects.

In the monocular mode, F_t increment thresholds increase as the F_c-F_t wavelength difference approaches the homochromatic condition as a limit. Functions obtained under achromatic conditions (Figure 5) have shapes that are approximately equivalent to the chromatic functions obtained under the same mode of stimulation. The F_t thresholds, however, are often higher under achromatic stimulating conditions. Steady-state increment threshold functions as measured by the 3000 ms condition are markedly lower than virtually all

(Text continued on page 70)

Figure 10. Excitability functions obtained with haploscopic stimulation. F_c wavelength 655 nm (red). Observer: JCS.

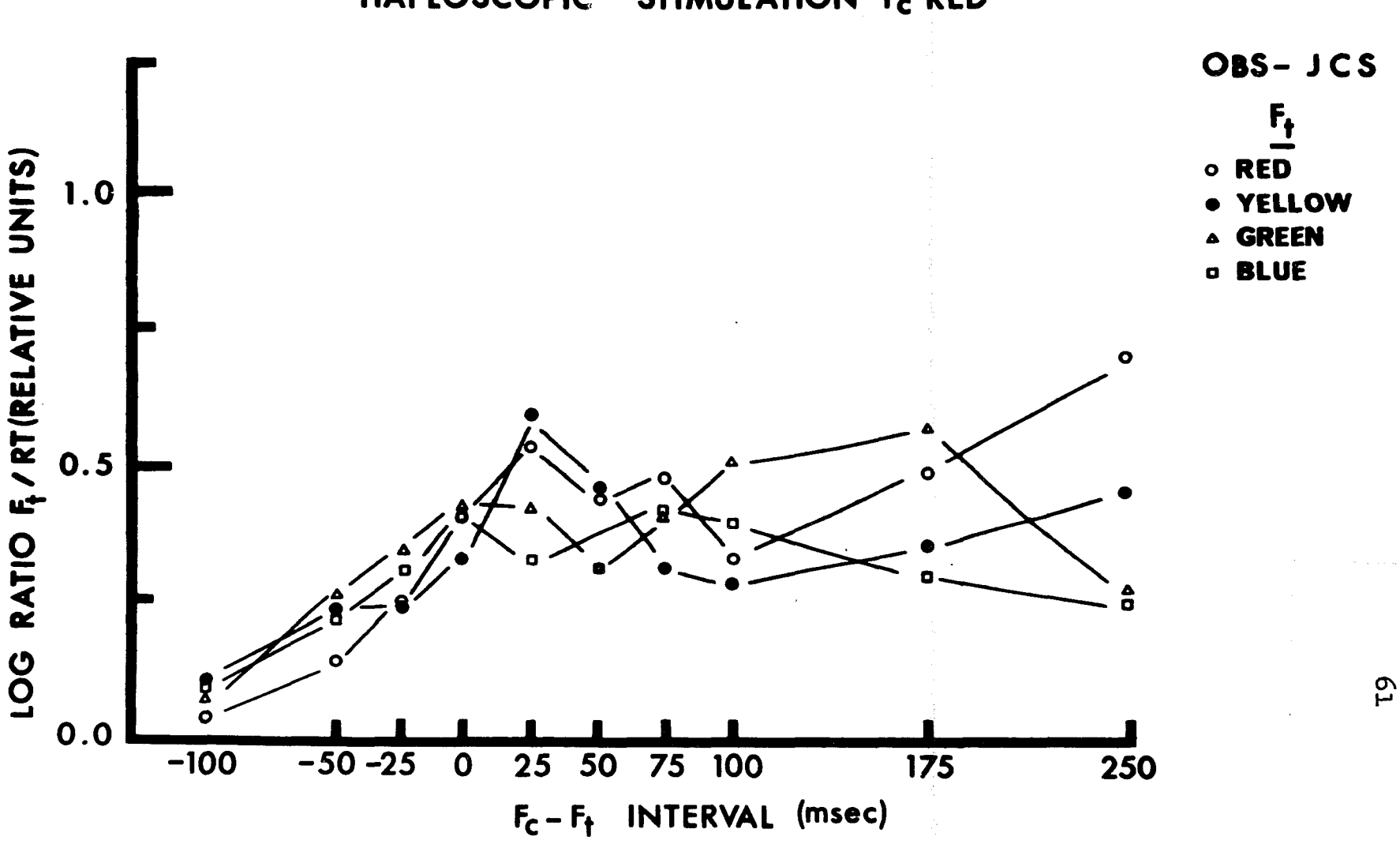

HAPLOSCOPIC STIMULATION F_c RED
OBS- JCS
F_t
RED
YELLOW
GREEN
BLUE
LOG RATIO F_t / RT(RELATIVE UNITS)
1.0
0.5
0.0
-100
-50
-25
0
25
50
75
100
175
250
$F_c - F_t$ INTERVAL (msec)

Figure 11. Excitability functions obtained with haploscopic stimulation. F_c wavelength 655 nm (red). Observer: KAG.

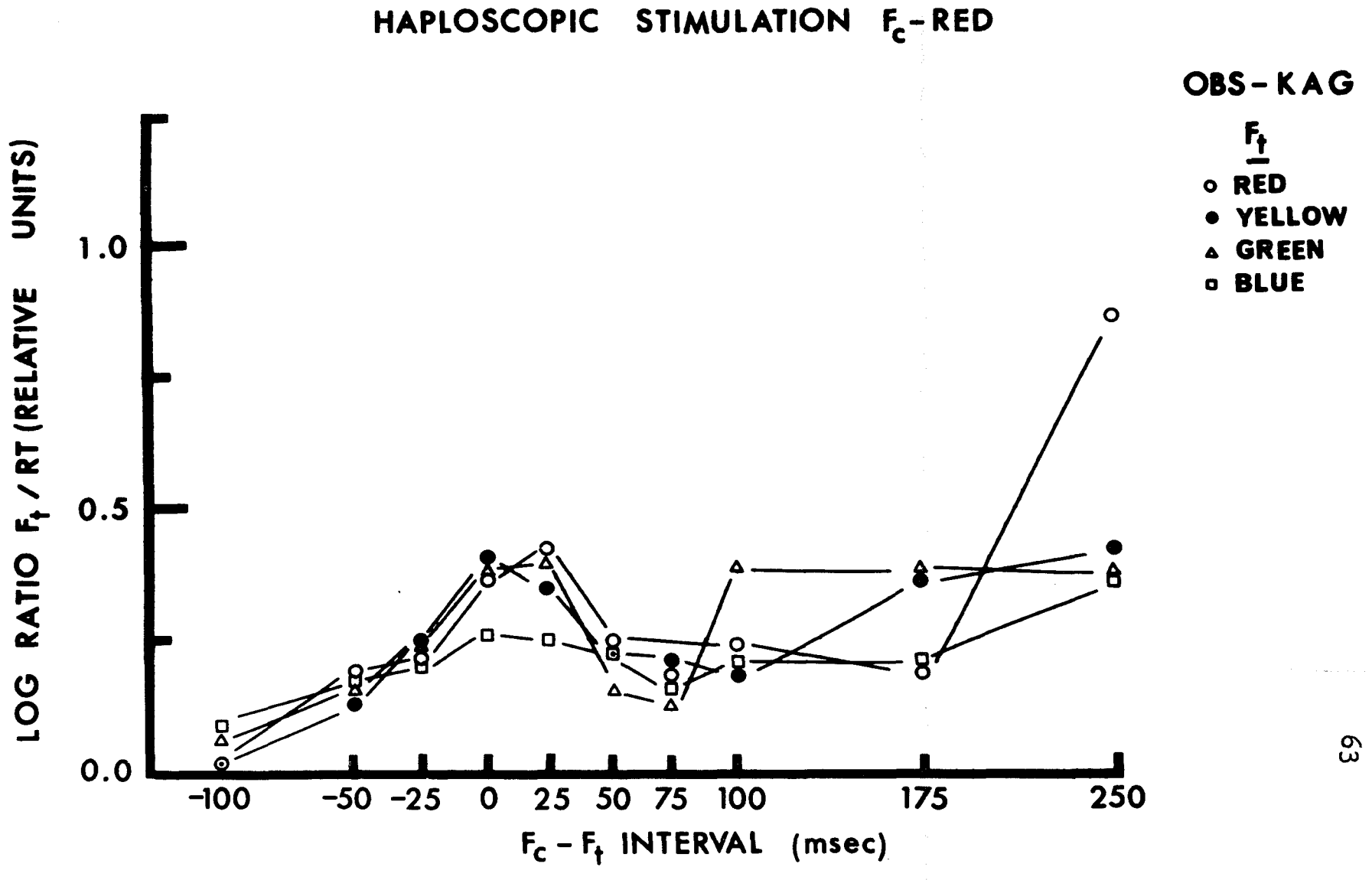

HAPLOSCOPIC STIMULATION F_c - RED
OBS - KAG
F_t
RED
YELLOW
GREEN
BLUE
LOG RATIO F_t / RT (RELATIVE UNITS)
1.0
0.5
0.0
-100
-50
-25
0
25
50
75
100
175
250
$F_c - F_t$ INTERVAL (msec)

Figure 12. Excitability functions obtained with haploscopic stimulation. F_c wavelength 472 nm (blue). Observer: JCS.

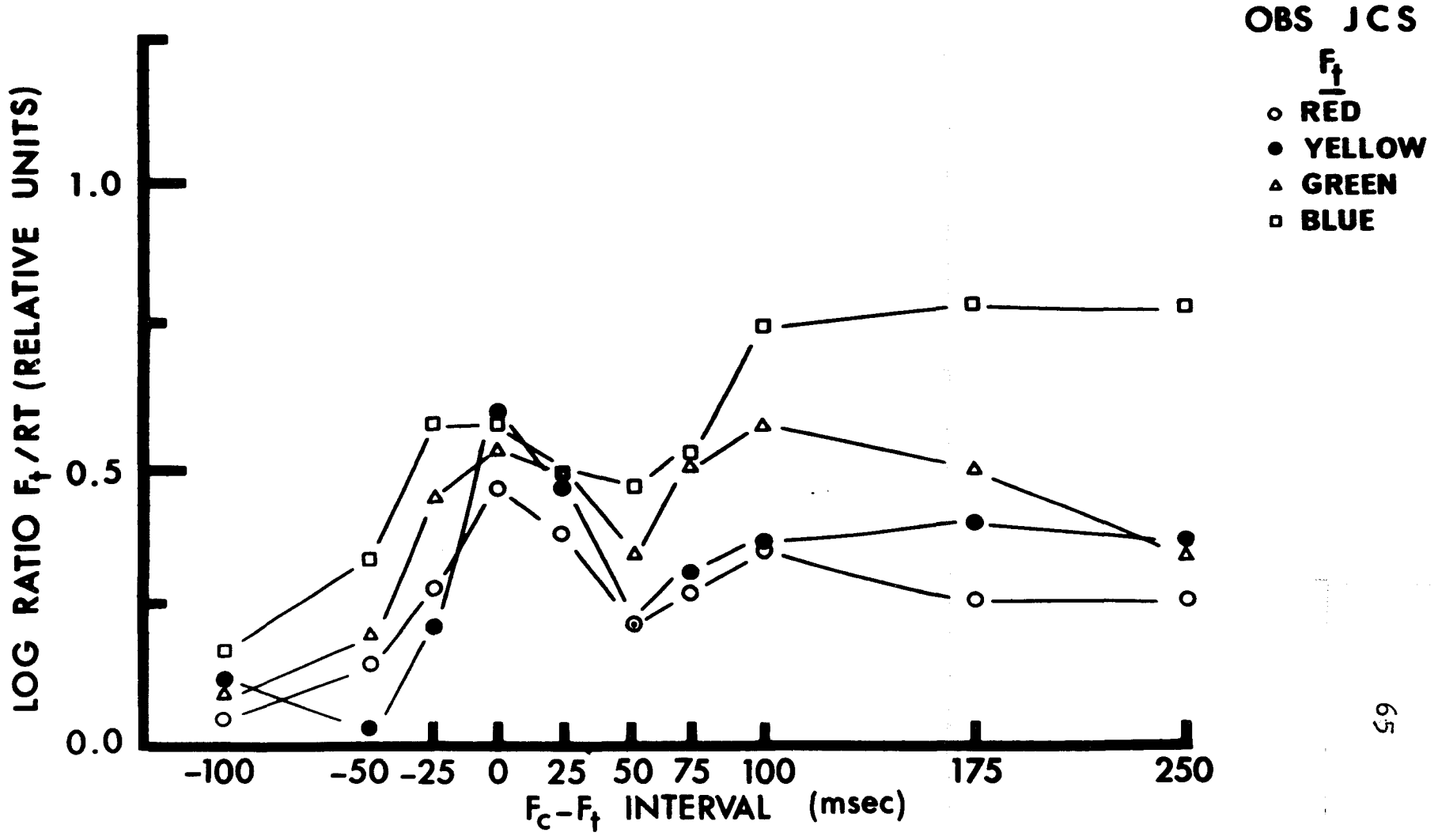

HAPLOSCOPIC STIMULATION F_c - BLUE
OBS JCS
F_t
RED
YELLOW
GREEN
BLUE
LOG RATIO F_t/RT (RELATIVE UNITS)
1.0
0.5
0.0
-100
-50
-25
0
25
50
75
100
175
250
$F_c - F_t$ INTERVAL (msec)

Figure 13. Excitability functions obtained with haploscopic stimulation. F_c wavelength 472 nm (blue). Observer: KAG.

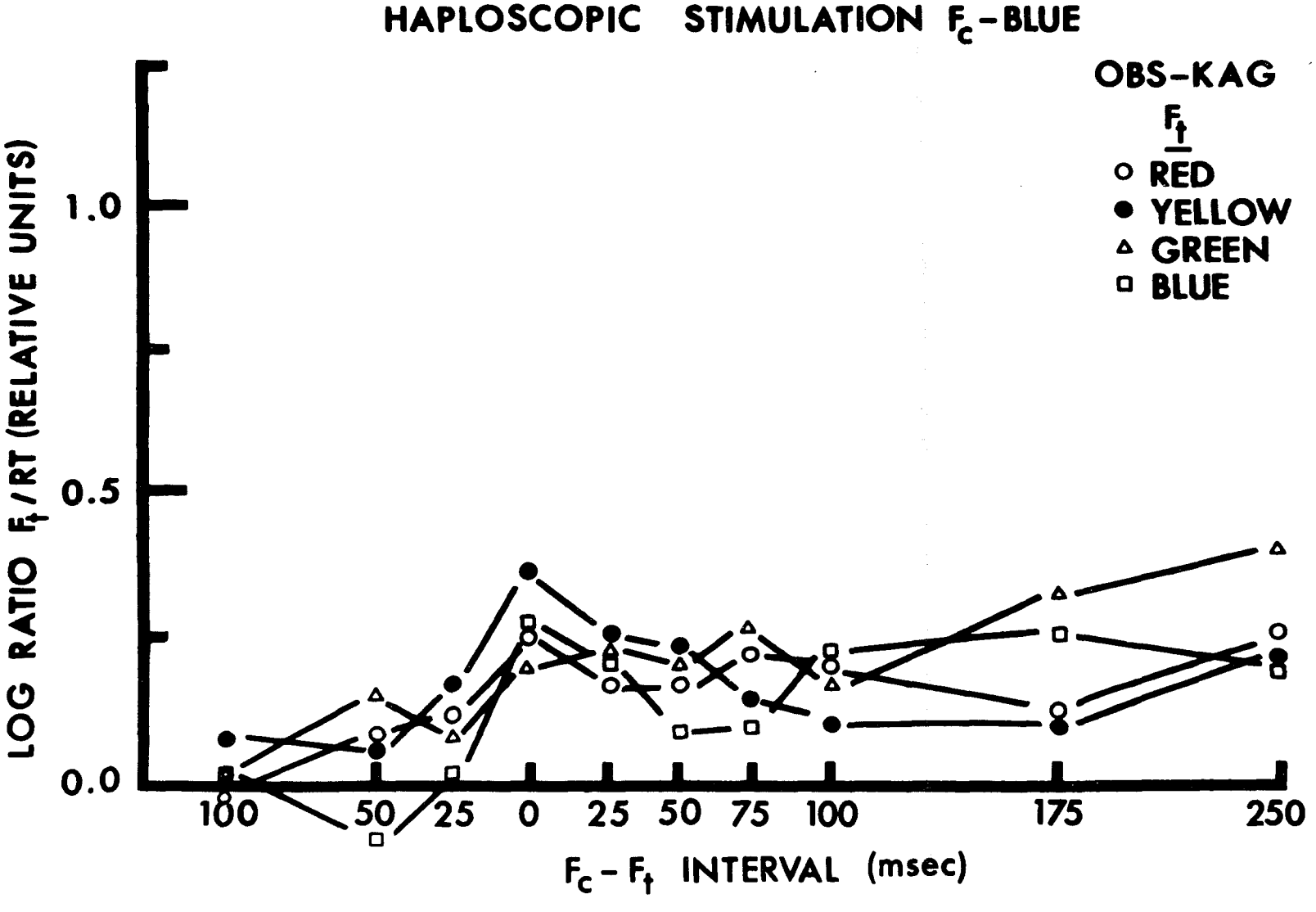
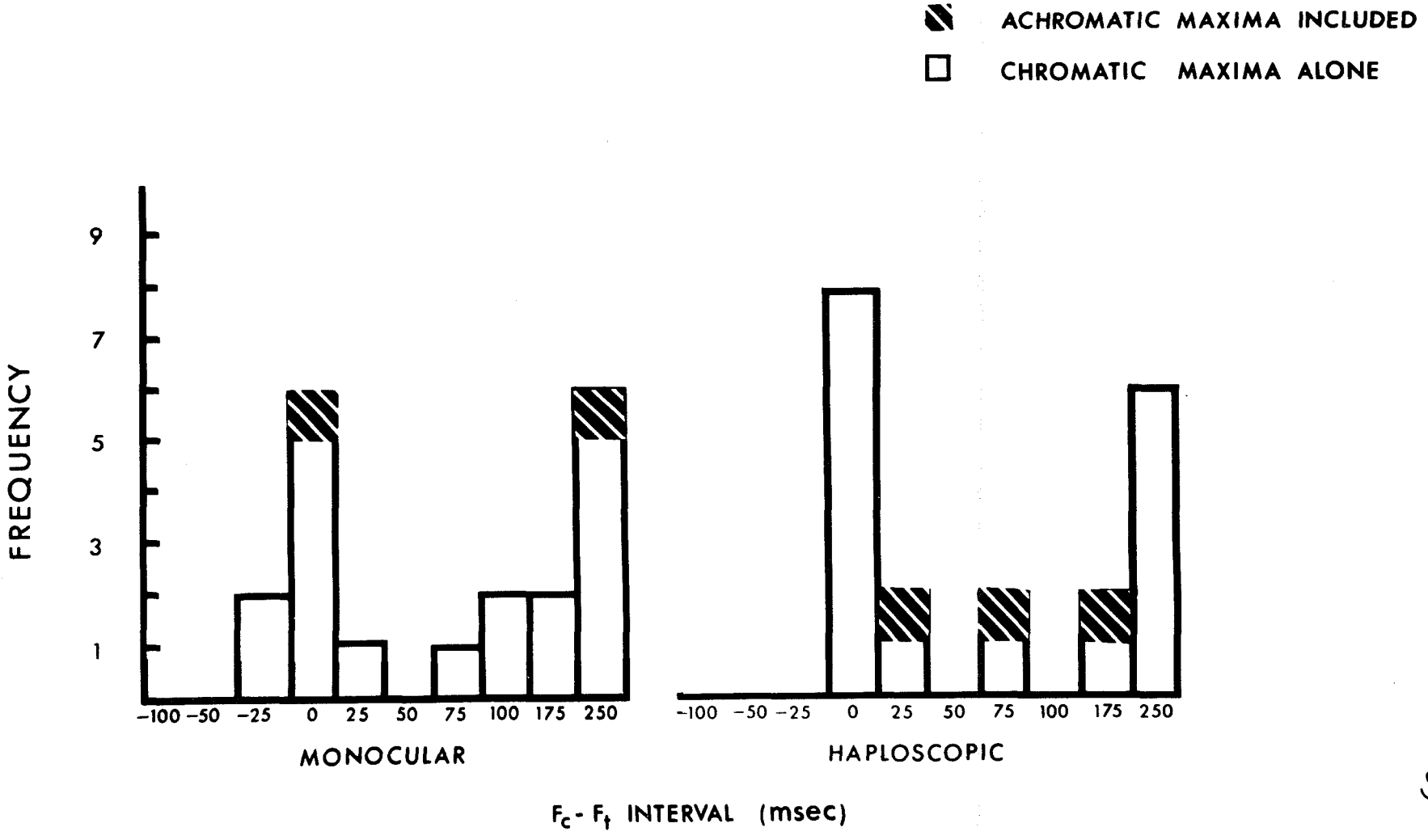

HAPLOSCOPIC STIMULATION F_c – BLUE
OBS-KAG
F_t
RED
YELLOW
GREEN
BLUE
LOG RATIO F_t / RT (RELATIVE UNITS)
1.0
0.5
0.0
100
50
25
0
25
50
75
100
175
250
$F_c - F_t$ INTERVAL (msec)

Figure 14. Frequency of F_t increment threshold maxima (on the ordinate) as a function of the F_c-F_t temporal interval (on the abcissa, in ms). Numbers represent the total of both Os.

FREQUENCY OF MAXIMA AS A FUNCTION OF INTERVAL

(TOTAL OF BOTH OBSERVERS)



F_t values obtained where F_c was 250 ms. Steady-state increment thresholds consistently increase as the F_c-F_t wavelength difference approaches the homochromatic condition.

Figures 15 through 18 present data derived from the excitability functions in Figures 6 through 13. Figures 15 and 16 each show the effect, for a single O, of systematically varying the wavelength difference between F_c and F_t on the increment thresholds, when such effects are interpreted in terms of four threshold indices: the average (mean) amplitude of the complete excitability function (labeled "mean of all intervals"); the average amplitude of the -50 and -25 ms F_c-F_t intervals ("mean of -50 and -25 intervals"); the average amplitude of the 25 and 50 ms F_c-F_t intervals ("mean of 25 and 50 intervals"); and the amplitude of the maximum F_t increment threshold, regardless of its temporal location ("maxima"). This format is intended to display as a function of wavelength, respectively, overall differences in the adaptive effect of F_c, backward masking effect, forward masking effect (each averaged over the two intervals with the greatest masking effect so as to reduce extraneous variability), and maximum effects as a single index free from averaging.

If trichromatic color mechanisms predominantly determine the psychophysical response, then the F_t increment threshold should vary as an inverse monotonic function of the F_c-F_t wavelength difference; if opponent-process coding predominates, then marked deviation from such a monotonic function would result when opponent F_c-F_t wavelength combinations are used (the direction of these deviations would also be determined by the temporal relationship of F_c to F_t). Figures 15 and 16 allow the following generalizations to be made: for the monocular mode, the magnitude of the derived F_t increment threshold indices are inversely related to the F_c-F_t wavelength difference. Only small deviations from the essentially monotonic relationship obtain for negative or positive F_c-F_t intervals or, in the case of O KAG (Figure 16), where the minimum adaptive effects tend to occur at opponent F_c-F_t wavelengths rather than at the spectrally most-distant F_c-F_t pair. For the haploscopic mode, the indices reveal virtually no wavelength-related effect on the F_c increment threshold for KAG and only a weak and highly variable effect, especially for the red F_c, for the case of O JCS. As in the monocular data, no temporally-related deviations were found.

(Text continued on page 76)

Figure 15. Derived indices of the F_t increment threshold as a function of the F_c-F_t spectral separation. Log ratio F_t/RT in relative units (on the ordinate) vs. F_t wavelength in nm (on the abcissa). See text for explanation. Observer: JCS.

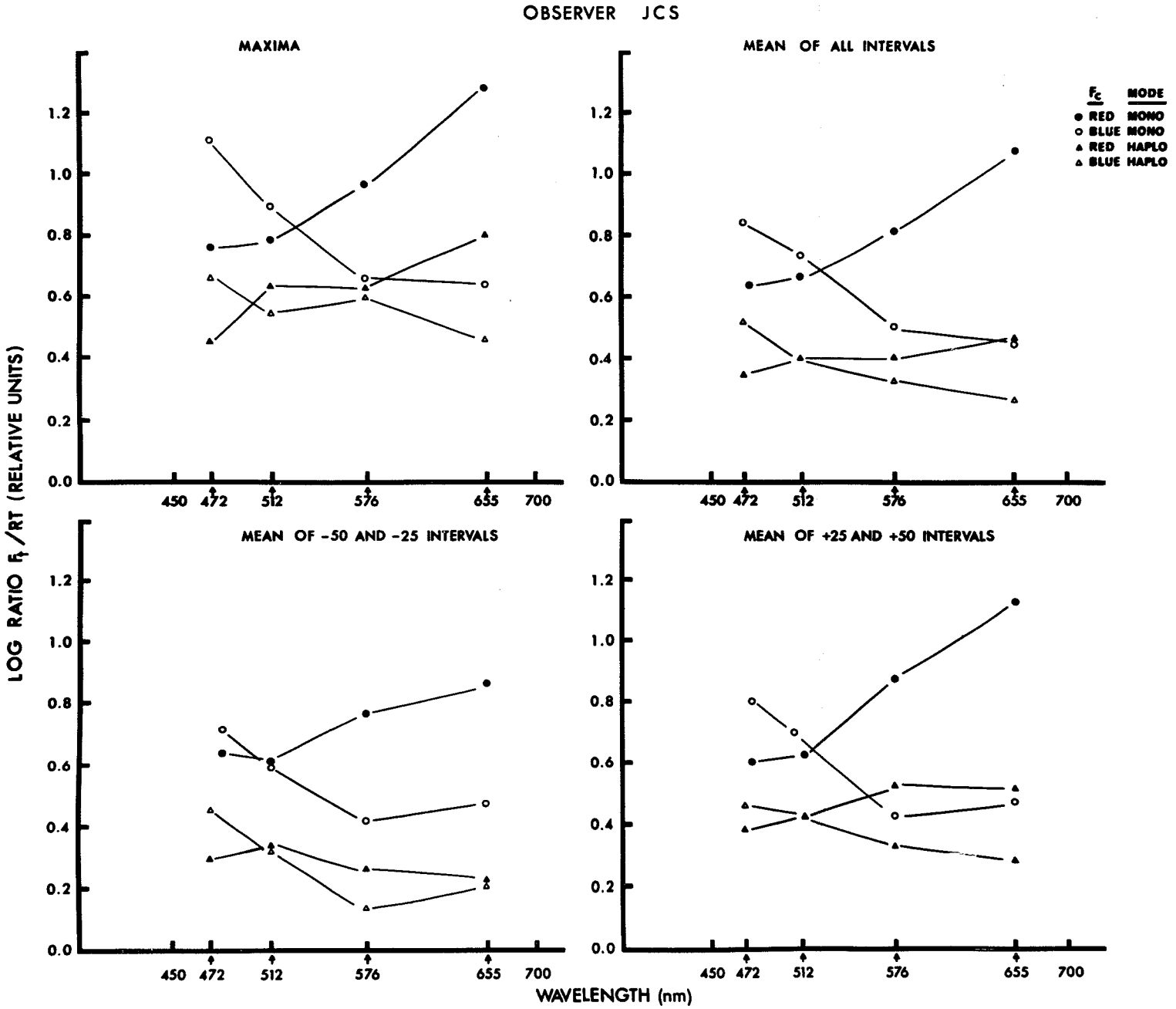
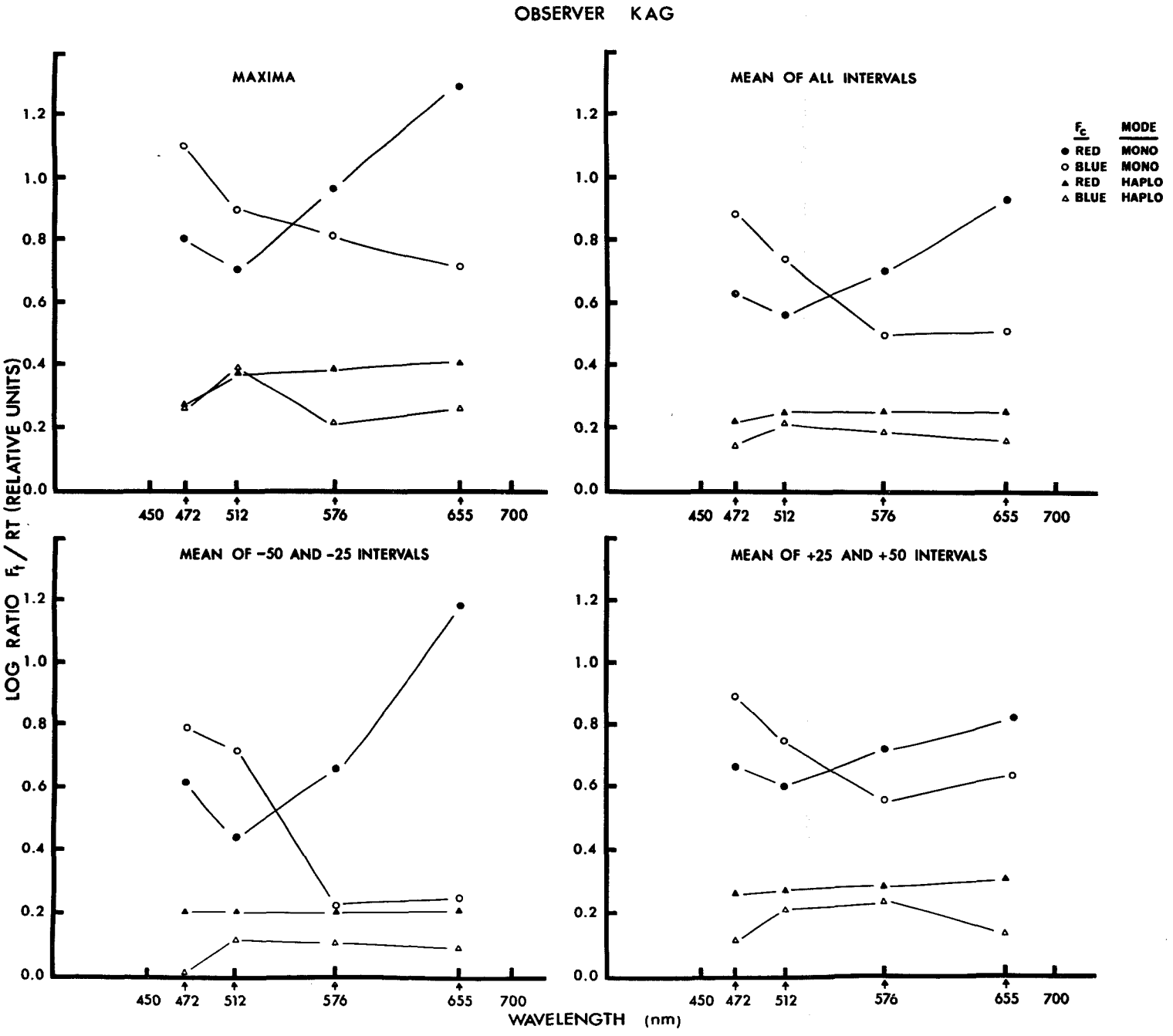

OBSERVER JCS
MAXIMA
MEAN OF ALL INTERVALS
MEAN OF -50 AND -25 INTERVALS
MEAN OF +25 AND +50 INTERVALS
LOG RATIO F_1/RT (RELATIVE UNITS)
WAVELENGTH (nm)
F_c MODE
RED MONO
BLUE MONO
RED HAPLO
BLUE HAPLO
0.0
0.2
0.4
0.6
0.8
1.0
1.2
450
472
512
576
655
700

Figure 16. Derived indices of the F_t increment threshold as a function of the F_c-F_t spectral separation. Observer: KAG.


OBSERVER KAG
MAXIMA
MEAN OF ALL INTERVALS
MEAN OF −50 AND −25 INTERVALS
MEAN OF +25 AND +50 INTERVALS
LOG RATIO F_t / RT (RELATIVE UNITS)
WAVELENGTH (nm)
F_c MODE
RED MONO
BLUE MONO
RED HAPLO
BLUE HAPLO
0.0
0.2
0.4
0.6
0.8
1.0
1.2
450 472 512 576 655 700

Figures 17 and 18 depict excitability functions derived by averaging the F_t increment thresholds across the four F_t wavelengths. These figures indicate that, for the monocular data of JCS and the haploscopic data of KAG, the increment thresholds obtained where F_c was red are markedly higher than for the case where F_c was blue.

Figure 17. Excitability function obtained by averaging the increment thresholds obtained at each F_c-F_t interval across the four F_t wavelengths. Data is presented for both the monocular and haploscopic conditions. Observer: JCS.

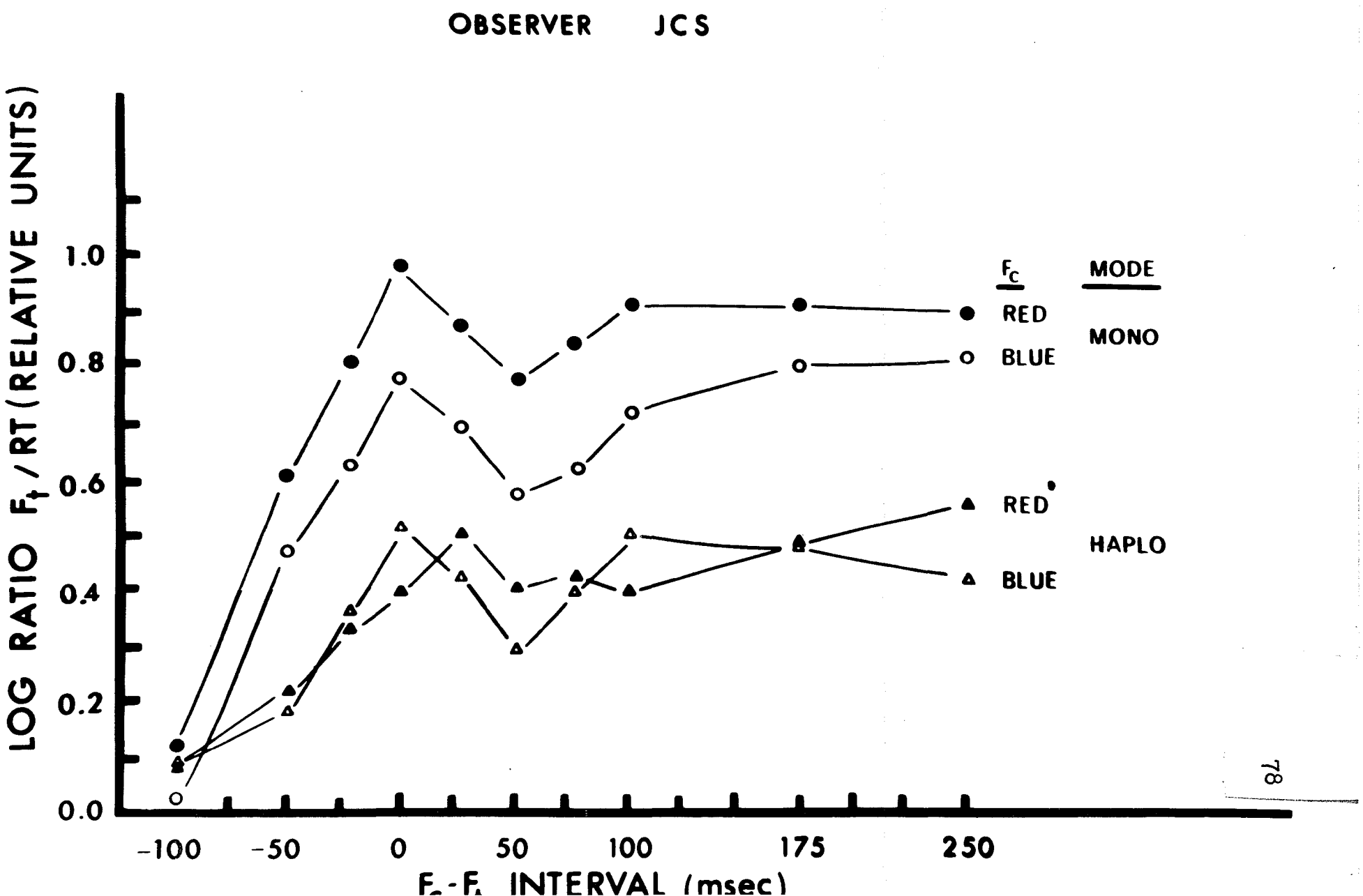
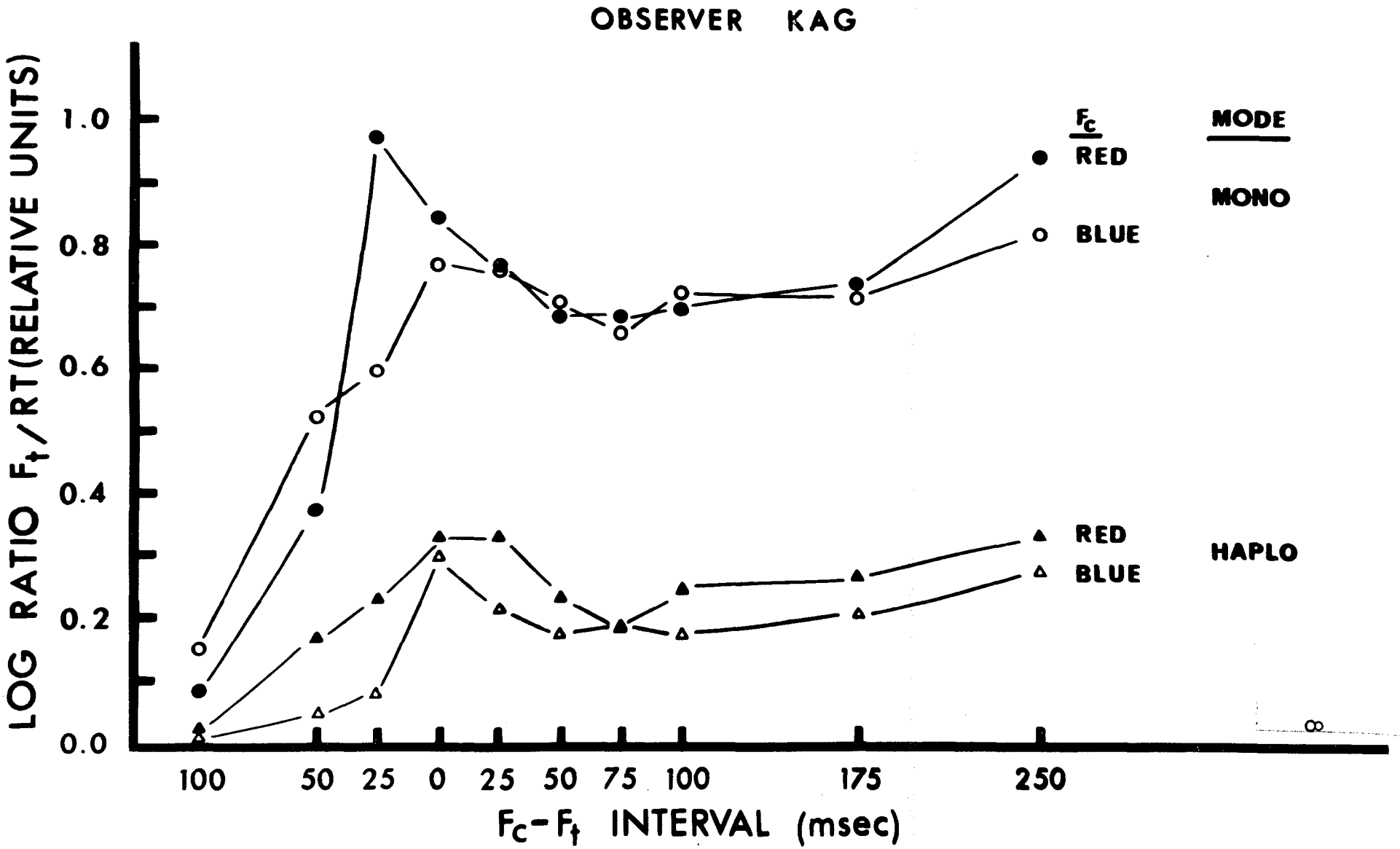

OBSERVER JCS
LOG RATIO F_t / RT (RELATIVE UNITS)
1.0
0.8
0.6
0.4
0.2
0.0
-100
-50
0
50
100
175
250
F_c - F_t INTERVAL (msec)
F_c
MODE
RED
BLUE
MONO
RED
BLUE
HAPLO

Figure 18. Excitability function obtained by averaging the increment thresholds obtained at each F_c-F_t interval across the four F_t wavelengths. Data is presented for both monocular and haploscopic conditions. Observer: KAG.


OBSERVER KAG
LOG RATIO F_t/RT (RELATIVE UNITS)
1.0
0.8
0.6
0.4
0.2
0.0
100
50
25
0
25
50
75
100
175
250
$F_C - F_t$ INTERVAL (msec)
F_C
MODE
RED
BLUE
MONO
RED
BLUE
HAPLO

FOOTNOTES

[1]The F_t increment threshold was plotted in units relative to the F_t resting threshold in order to compensate for the difference in F_t wavelength. In this approach equal adaptive effect of F_c upon F_t resting threshold. This is analogous to equating the two conditioning flashes by raising them an equal amount above their respective threshold values. The relative units also allowed a clear and uniform way of presenting the data in graphical form. The use of absolute units was impractical due to the complexity of accounting for the emission characteristics of the tungsten source and the filter transmission parameters.

[2]The decrease in F_t threshold occurring at 50 ms for the blue F_c, JCS, conditions (Figures 8 and 12) was checked and found to be reliable. Thus, these data should not be attributed to changes in O organismic variability. Irregularities such as these were also found by Bush (1955).

CHAPTER V

DISCUSSION

The data presented in Figures 5 through 8 and the derived index functions in Figures 15 and 16 agree with Bush's (1955) study, showing that the magnitude of the F_t increment threshold is directly related to the proximity of F_c and F_t wavelengths. No reliable deviation from a monotonic function is observed as would be predicted by an opponent-process theory of color vision.

Bush's (1955) data also reveal that, in general, the threshold <u>difference</u> between excitability functions obtained with chromatic stimuli decrease as the F_c-F_t spectral distance increases, a finding that is confirmed in the present study. Bush, however, found relatively large differences between the threshold obtained with a green or blue F_t paired with a red F_c (see Figure 2). The present study found almost no difference for either these conditions or for the complimentary situations (not considered by Bush) when a blue F_c is paired with a yellow or red F_t. It appears likely that the failure to obtain similar results was due to differences in the

stimulating conditions employed in the respective investigations. The Bush study used a F_c luminance of 1.2 log mL presented to the dark adapted eye. The present study used a F_c with a luminance of about 1.4 log mL presented to an eye that was light adapted to a constant adapting background of 0.0 log mL. This difference in the adaptation level most probably reduced the magnitude of the "on" effect, since the ΔI incurred by F_c onset in Bush's study was almost 4 log units (it was only 1.4 log units in the present case). Frumkes (1970, personal communication) found that with a constant luminance F_c, reduction of adaptation level produced a marked influence upon the F_t increment threshold. In the present study, it was not possible to employ higher F_c luminance due to the limitations of the apparatus; if lower adapting field luminance were used, the adaptation level would be below the photopic range. This shift would result in obtaining threshold data based on the blue-sensitive rod system, the nature of which is already well known. If the F_c intensity had been increased to a higher level above the adapting background, reliable differences between the spectrally most distant F_t wavelengths would most probably have been obtained.

Within the range of values used, however, the results of the present experiment are in agreement with the data of Stiles (1959). Stiles' data uniformly support his contention that separating F_c from F_t in wavelength decreases the number of F_c quanta able to act on the mechanism responding to F_t (decrease the "effective" brightness of F_c). Further comparisons with the work of Stiles are precluded since, in this experiment, the spectral relationship of F_c to F_t was not varied in the small parametric steps required by the Stiles technique. This approach is suggested for further research and could be developed as an extension of the method used by Boynton (1956).

Although this study did not obtain evidence in support of cpponent-process theory, the electrophysiological data supporting the presence of such opponent-processes in the visual nervous system is irrefutable. As discussed previously, this evidence consists primarily of studies of receptor field "coding" at the neuroretinal and geniculate levels of primates, and the neuroretinal level of fish. (For a good review of such work, see Sheppard, 1968.) In view of the strength of such data, together with the equally undeniable fact of the basic trivariance of color vision (Le Grand, 1968), it is apparent to the author that any theoretical approach

to function of the visual nervous system must be capable of accounting for both classes of data. In this regard it should be pointed out that there is no necessity for information obtained at the photoreceptor level, based on a trichromatic receptor system, to maintain similar "trichromatic" projections to cortex. It is equally possible that a neural encoding of peripheral trichromatic potentials into opponent-process signals are propagated centrally where they are "decoded" into the states of cortical activity leading to the perceptual response--the nature of which is basically trichromatic. Gouras (1970) has obtained electrophysiological evidence from the Rhesus monkey supportive of this position.

It should be noted that the Os' criterion for determining the increment threshold might have been partially responsible for the lack of evidence supporting the opponent-process position. In the present study, as in the previous work by Stiles and Bush, the O was called upon to judge whether there was a difference between F_c and F_c plus F_t. At threshold values, O was instructed to make this discrimination on the basis of the smallest detectable difference between the two contingencies. Both Os reported that the criterion for this decision was, even for the heterochromatic combinations, a brightness increment rather than a

chromatic shift. The increment threshold might have been mediated by an achromatic luminosity system analogous to Granit's photopic dominator (Granit, 1947), responsible for the photopic luminosity curve, and not by a wavelength-specific system of color mechanisms (analogous to Granit's modulators). This possibility is further supported by Hurvich and Jameson's (1957) paper indicating that when chromatic visual response is studied via chromatic adaptation, there are marked changes in the sensitivity of specific mechanisms as indicated by alterations of hue. These alterations have been specified by color neutralization experiments, the findings of which support a theory of opponent-process mechanisms. At the same time the achromatic (luminosity) response function changes very little as a function of chromatic adaptation. The changes that do occur suggest the presence of only non-opponent (trichromatic) mechanisms with close peak spectral sensitivities (Hecht, 1937). In general, spectral sensitivity functions are obtained by some form of brightness threshold measure. Those studies attempting to study the nature of mechanisms presumed to underly the photopic spectral sensitivity function with a threshold technique, most notably Stiles' increment threshold technique, obtain data supportive of a non-opponent-process system. It

may be that some of the divergent data obtained regarding whether the psychophysical response to different wavelengths of light is basically trichromatic or opponent-process are due to the investigative technique used. Color neutralization data may support opponent-process theory because of the dependence of such data on a system of "modulators"; whereas increment threshold data may support trichromatic theory because of the dependence of such data on the presence of a separate "dominator" system.

The "steady-state" (3000 ms) condition of the present study reveals that, without exception, the adaptive state which the mechanisms responding to F_t approaches as a function of continued exposure to F_c is directly related to the F_c-F_t spectral separation. This finding confirms the data and conclusions of the temporally kinetic phase of this study. Furthermore, as this condition is closely comparable with the technique of Stiles (1959), it may be more appropriate to consider the results of the present study as an extension of the findings of Stiles than as a contradiction of any opponent-process data.

It should also be pointed out that previous studies (e.g., Wiesel and Hubel, 1966) have interpreted the effects of incremental stimulation in terms of

opponent-process theory. In view of the foregoing considerations, such interpretations should be re-examined.

Data obtained under haploscopic stimulation (Figures 10 through 13) generally confirm the findings of earlier work in that they are attenuated compared to the monocular data. Noteworthy, however, is the finding that such data, reflecting central (retrochiasmal) effects, are virtually unaffected by the relative wavelength of the test and adapting stimuli. If these haploscopic data, summarized in Figures 14 and 15 are interpreted within the context of the Stiles rationale, it appears that the central color mechanisms have extremely broad spectral response, or that the central color system is simply not comprised of separate mechanisms.

As discussed previously, the facts of color mixture suggest that independence of color mechanisms <u>not</u> be maintained at all levels of the visual system. One could postulate that no wavelength-related haploscopic effects were found in the present experiment because there are <u>no</u> independent color mechanisms in the CNS. Alternatively, the possibility exists that there <u>are</u> central color mechanisms with relatively narrow spectral response, but that the reduced magnitude of the

haploscopic effect allowed the wavelength-related changes in the F_t increment threshold indicative of such narrow-band mechanisms to be lost in threshold variability. Unfortunately, this type of problem cannot be rectified, as it could be in the monocular mode, by increasing the F_c intensity, since Kandel (1959), and Battersby and Wagman (1962) have demonstrated the haploscopic increment threshold to be independent of F_c intensity. It is possible, however, to affect the magnitude of the haploscopic increment threshold through manipulation of spatial variables, with maximum F_c-F_t interaction occurring for the case of coincident target borders (Battersby, Oesterreich, and Sturr, 1964). Thus, it is suggested that future research employ F_c and F_t of equal size. This was not done in the present study in order to eliminate the possibility that F_c would fall outside F_t in the haploscopic mode. Misalignment resulting in the border of one target falling outside the border of the other target would allow discrimination of the two-flash threshold to be made on the basis of spatial displacement rather than intensity increment.

The assumption that central mechanisms allow greater interaction across wavelengths than do peripheral mechanisms may be further elucidated by another approach. Matin (1962) and Battersby and Defabaugh (1969) have

obtained data clearly indicating that binocular stimulation lowers the visual threshold in excess of the amounts predicted on the basis of probability summation between the two eyes (Pirenne, 1943). These studies, however, have employed achromatic stimuli. It is suggested that the presence of summation at the haploscopic threshold be studied using both heterochromatic and homochromatic stimuli. If central mechanisms have wide spectral response, then little difference should be found between the threshold otbained, for example, with a red stimulus presented to one eye and a blue stimulus presented homotopically to the other, as contrasted to red or blue stimuli presented binocularly. At the same time, the difference between heterochromatic and homochromatic summation thresholds measured monocularly should be considerable. Contrariwise, results showing definite wavelength effects would be salutary regarding the question of binocular summation. For, analogous to the rationale in the Matin (1962) study, if changes in the wavelength difference between haploscopically presented stimuli are found to affect the probability of seeing, it would constitute additional evidence that there are central neural mechanisms which allow binocular summation.

Figures 16 and 17 show excitability functions derived by averaging the F_t increment thresholds across the four F_t wavelengths. These figures generally confirm that thresholds obtained where F_c was red are higher (by a small amount) than for the case where F_c was blue. Since both F_c were equated at threshold, it appears that in raising each F_c 1.4 log units above their respective threshold values the effective brightness of the red F_c increased disproportionately. As previously discussed, it has been found (Sperling and Lewis, 1959) that threshold luminance matches (in the fovea) of different wavelengths yield comparable results to suprathreshold (e.g., flicker photometric) matches, excluding the effect of the Purkinje shift. It is possible that the value chosen for the constant adapting background (0.0 log mL), which resulted in F_c thresholds bordering on the mesopic range, together with the parafoveal locus of stimulation, in fact allowed the Purkinje shift to equivocate the threshold matching data. That is, visual sensitivity may have been greater in the blue spectral region at the threshold luminance than at the adapting level luminance. Thus the blue F_c would appear less bright than the red F_c when both were raised a constant amount. Alternatively, the classic work of Konig and Brodhun on the Weber constant (Holway and Pratt, 1936) indicates that red and blue

stimuli have different Weber fractions in the range of luminances used in the present study such that red would be predicted to yield a greater sensation for a given luminance than would blue. This effect disappears at higher luminances as the Weber fraction for different wavelengths tends to approach the same value as luminance is increased. While not directly related to the issues primarily considered in this investigation, it is suggested that some future research be devoted to a further examination of whether the sensory effect of wavelengths matched at one intensity remain equivalent at other intensities. The Bezolde-Brüke phenomenon that luminance level interacts with hue could then be extended to include effects of wavelength on determining brightness.

It was difficult because of the variability in the data to ascertain by inspection of the original excitability functions (Figures 5 through 13) the presence of a reliable secondary rise in the magnitude of the functions at F_c termination (the "off" effect). It <u>is</u> clear, however, that the increment thresholds for a particular (monocular) condition never fall below their respective "steady-state" values for any temporal interval more positive than -25 ms. This result indicates that the masking effect is responsible for some portion of the F_t increment threshold throughout the duration of F_c.

That this effect is, in fact, increasing towards the end of F_c can be demonstrated, as has been done in Figure 18, by plotting the frequency of the maxima of the original excitability functions (both monocular and haploscopic) as a function of the F_c-F_t temporal interval. This operation reveals a clearly bimodal distribution with peaks at the onset and termination of F_c, thus more clearly delineating the presence of the "off" effect. There is little doubt, especially in view of Crawford's (1947) finding (see Figure 1) that relatively high F_c luminance is required to obtain the "off" effect, and that had it been feasible to employ higher F_c luminance or a closer spatial "fit" between F_c and F_t such kinetic phenomena could have been made larger.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The present study was an evaluation of the increment threshold of a small "test flash" of light (F_t) superimposed upon a "conditioning flash" (F_c) when the relative wavelength of F_c and F_t was varied over two conditions of stimulation: F_c and F_t to OD (monocular stimulation); F_c to OS, F_t homotopically to OD (haploscopic stimulation). The paired flashes were presented at various temporal separations. These experiments attempted to relate the increment threshold to the neural organization of the visual system underlying the transmission of wavelength information.

A four-channel Maxwellian view optical system was used to present the paired stimuli at $6^{\circ}40'$ along the right horizontal meridian. Two observers were used. F_t was a 1° circular target of 5 msec duration; F_c a $1^{\circ}20'$ concentric circular target of, in the main experiment, 250 msec duration. Both stimuli were presented in constant contrast to a 0.0 log mL achromatic adapting background. All possible combinations of two F_c wavelengths (472 and 655 nm) and four F_t wavelengths (472,

512, and 655 nm) were used in the main experiment. F_c wavelengths were equated for sensory effect by a threshold matching technique and F_t was recorded as increment above its resting threshold, as obtained by a modified psychophysical method of adjustment.

The data were plotted as "excitability functions" (F_t threshold at several temporal intervals under a given condition of F_c-F_t wavelength combination and mode of stimulation) after the method of Crawford (1947). From these data the average F_c threshold was derived as a function of 1) the F_c-F_t wavelength difference and 2) the F_c-F_t interval. Additional data were obtained under achromatic stimulation and steady-state adaptation. The results showed that:

1. F_t threshold in the monocular mode was a direct monotonic function of the spectral proximity of the F_c-F_t pair.

2. F_t threshold was greatly attenuated in the haploscopic as compared to the monocular mode.

3. F_t threshold in the haploscopic mode was independent of the spectral characteristics of the stimuli, suggesting that central processes have broad spectral response characteristics.

These results were discussed in terms of characteristics of neural mechanisms underlying the transmission and integration of wavelength-related information.

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