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SCOTOPIC-PHOTOPIC INTERRELATIONSHIPS IN
METACONTRAST AND PARACONTRAST.

City University of New York, Ph.D., 1976
Psychology, physiological

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SCOTOPIC-PHOTOPIC INTERRELATIONSHIPS IN METACONTRAST AND PARACONTRAST

by

Michael C. Barris

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1976

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

Aug. 2, 1976
date

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Abstract

SCOTOPIC-PHOTOPIC INTERRELATIONSHIPS IN METACONTRAST AND PARACONTRAST

by

Michael C. Barris

Adviser: Dr. Thomas E. Frumkes

The interrelationship between the scotopic and photopic systems was investigated in a series of metacontrast and paracontrast experiments. A Maxwellian view optical system was used to present stimuli to three dark-adapted observers. A 2° diameter, 10-msec duration test flash (F_t) was presented at 7° on the horizontal meridian in the temporal visual field of the right eye. A 10-msec annular adapting flash (F_a) which had a 2° inner diameter and a 10° outer diameter was presented concentrically with the F_t. The temporal interval between the onsets of the stimuli ($F_a - F_t$ interval) and the wavelength and illuminance of the flashes were systematically varied in the various phases of the study. (A negative $F_a - F_t$ interval indicates that the F_t precedes the F_a; a positive interval indicates the opposite.)

In Experiment 1, the threshold of a 512 nm wavelength F_t was determined as a function of the scotopic illuminance of either a 512 nm or 655 nm wavelength F_a. With both F_as, the F_t threshold monotonically increased as the scotopic illuminance increased, regardless of the $F_a - F_t$ interval. However, at certain $F_a - F_t$ intervals, the scotopic illuminance of the F_a alone determined F_t threshold. At different $F_a - F_t$ intervals, the 655 nm wavelength

F_a was either more or less effective than the 512 nm wavelength F_a. These results are impossible to reconcile with the concept that only one type of receptor stimulated by the F_a is influencing F_t threshold.

In Experiment 2, a F_t 512 nm in wavelength was presented at a fixed illuminance of $\bar{1}.9$ log scotopic trolands (0.5 log units above absolute threshold). Because of its wavelength and illuminance, it was assumed to be detected solely by the scotopic system. The illuminance of either a 512 nm wavelength or a red-hued (Wratten 29 filter) F_a which masked the F_t was determined at many F_a - F_t intervals. Regardless of F_a wavelength, the F_a illuminance necessary to mask the F_t first decreased, and then increased as the F_a - F_t interval became longer. In general, however, the red-hued F_a was more effective in masking the F_t at negative F_a - F_t intervals, while the 512 nm wavelength F_a was more effective at positive F_a - F_t intervals. Only at the -100, -50, and +150 msec F_a - F_t intervals were the two different F_as equal in their effect on the F_t.

Experiment 3 was performed in order to ascertain that the scotopic system alone was detecting the F_t in Experiment 2. The illuminance of two F_as of different wavelength that masked the F_t was determined at three F_a - F_t intervals. With these six different conditions (three intervals at two F_a wavelengths), the threshold log relative quanta of a variable wavelength F_t was determined in the presence of the F_a. In all cases, the F_t threshold log relative quanta described the sensitivity of the C.I.E. scotopic observer corrected for quanta. Therefore, in Experiment 2, the F_t must always be detected by the scotopic system.

In Experiment 4, a F_t, 512 nm in wavelength, was again presented at a fixed illuminance of $\bar{1}.9$ log scotopic trolands (0.5 log units above absolute threshold). The log relative quanta of a variable wavelength F_a which masked the F_t was determined at four F_a - F_t intervals. When the F_a preceded the F_t by 100 or 200 msec, the log relative quanta of the F_a necessary to mask the F_t was predictable by considering the F_a sensitivity to only the scotopic system. When the F_t preceded the F_a by 50 or 150 msec, however, the sensitivity of the scotopic system alone did not predict the log relative quanta of the F_a necessary to mask the F_t. With the red-hued F_as, the log relative quanta necessary to mask the F_t was considerably less than that predicted by scotopic sensitivity.

The results of these experiments show that, in metacontrast and paracontrast situations in which a F_t is detected only by the scotopic system, the type of receptor which influences F_t threshold is determined by the F_a - F_t interval. If the F_a precedes the F_t, the influence of the F_a on the scotopic system alone determines F_t threshold. These results are related to the difference in latency between the scotopic and photopic systems.

Acknowledgements

Dr. Thomas E. Frumkes guided this study from its inception. His creative insights led it to a successful conclusion. Also deserving of gratitude is Dr. William S. Battersby, whose teaching provided a solid basis for the study and whose loan of the optical system made it possible. The other members of the Dissertation Defense Committe, Dr. Mitchell Kietzman, Dr. Israel Abramov, and Dr. Ethel Matin, deserve appreciation for their constructive comments.

I deeply appreciate the financial and moral support of a Sigma Xi Grant-in-Aid of Research.

Dr. Lynn Gross Simon is gratefully remembered for the loan of crucial interference filters and for competent advice on metacontrast phenomena. Dona L. Galeno, Alan R. Kaufman, and Gay Holstein, whose avid interest and dependable service spurred this study, served as experimenters and observers. Finally, Dr. Leonard Temme and Rolf Nygaard provided counsel, support, and aid in ways too numerous to enumerate.

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Chapter 1

Introduction

Max Schultze's (1866) identification of retinal rods and cones formed the basis of the duplicity theory of vision. This theory maintains that retinal rods are involved with scotopic (night) vision and retinal cones with photopic (day) vision. A problem arising from the duplicity theory is the relationship between the two systems: Do the systems inhibit each other; do they summate with each other; or, are they completely independent?

In recent years, the question of scotopic-photopic interaction has been specifically addressed by psychophysical studies involving dual-flash threshold techniques (Stiles, 1939, 1959; Alpern, 1965; Westheimer, 1970; Frumkes, Sekuler, & Reiss, 1972; Ingling, 1972; Frumkes, Sekuler, Barris, Reiss, & Chalupa, 1973; Lennie & MacLeod, 1973; Makous & Boothe, 1974; Martinez & Sturr, 1975; Foster, 1976; Blick & MacLeod, in press; Temme & Frumkes, in press; Frumkes & Temme, in press).

Of these studies, the one most frequently cited as evidence for scotopic-photopic independence is that of Alpern (1965), which used an afterflash, or metacontrast, paradigm. Alpern implies that metacontrast is the interaction of neural signals stimulated by light flashes that are separated both spatially and temporally. In his study, he presented all stimuli at 6° from the fixation point of the dark-adapted observer. His test flash (F_t) was a 2.5° square 5 msec in duration. Since his F_t was 527 nm in wavelength and was generally dim enough to appear hueless, it probably was detected by the scotopic system in most phases of this study. His adapting flash (F_a, or afterflash in his terminology) was also 5 msec in duration, but it was presented 50 msec after the onset of the F_t. The wavelength of the F_a was either 500 or 635 nm. When these F_as were equated for their influence on the scotopic system, the 635 nm F_a had a much greater influence on the photopic system than the 500 nm wavelength F_a. The F_as were 9^o disks which eccentrically surrounded but did not overlap the F_t. In most cases, the F_t threshold illuminance was determined as a function of F_a illuminance.

Alpern (1965) found that F_t threshold illuminance monotonically increased as the illuminance of the F_a of different wavelengths increased. When the functions for the F_as of different wavelengths were compared (see Fig. 12), they superposed if the abscissae were expressed in terms of scotopic illuminance, i.e, when they were equated for the scotopic system. If the abscissae of these same functions were expressed in terms of photopic illuminance, the 527 nm wavelength F_a was much more effective in influencing F_t threshold. In this case, if the functions were equated for the photopic system, they did not overlap. Alpern concluded that only the scotopic component stimulated by the F_a raised the scotopic F_t threshold.

Since 1965, Alpern (e.g., Alpern, 1976) has generalized broadly from the results of this study. He has stated that all receptor systems act independently of each other in many perceptual situations. However, there are two methodological factors in his study which might have influenced his results. First of all, Alpern (1953) himself and many other investigators (for reviews, see Kahneman, 1968; Weisstein, 1972; Lefton, 1973; Matin, 1975; Breitmeyer & Ganz, 1976) have demonstrated that the influence of an F_a upon the brightness or threshold of a F_t is dependent upon the interval between the two stimuli. Because of the widely-known differences between the latency of photopic and scotopic systems (Wooten, 1972; Walters, 1971; Gouras, 1966; Gouras & Link, 1966; Steinberg, 1969; Niemeyer & Gouras, 1973; Fain, 1975), his choice of a single interval between the F_a and F_t could have biased his data. If he had used other intervals, he might have noticed different effects. Second, his data might be specific to the particular spatial configuration that he used. If he had varied the diameter of his flashes or changed their position in the observer's visual field, he might have noticed different effects.

Alpern's claim of scotopic-photopic independence in dual-flash situations has not gone unchallenged. For example, Frumkes et al. (1973) studied scotopic-photopic interrelationships using a methodological paradigm (the rapid adaptation technique of Crawford, 1947) similar to the metacontrast situation. In their experiments, stimuli were presented concentrically at 7° from the fixation point of the dark-adapted observer. The F_t was a 55' diameter disk, 10 msec in duration. Its wavelength was governed by either 420 or 680 nm narrow passband interference filters. These investigators assumed that the 420 nm wavelength stimuli were principally detected by the scotopic system and the 680 nm wavelength stimuli by the photopic system. In general, F_t threshold illuminance was determined as a function of the temporal onset interval between the F_a and F_t (F_a - F_t interval).

When the two flashes were identical in wavelength, Frumkes et al. (1973) found that F_t threshold illuminance was greatest when the two stimuli were presented simultaneously. The F_t threshold illuminance decreased as the F_t was presented either earlier or later than the F_a. A similar inverted U-shaped function was obtained when the two stimuli were different from each other in wavelength. However, when the F_a wavelength was 680 nm, maximum threshold illuminance for the 420 nm wavelength F_t occurred when it was presented before the F_a. To the extent that the 420 nm wavelength stimuli influence the scotopic system exclusively and the 680 nm wavelength stimuli the photopic system, the data suggested scotopic-photopic interaction. Frumkes et al. (1973) interpreted the shift in the time course of their functions as the result of the difference in latency between the scotopic and photopic systems. Nevertheless, they produced no conclusive evidence that their 420 or 680 nm wavelength stimuli discretely affected only one type of receptor.

Three factors could determine the different conclusions reached by Alpern (1965) and Frumkes et al. (1973). First, the spatial parameters differed between these two studies. Specifically, Frumkes et al. (1973) used a disk F_t superposed on a disk F_a, while Alpern (1965) used a square F_t with an eccentric surrounding flash. However, in light of recent replications of the experiments of Frumkes et al. (1972) using disk F_ts and concentric annuli as stimuli (Ingling, 1972; Foster, 1976), this factor by itself probably does not account for the discrepancy. Second, none of the studies cited above adequately demonstrated which type of receptor population was affected by the various wavelength stimuli. Third, Alpern's (1965) conclusion of scotopic-photopic independence may be specific to the single F_a - F_t interval that he used. This is probable in light of observations (Frumkes et al., 1972, 1973; Ingling, 1972; Foster, 1976) that show the F_a - F_t interval as an important variable in determining scotopic-photopic interactions.

The present investigation is a study of scotopic-photopic interaction under metacontrast and paracontrast conditions. In brief, the threshold illuminance of a 512 nm wavelength F_t was determined as a function of the illuminance and wavelength of an F_a as well as F_a - F_t interval. By determining action spectra, it was possible to specify with a fair degreee of certainty which type of receptor population detected the different stimuli. The results show that the interrelationship between the photopic and scotopic systems in metacontrast and paracontrast is highly dependent on the F_a - F_t interval.

Chapter 2

Literature Review

The duplicity theory of vision evolved in the nineteenth century as an attempt to explain visual phenomena related to differences in the prevailing level of illumination (for early literature references, see LeGrand, 1975). As early as 1819, Purkinje noted that, at low levels of illumination, acuity is sharper, vision is hueless, and sensitivity is greater with shorter wavelengths of light. In contrast, at higher levels of illumination, acuity is sharper, different hues are easily discriminated, and sensitivity is greater with longer wavelengths. In 1866, Schultze described two types of photoreceptors in the vertebrate retina, the rods and the cones. Fifteen years later, Parinaud and von Kries related this anatomical duplicity to the apparent functional duplicity of human vision. They described vision in dim light as scotopic and attributable to rods, while vision in bright light was described as photopic and due to cones. Since that time, several converging lines of evidence have been offered as support for the duplicity theory.

A problem arising from the duplicity theory of vision is the nature of the transition between the scotopic and photopic systems[1].

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[1] The term, scotopic system, is used here to refer to the functional and structural system which is connected to the rods, while the term, photopic system, refers similarly to the system connected to the cones. This nomenclature is preferable to the terms, rod and cone systems, which imply that only photoreceptors are involved in each system. In fact, several orders of neurons are involved.

Do they always function independently of one another or are they coupled in some manner?

Anatomical evidence in the primate. Much evidence shows that rods and cones terminate on different bipolar cells in the primate retina (Dowling & Boycott, 1966; Boycott & Dowling, 1969), suggesting that the scotopic and photopic systems operate independently of one another. However, there are several structural features which suggest that rods and cones may interact in the retina. Raviola and Gilula (1973) have documented the existence of gap junctions between rods and cones in vertebrate animals, including monkeys. To the extent that the gap junctions have been identified as the structural basis for electrical synapses in nonmammalian neural systems, they may provide a direct route for rod-cone interaction in primates. Moreover, Kolb (1970) has shown that all of the primate horizontal cells which she studied had dendritic connections with cones and axonal processes passing to rods. Finally, several anatomists (Polyak, 1941; Dowling & Boycott, 1966; Kolb & Famiglietti, 1974) have shown that rod and cone bipolar cells converge on the same ganglion cell in a variety of mammals.

In summary, there are several structural bases for interaction between scotopic and photopic signals at several different loci within the retina.

Physiological evidence in cat and primate. Physiological evidence for scotopic-photopic interactions has been well documented by recordings from every cell type within the vertebrate retina. Unfortunately, a good deal of this evidence (e.g., Schwartz, 1975; Fain, 1975) stems from the retinas of cold-blooded animals. Nevertheless, there is ample evidence for scotopic-photopic interaction in the cat and primates. Recording intracellularly from cat cones, Nelson (1975) has shown that cones are influenced by rod signals. Other investigators (Steinberg, 1969; Niemeyer & Gouras, 1973; Nelson, von Lützow, Kolb, & Gouras, 1975) have noted that horizontal cells receive both scotopic and photopic signals. However, the nature of their interaction is unclear. These cellular studies are paralleled by records of the late receptor potential, an electroretinogram (ERG) component, obtained in the primate (Whitten & Brown, 1973). Considering these papers, it is reasonable to conclude that some interaction between the scotopic and photopic systems is occurring in the distal portions of the retina.

A number of studies in the cat (Andrews & Hammond, 1970a, 1970b; Hammond & James, 1971; Rodieck & Rushton, 1976) have clearly documented that scotopic and photopic signals can interact in an inhibitory manner at the ganglion cell level.

Collectively, there is ample electrophysiological and anatomical evidence for interaction between the scotopic and photopic systems within the retina. The specific pathways involved in the mammalian retina, however, have yet to be outlined.

Psychophysical evidence in the human. Some psychophysical evidence obtained with human observers supports the hypothesis of independence between the scotopic and photopic systems. However, other psychophysical evidence suggests that either summation or inhibition occurs between the two systems.

One line of work is based on experiments assessing the color-mixing properties of the human observer. Traditional studies (e.g., Wright & Pitt, 1934; Hurvich & Jameson, 1957) suggest that color vision can be attributed to three different cone (photopic) mechanisms. However, a growing body of literature written from the theoretical viewpoint of Helmholtz (Trezona, 1970, 1973, 1974), Hering (Stabell, B., & Stabell, U. 1973, 1974; Stabell, U., & Stabell, B., 1973, 1975a, 1975b), and Land (McCann & Benton, 1969; McCann, 1972) indicate that rods must play a role in determining both the hue and saturation of a stimulus. The difference between results claiming interaction or independence seems to be quite clear: if large or extrafoveal stimuli are used, the scotopic as well as the photopic response must be considered to account fully for the results of color matching and color additivity experiments.

A second line of work involves the study of flicker. Traditional flicker studies indicate that critical flicker frequency (CFF) increases with stimulus illuminance (e.g., Hecht & Shlaer, 1936). These functions are two-limbed; the lower limb is attributed to the scotopic system, and the upper limb is attributed to the photopic system. Such interpretations which involved the duplicity theory were questioned as early as 1929 (Lythgoe & Tansley, 1929). Recently, scotopic-photopic interactions have been indicated both psychophysically and electrophysiologically in flicker paradigms. MacLeod (1972) concluded that scotopic signals evoked by a flickering stimulus completely cancelled photopic signals evoked by the same stimulus at mesopic illuminance levels where both the scotopic and photopic systems were stimulated. Walters (1971) examined psychophysical reports of hue desaturation in flicker studies. He found ERG evidence that the scotopic system was effective when the observer reported that the stimulus hue was desaturated. Consequently, he postulated an interaction between the scotopic and photopic systems to account for the desaturation.

A third line of work derives from studies of dark adaptation. Most dark adaptation studies have concluded that the scotopic and photopic systems adapt independently (for reviews, see Hecht, 1937; Rushton, 1961; Hayhoe, MacLeod, & Bruch, 1976). However, some workers have reported evidence for scotopic-photopic interaction during dark adaptation. Hough and Ruddoch (1969a, 1969b) compared Purkinje shifts in the spectral sensitivity functions of observers with normal color vision with those of tritanopic observers. They concluded that the short wavelength chromatic mechanism, which is missing in the tritanope, inhibits the scotopic system. Lythgoe (1932) and Spillman & Conlon (1972) have shown that the threshold illuminance for hue perception is greater after the rod-cone break of the traditional dark adaptation curve. This indicates that photopic activity is suppressed by the scotopic system. The conclusion of independence or interaction apparently depends upon the behavioral measure used and the particular aspect of the data emphasized by the investigator.

A fourth line of work involves experiments studying the summation of signals stimulated by two flashes. Ikeda & Urakubo (1969) have applied the summation index technique of Boynton, Ikeda, & Stiles (1964) to the study of summation between photopic and scotopic signals, although their results were inconclusive. Frumkes et al. (1973) found that both scotopic and photopic test flash (F_t) threshold was reduced when it was paired with subliminal scotopic and photopic adapting flashes (F_as). The amount of summation between the flashes was dependent on the temporal onset interval between the F_a and the F_t (F_a - F_t interval). Scotopic-photopic interaction was indicated only when the greater latency of the scotopic system was considered.

A fifth line of research stems from the increment threshold studies of Stiles (1939, 1959). In his original studies, the threshold of a F_t 2^o in diameter and 200 msec in duration was determined as a function of the irradiance of a continuously-exposed adapting field 10^o in diameter. Stiles obtained a series of F_t threshold versus adapting field irradiance (tvi) functions by systematically varying the wavelength of both flashes. He concluded that the spectral mechanisms detecting the F_t functioned independently of each other. For example, when the stimuli were presented parafoveally and the flashes were relatively dim, all the tvi functions had the same shape. The functions were displaced laterally if the adapting field wavelength was varied. Action spectra of the invariant-shaped tvi functions were nearly identical to the C.I.E. scotopic luminosity function. Therefore, Stiles concluded that the only influence of the adapting field on F_t threshold was the extent of its influence on the spectral mechanism which actually detected the F_t. In this case, the spectral mechanism was the scotopic mechanism. This is striking evidence for scotopic-photopic independence since his long-wavelength adapting fields always stimulated cones as well as rods, as was evident from their red hue (see Aguilar & Stiles, 1954).[2]

Several recent reports, however, indicate that some photopic mechanisms can influence photopic thresholds in the increment threshold situation. For example, Frumkes & Temme (in press) repeated some of the experiments of Stiles (1939), but they also varied the diameter of their adapting field. They showed that the scotopic influence of an adapting field 8° in diameter on the threshold of a F_t detected by the scotopic system was predicted by the scotopic sensitivity function. These results were equivalent to those of Stiles (1939). When the adapting field was about 1°

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[2] When similar experiments were performed in the fovea, the tvi curves were not invariant in shape. According to his original analysis (Stiles, 1939, 1959), these foveal experiments revealed the presence of five different photopic mechanisms. These experiments, however, are not related to the current study of scotopic-photopic interrelationships.

in diameter, however, Frumkes & Temme (in press) showed that longer-wavelength adapting fields (which stimulated the photopic as well as the scotopic system) were more effective than shorter-wavelength adapting fields in their influence on F_t threshold. With an analysis which involved action spectra, they showed that the scotopic system alone could not be influencing the scotopic F_t threshold when small adapting fields were used. These results, as well of those of other investigators (Lennie & MacLeod, 1973; Makous & Boothe, 1974; Martinez & Sturr, 1975; Blick & MacLeod, in press) clearly show that the spatial relationship between stimuli are crucial features in determining whether the scotopic system mediating the F_t threshold is independent of photopic influence.

In recent years, only one other increment threshold study (Westheimer, 1970) has suggested that the scotopic threshold is independent of the photopic system. Westheimer (1970) presented a F_t 5' in diameter, 10 msec in duration, and 527 nm in wavelength to the parafoveal retina in order to assess its scotopic threshold. This F_t was superposed on a continuously-exposed red-hued stimulus 8^o in diameter and 200 photopic trolands in illuminance. Some phases of this study involved a third continually-exposed stimulus, which was an annulus with a 65' inner diameter and a 86' outer diameter. This sensitizing annulus lowered F_t threshold, regardless of its wavelength. Moreover, red- and green-hued annuli equated for their influence upon the scotopic system produced an equivalent influence on F_t threshold. Thus, Westheimer (1970) concluded that this sensitizing effect involved one other example of scotopic-photopic independence. However, Westheimer's (1970) results were probably attributable to the particular size of his stimuli. For example, the results of Frumkes & Temme (in press) suggest that Westheimer's (1970) sensitizing annulus would have to be somewhat smaller to produce scotopic-photopic interaction. In fact, when a smaller sensitizing annulus was used in a paradigm almost identical to Westheimer's (1970) paradigm, scotopic-photopic interaction was indicated (Lennie & MacLeod, 1973).

Alpern (1965) used a rationale similar to that of Stiles (1939, 1959) and Westheimer (1970) to study scotopic-photopic interactions in the afterflash (metacontrast) paradigm. A F_t, which was a 2.5° square 5 msec in duration and 527 nm in wavelength, was presented to the dark-adapted parafoveal retina. This F_t was generally detected by the scotopic system. A much larger 5 msec duration stimulus, which surrounded but did not overlap the F_t, was presented 50 msec after the F_t. This F_a was either red or green in hue. Alpern found that F_t threshold increased as the F_a illuminance increased. If the red- and green-hued F_as are equated for scotopic illuminance, they produce identical effects on the scotopic F_t threshold, thus suggesting scotopic-photopic independence.

I propose that Alpern's (1965) conclusion may be valid only for the specific stimulus parameters which he used. In order to consider this more fully, a brief review of contrast flash experiments is necessary.

Basic findings of contrast flash experiments. Stigler (1910) was the first to examine the influence of contrast flashes (F_as). In this paradigm, the influence of an F_a on the perceptual attributes of a spatially-adjacent F_t is examined when the F_a - F_t interval is parametrically varied. In Stigler's (1910) study, the apparent brightness of the F_t was the dependent variable. Stigler (1910) noted that presentation of the F_a generally made the F_t appear dimmer to the observer. This effect was much greater when the F_t preceded the F_a (the metacontrast situation) than when the F_a preceded the F_t (the paracontrast situation).

Since the work of Stigler (1910), metacontrast has been the subject of much study, as is evident in many reviews (Alpern, 1952; Raab, 1963; Blanc-Garin, 1967; Kahneman, 1968; Weisstein, 1972; Lefton, 1973; Matin, 1975; Ganz, 1975; Breitmeyer & Ganz, 1976). There are several general findings. If the F_t and F_a are approximately the same size, luminance, and duration, and if F_t brightness is the dependent variable, the influence of the F_a is greatest when it precedes the F_t by 50 to 100 msec. As the F_a - F_t interval is changed from this optimal setting, the influence of the F_a becomes smaller. This relationship has commonly been called Type B masking (Kolers, 1962; Kahneman, 1968).

If F_t threshold is the dependent variable, or if F_t brightness is the dependent variable but the F_a is much larger, longer, or greater in illuminance than the F_t, Type A masking (Kolers, 1962; Kahneman, 1968) is obtained. In Type A masking, the influence of the F_a is most marked when the two flashes are simultaneous and decreases when either the F_t precedes (metacontrast) or follows (paracontrast) the F_a. Type A masking is similar to other forms of visual masking. However, Type B masking is different.

<u>Scotopic-photopic interrelationships in dual-flash situations</u>. In his study of scotopic-photopic interrelationships, Alpern (1965) determined the F_t threshold as a function of F_a illuminance. He presented the F_a 50 msec after the F_t for three reasons. First, in a previous study using a Type B paradigm, Alpern (1953) had noted maximal masking at this interval. Second, these functions could be interpreted using the rationale of Stiles (1939, 1959). Finally, the use of this interval clearly distinguished his situation from the increment threshold situation of Stiles (1939, 1959).

My contention is that Alpern's (1965) use of this single $F_a - F_t$ interval could have influenced his demonstration of scotopic-photopic independence in the metacontrast situation. First, by using F_t threshold as his dependent variable, Alpern's (1965) situation would produce a Type A situation where masking would be maximal when the two flashes were simultaneous. This was not the interval which Alpern (1965) used. Second, many investigators including Alpern (1953) himself have shown that the relationship between F_t threshold and F_a illuminance in the Type A masking situation depends on $F_a - F_t$ interval in a complex manner. Once again, the choice of a single interval could influence the data obtained. Third, there are several psychophysical (e.g., Frumkes et al., 1972, 1973) and electrophysiological (Walters, 1971; Wooten, 1972) demonstrations in the human observer that show that the scotopic system has a considerably slower latency than the photopic system. Therefore, if a F_a which stimulates the photopic system influences the threshold of a F_t which stimulates the scotopic system, its effect would probably not be apparent even when the F_a follows the F_t by 50 msec.

This contention is supported by several studies. Frumkes et al. (1972, 1973) determined the threshold of a 420 nm wavelength F_t at various F_a - F_t intervals with respect to a larger-diameter F_a either 420 or 680 nm in wavelength. They assumed that the 420 nm wavelength stimulus affected only the scotopic system and that the 680 nm wavelength stimulus the photopic system primarily. When the stimuli were presented homochromatically at a wavelength of 420 nm, they found that F_t threshold was maximal when the two flashes were presented simultaneously and decreased as the F_t either preceded or followed the F_a. When the F_a wavelength was 680 nm, a similar inverted U-shaped function was obtained. However, this function was shifted so that maximal F_t threshold occurred when the F_t preceded the F_a. They interpreted these findings as an indication that the photopic system could inhibit the photopic system provided that the greater latency of the scotopic system was taken into account. The spatial configuration of the F_a [Frumkes et al. (1972, 1973) used a disk rather than the surrounding field used by Alpern (1965)] was not a determinant of these results, since similar results have been obtained with an annular F_a (Ingling, 1972; Foster, 1976).

Rationale of the present study. The rationale of the present study follows that of Stiles (1939, 1959), Alpern (1965), and Westheimer (1970). A 512 nm wavelength F_t is presented to the parafoveal retina of the dark-adapted observer. Because its illuminance is always less than 1.5 log units above absolute threshold, the F_t is assumed to be detected by only the scotopic system. The influence of an F_a on F_t visibility (generally threshold) is determined at many different F_a - F_t intervals.

If the threshold of the scotopic system is independent of the photopic system, the only variables influencing F_t threshold should be the scotopic illuminance of the F_a and F_a - F_t interval. Specifically, the wavelength and photopic illuminance of the F_a should have no influence on F_t threshold. If, however, the photopic system influences scotopic threshold, F_as which stimulate the photopic system to a greater extent (i.e., F_as with longer wavelengths) should exert a greater influence on F_t threshold. If the difference in latency between the scotopic and photopic systems is a crucial variable in determining interaction between these systems, this should be observed when the F_a precedes the F_t.

Action spectra obtained with the F_t or F_a should conform to the scotopic luminosity function corrected for quanta if the F_t or F_a is always detected by the scotopic system. Deviations from that function should indicate a contribution of the photopic system.

Chapter 3

Apparatus

A four-channel Maxwellian view optical system was used to present all stimuli to the observers. Frumkes & Sturr (1968) have described the optics of an identical system, and Battersby & Schuckman (1970) have described the electronic controls.

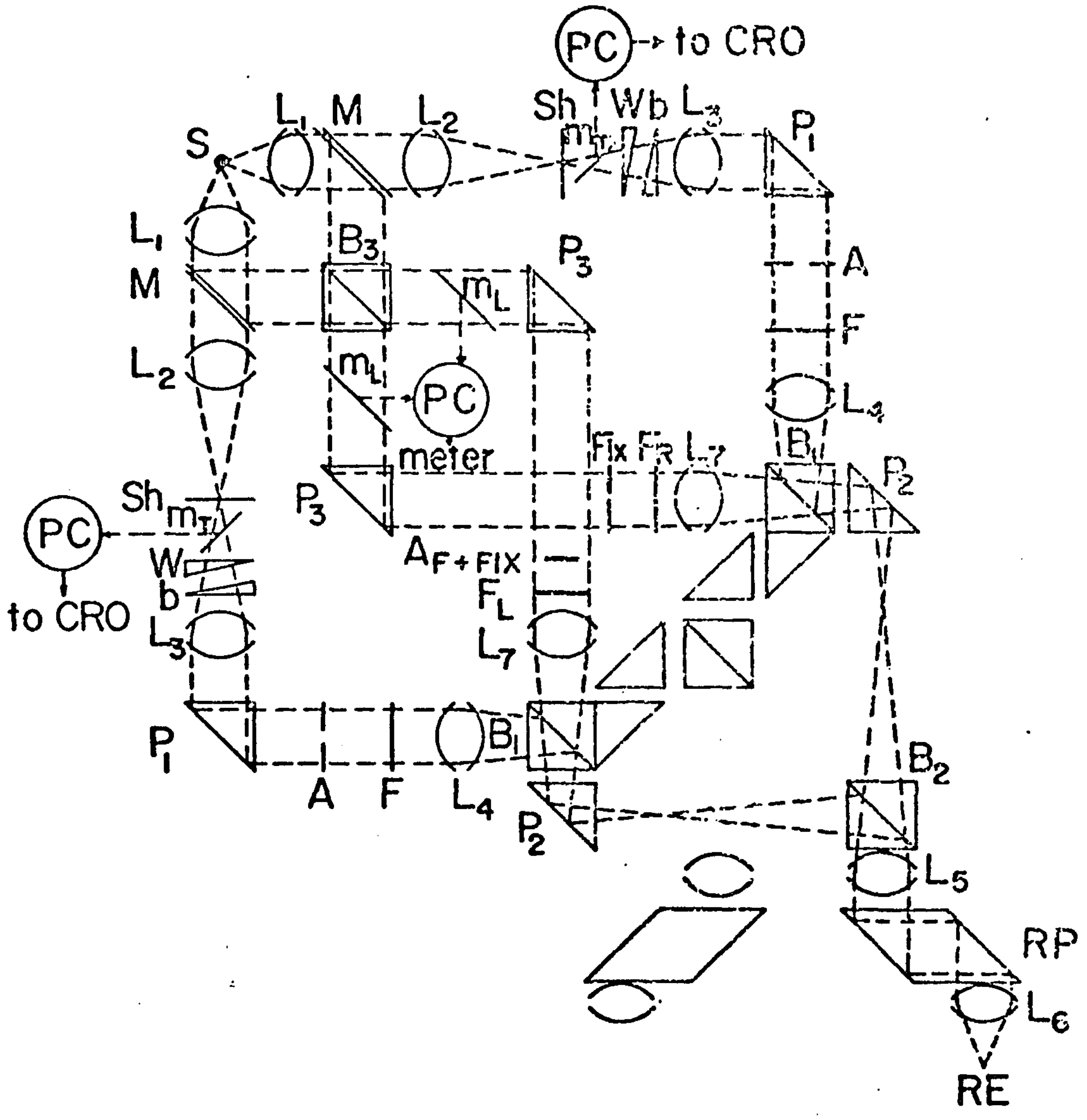
Optical system. Fig. 1 is a schematic diagram of the optical system which is composed of two symmetrical major and two symmetrical minor channels. Since this system was designed for dichoptic and monocular stimulation, only the light beams used in this monocular study are indicated with the dotted lines.

S indicates the light source, which was an 18 ampere tungsten filament incandescent lamp (General Electric CPR Projector Lamp). The lamp was powered by a 6-volt power supply (Electro Products Model H). The output of the power supply was controlled by a rheostat, and the current was monitored by an ammeter. According to the manufacturer's specifications, the approximate color temperature of the lamp is $2250^{o}K$ at the rated power. The lamp was always underpowered at approximately 16.5 amperes in order to increase its life. The same lamp was used in the collection of all the data reported here.

The two symmetrical major channels in the optical system governed the flash parameters. In each channel, L_1 indicates the initial collimating lens which collects the light from the source. L_2 indicates a focusing lens which brings the light beam into focus in the plane of the shutter, indicated by Sh. The

Fig. 1. Schematic diagram of the four-channel Maxwellian view optical system discussed in the text.

Fig. 1


PC
to CRO
Sh
m_I
Wb
L3
P1
S
L1
M
L2
B3
P3
mL
A
F
L4
mL
PC
meter
Fix
FR
L7
B1
P2
Sh
mI
PC
W
b
to CRO
L3
P3
AF+FIX
FL
L7
P1
A
F
L4
B1
P2
B2
L5
RP
L6
RE

shutter controls the duration of the stimulus. W indicates a variable neutral density wedge, which is balanced by a fixed wedge, indicated by b. The wedges control the illuminance of the stimulus. L_3 indicates a collimating lens. P_1 indicates a right-angle prism. A indicates an aperture which determines the size and spatial position of the stimulus. F indicates a filter rack which contains wavelength-controlling filters and illuminance-controlling neutral density filters. L_4 indicates a focusing lens. B_1 indicates a beamsplitter which combines one major and one minor channel. P_2 indicates a right-angle prism which directs the combined beam to the final beamsplitter, indicated by B_2. This final beamsplitter combines all four channels and leads these beams to a collimating lens, indicated by L_5. RP indicates a rhomboid prism, which adjusts the beam to a convenient position for the observer. L_6 indicates the final eye lens which focuses the beam in the plane of the pupil of the observer's right eye, indicated by RE.

Two symmetrical minor channels of the optical system provide an adaptation field, a fixation target, and a source radiance monitor. M indicates a partially-reflecting mirror which diverts light from a major channel into a minor channel. B_3 indicates a beamsplitter which combines the two minor channels. Two beams enter the beamsplitter and are combined, and then the two combined beams leave. P_3 indicates a right-angle prism. $A_{F + FIX}$ and Fix indicate apertures which govern the spatial configuration of the fixation stimuli. F_R and F_L indicate racks for filters which control the wavelength and the illuminance of the fixation channels. L_7 indicates a focusing lens which conveys the light beam to the beamsplitter, indicated by B_1, for combination with a major channel.

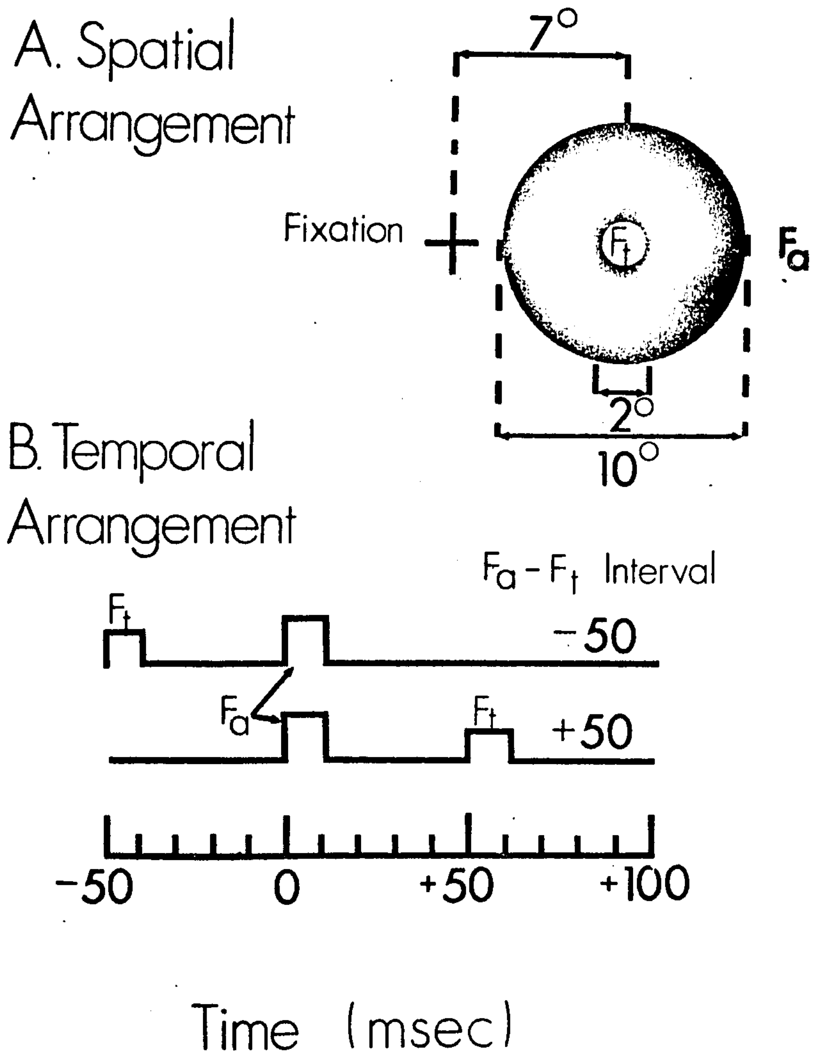
Source monitor. To monitor the radiance of the light source, partially-reflecting mirrors, indicated by m_L, divide the beams in the two minor channels and present the beams to a photocell, indicated by PC. The current of the photocell is monitored by a microammeter. The experimenter adjusted the rheostat controlling the light source current whenever he found that the microammeter reading had departed from its calibrated reading.

Spatial control. The spatial configuration of each stimulus was governed by a target mounted at the position indicated by A. Each target was mounted in a micromanipulator which permitted precise movement vertically and horizontally. A projection technique showed that an aperture 1 mm in diameter resulted in an image 1.8° in diameter. Since a stimulus of any size can be mounted on the micromanipulator, which is also calibrated, both the retinal position and size of all stimuli can be accurately determined. The test flash (F_t) target was an aperture drilled in a metal plate, which provided a 2° disk in Maxwellian view. The adapting flash (F_a) target was a photographic film, which provided an annulus with a 2° inner diameter and a 10° outer diameter in Maxwellian view. These stimuli are illustrated in Fig. 2a. The F_t was centered at a point 7° from the fixation

Fig. 2a. Spatial arrangement of the F_t and F_a. The F_t is a 2° diameter disk located 7° from the fixation point on the horizontal meridian in the temporal visual field of the right eye. The F_a is an annulus with a 2° inner diameter and a 10° outer diameter concentric with the F_t.

Fig. 2b. Temporal arrangement of the F_t and F_a as they appear on the monitoring oscilloscope. The term, $F_a - F_t$ interval, refers to the temporal interval between the onsets of the F_a and the F_t. The F_t is represented by a low amplitude pulse, while the F_a is represented by a higher amplitude pulse. The trace labelled -50 illustrates the situation where the F_t onset precedes the F_a onset by 50 msec. The trace labelled +50 illustrates the situation where the F_t onset follows the F_a onset by 50 msec.

Fig. 2


A. Spatial Arrangement
7°
Fixation
Ft
Fa
2°
10°
B. Temporal Arrangement
Fa - Ft Interval
Ft
-50
Fa
Ft
+50
-50
0
+50
+100
Time (msec)

point on the horizontal meridian of the temporal visual field of the right eye. The annulus was adjusted until it was concentric with the F_t.

Temporal control. The duration of the stimuli and the temporal onset intervals between the F_a and F_t (F_a - F_t intervals) is governed by the shutters and their electronic controls. One Tektronix 162 Waveform Generator provides an adjustable recycling rate. During this experiment, the recycling rate was always one cycle for every four seconds. A second Waveform Generator provides a time base for the stimulus-monitoring oscilloscope (Tektronix 360) and two Tektronix 161 Pulse Generators. One Pulse Generator controls the duration, onset, and waveform of the F_t. The second Pulse Generator governs these parameters for the F_a. Each Pulse Generator controls a shutter power supply of local design which drives a galvanometer motor with a shutter attached.

Temporal parameters of the stimuli are monitored by photocells and associated electronic circuitry mounted behind the shutters in each major channel. In the schematic diagram, they are indicated by PC, and the partially-reflecting mirror providing the beam is indicated by m_T. Currents from these photocells are displayed on the monitoring oscilloscope, indicated by CRO. The experimenter can continuously monitor all temporal parameters with this arrangement.

Fig. 2b illustrates the appearance of the oscilloscope traces for two F_a - F_t intervals. The F_t is represented by a low amplitude pulse, and the F_a is represented by a higher amplitude pulse.

The duration of both pulses was always 10 msec. The trace labelled -50 msec illustrates the situation where the F_t onset precedes the F_a onset by 50 msec. The trace labelled +50 msec illustrates the situation where the F_t onset follows the F_a onset by 50 msec. The term, F_a - F_t interval, is used throughout this study to refer to the temporal interval between the onsets of the F_a and F_t.

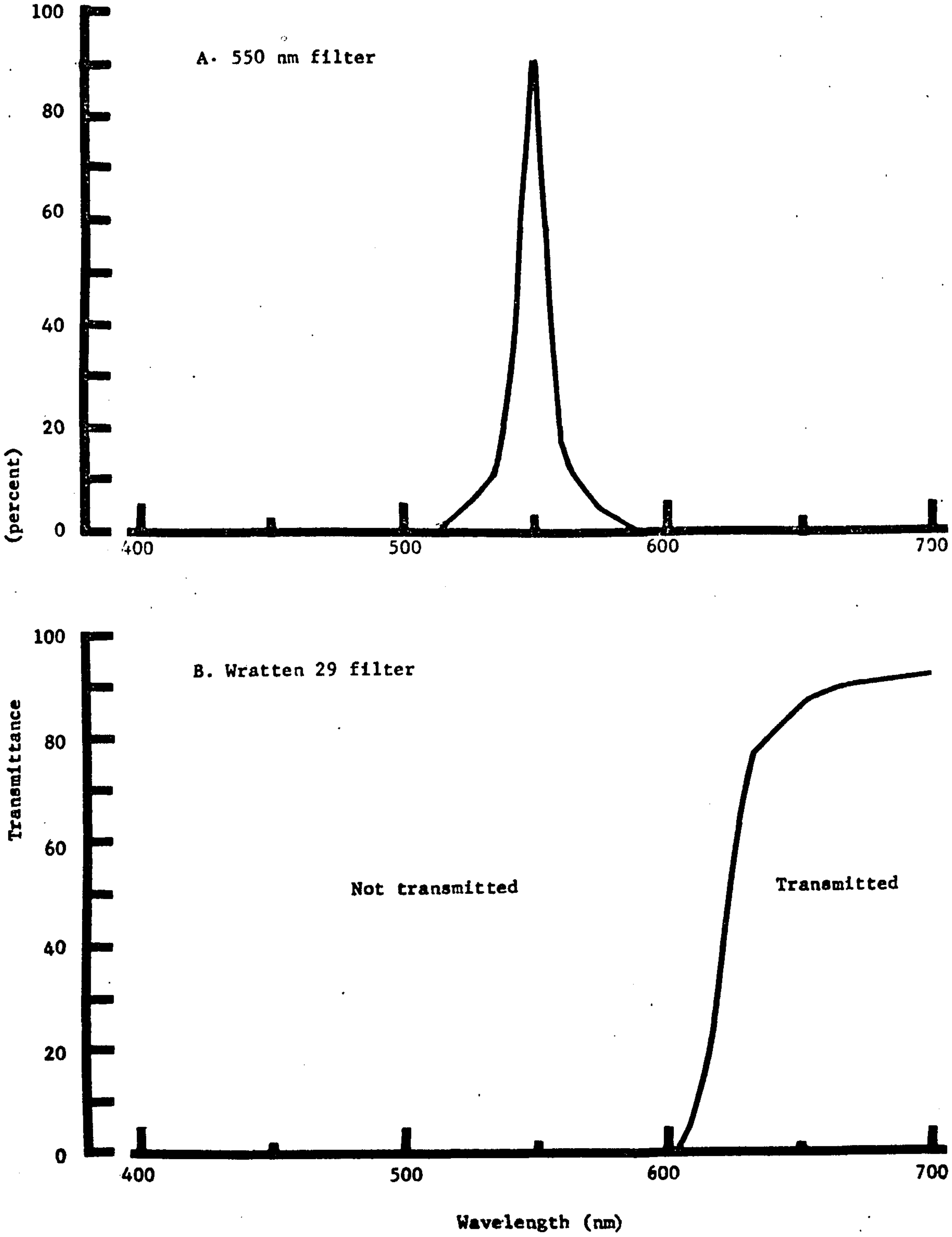
<u>Illuminance control</u>. The illuminance of the major channels is controlled by four-log-unit, circular, and balanced neutral density wedges geared to indicator dials. Forty revolutions of the indicator dial result in one revolution of the variable wedge. Therefore, one revolution results in an illuminance change of 0.1 log units. Further illuminance control in the major channels is provided by adding neutral density filters at the position indicated by F. Illuminance control of the minor channels is acheived by placing neutral density filters at F_L and F_R.

<u>Wavelength control</u>. Stimulus wavelength was governed by Baird-Atomic B-16A interference filters with peak wavelengths of 420, 472, 495, 512, 525, 577, 615, 630, 655, and 680 nm. F indicates the location of these filters in the optical system. Spectrophotometric data reported by the manufacturer show that approximately 45-90% of the photons with the peak wavelength are transmitted. The half bandwidth of each filter is approximately 10 nm. Fig. 3a illustrates transmittance as a function of wavelength for a filter of this type with a peak wavelength of 550 nm.

Fig. 3a. Transmittance as a function of wavelength for an interference filter with a peak wavelength of 550 nm (from Wyszecki and Stiles, 1967, p 174).

Fig. 3b. Transmittance as a function of wavelength for a Kodak Wratten 29 absorption filter (from Wyszecki and Stiles, 1967, p 148).

Fig. 3


A· 550 nm filter
100
80
60
40
20
0
(percent)
400
500
600
700
B. Wratten 29 filter
100
80
60
40
20
0
Transmittance
Not transmitted
Transmitted
400
500
600
700
Wavelength (nm)

In addition, a Kodak Wratten 29 absorption filter was used in the F_a channel in Experiments 2 and 3. Transmittance as a function of wavelength for this filter is indicated in Fig. 3b. This filter does not permit appreciable transmittance of photons with wavelengths less than 600 nm. Its predominant transmittance involves photons with wavelengths greater than 660 nm. This filter was used because of the inability to obtain adequate illuminance with monochromatic long-wavelength filters.

Illuminance calibration. The illuminance of the spectrally-unfiltered channels of the optical system was determined with the procedure outlined by Westheimer (1966). First, a perfectly diffusing surface with a specific reflectivity, r, was placed at a given distance, x, beyond the filament image. During experimentation, this image was in the plane of the observer's pupil. Second, the luminance of the surface, $\bar{B}$ millilamberts, was measured with a Macbeth illuminometer. Finally, the retinal illuminance was calculated with equation 1. E is the retinal illuminance

Equation 1. $$E = 10^7 \bar{B} x^2/r$$

in trolands, $\bar{B}$ is the surface luminance in millilamberts determined in the second step, x is the distance in meters between the filament image and the diffusing surface, and r is the reflectivity of the diffusing surface. This procedure is required to specify the illuminance of the stimuli at the retina. Luminance measures at a point in space do not adequately describe the stimuli at the retina.

The illuminance of the 512 nm wavelength stimuli was calibrated by performing brightness matches between a spectrally-unfiltered (approximate color temperature = 2250°K) stimulus $\bar{1}.0$ log scotopic trolands in illuminance and a 512 nm wavelength annular stimulus. The duration of both stimuli was one sec. At this illuminance level and wavelength, the hue of the two stimuli appeared identical. Therefore, it is reasonable to assume that only the scotopic system is determining threshold. This brightness match was used as the basis for calibrating the illuminance of stimuli of all other wavelengths.

Calibrating the illuminance of stimuli of other wavelengths, particularly the red-hued long-wavelength stimuli, was more difficult, since all commonly-used procedures involve several tenuous assumptions. Therefore, three procedures were used to determine the scotopic illuminance of the red-hued stimuli. In the first procedure, brightness matches were made between these annular stimuli and a 512 nm wavelength disk stimulus presented at an illuminance of $\bar{1}.0$ log scotopic trolands. This procedure assumes that the apparent brightness of both stimuli is determined by the scotopic system. In the second procedure, the absolute threshold illuminance of red-hued flashes 2° in diameter and 10 msec in duration was arbitrarily equated in illuminance to the absolute threshold illuminance of a 512 nm wavelength stimulus with the same diameter and duration. This procedure assumes that the absolute threshold of both stimuli are determined by the scotopic system, although several investigators (e.g., Wald, 1945) suggest that peripheral cones are more sensitive than rods at these wavelengths. In the third procedure, increment threshold functions were obtained with a 512 nm wavelength F_t 2° in diameter and 10 msec in duration presented on a continuous adapting field 10° in diameter. The adapting field wavelength was governed by either a 512 nm, 655 nm, or a Wratten 29 filter. Functions obtained with adapting fields of different wavelengths were always identical in shape. Using the example given in Fig. 4, the experimenters laterally shifted the graph of the function obtained with a 655 nm wavelength adapting field with respect to the graph of the function obtained with a 512 nm wavelength adapting field until the two functions superposed. Common points on the superposed functions were taken as equivalent in scotopic illuminance for the 512 and 655 nm wavelength stimuli. The numerical difference between the abscissa values of the common points expressed in arbitrary dial units provided the value for calibrating the unknown illuminance of the 655 nm wavelength stimulus with the known illuminance of the 512 nm wavelength stimulus. This procedure is warranted on the basis of Stiles' (1939, 1959) data, although he assumed strict scotopic-photopic independence.

Each of the three methods used with two observers gave an estimate of scotopic illuminance. Table 1 presents the arbitrary dial settings of a stimulus with its spectral composition controlled by a 655 nm wavelength or a Wratten 29 filter which are required

Fig. 4. The F_t threshold illuminance as a function of illuminance for a continuously-exposed solid disk adapting field 10^o in diameter. Closed circles and solid lines indicate the function obtained when the adapting field wavelength is 512 nm. Open circles and broken lines indicate the function obtained when the adapting field wavelength is 655 nm. The functions on the upper set of coordinates were obtained with observer MCB, and the functions on the lower set of coordinates were obtained with observer ARK. The F_t threshold illuminance for the F_t presented alone is represented by the closed diamond symbol over the abscissa position marked "minus infinity". The crossbars indicate 95% fiducial limits. The increment threshold functions of different wavelengths are displaced laterally by approximately 0.2 log units because the abscissa calibration is based on the mean value determined with three different techniques rather than the increment threshold technique alone.

Fig. 4

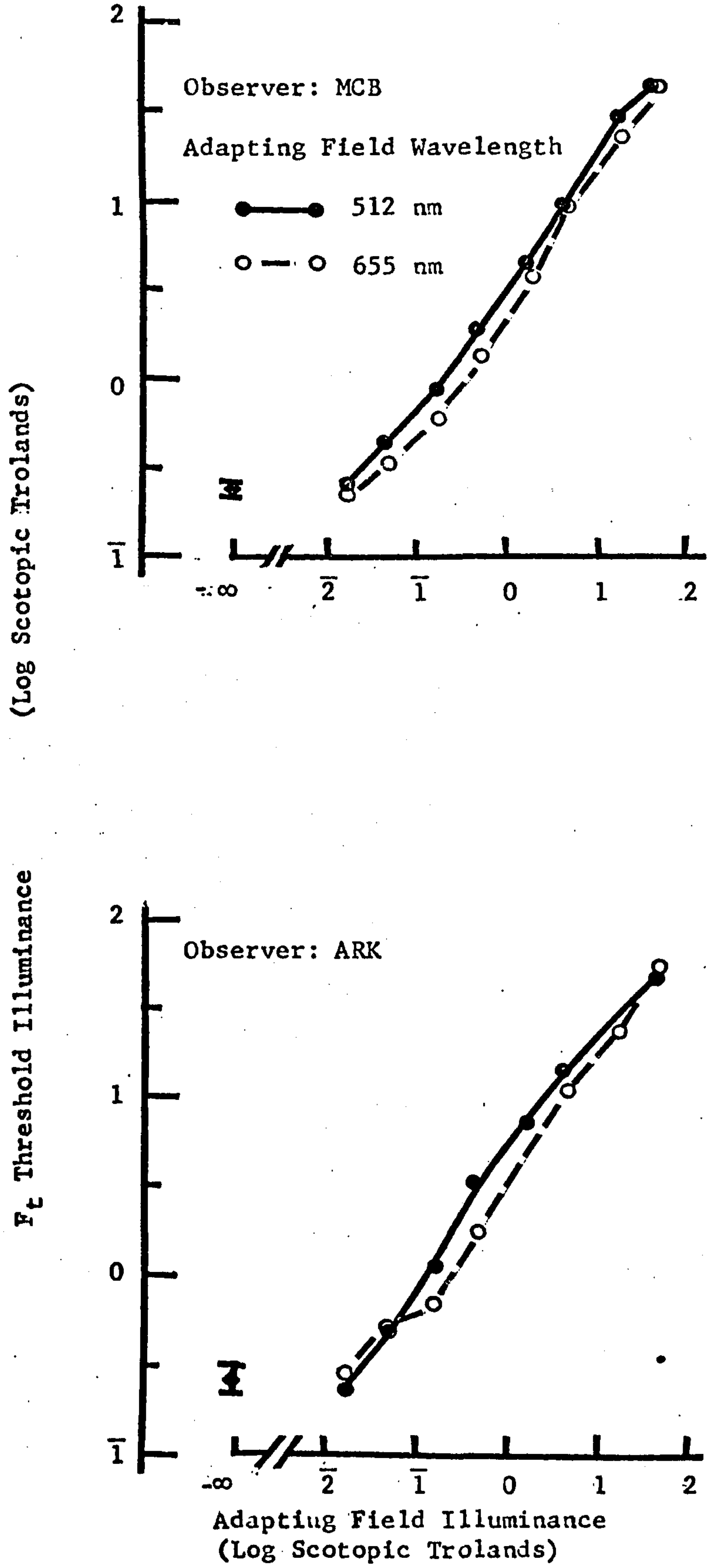

Observer: MCB
Adapting Field Wavelength
512 nm
655 nm
2
1
0
$\bar{1}$
-∞
$\bar{2}$
$\bar{1}$
0
1
2
Observer: ARK
2
1
0
$\bar{1}$
-∞
$\bar{2}$
$\bar{1}$
0
1
2
F_t Threshold Illuminance
(Log Scotopic Trolands)
Adapting Field Illuminance
(Log Scotopic Trolands)

Table 1

Arbitrary dial settings of a stimulus with spectral composition controlled by a Wratten 29 filter which are required to match a zero setting of a 512 nm wavelength stimulus.

	Observer		
Method	MCB	ARK	Mean of two observers
Brightness match	1.34	1.03	1.18
Absolute threshold	1.41	1.31	1.36
Increment threshold	1.12	1.05	1.08
Mean of three methods	1.29	1.13	1.20

Arbitrary dial settings of a stimulus with spectral composition controlled by a 655 nm wavelength filter required to match a zero setting of a 512 nm wavelength stimulus.

	Observer		
Method	MCB	ARK	Mean of two observers
Brightness match	2.12	2.02	2.07
Absolute threshold	2.05	2.56	2.30
Increment threshold	2.20	2.05	2.12
Mean of three methods	2.12	2.21	2.16

to match a zero arbitrary dial setting of a 512 nm wavelength stimulus. This information is given for two observers and three methods. The arithmetic mean of these six measures provided the basis for calibrating the illuminance coordinates used in this study.

Irradiance calibration. An E.G. and G. Model 580/585 Spectroradiometer/Radiometer was used to measure the energy in each channel with each of the 11 monochromatic interference filters. These energy values were converted to log quanta relative to the number of quanta transmitted with the 420 nm wavelength filter. This filter was chosen as the reference because it transmitted less energy than any of the other filters. For example, in one specific channel, the 420 nm wavelength filter transmitted 0 log relative quanta, the 512 nm wavelength filter transmitted 0.862 log relative quanta, and the 680 nm wavelength filter transmitted 1.360 log relative quanta.

Fixation target. A continuous fixation target is provided in the optical system at the point indicated by Fix and F_R. At low levels of adaptation field illumination, this target appears as four red disks approximately 15' in diameter. These disks outline a 3° square. The spatial configuration of these disks is governed by a photographic film placed in front of a circular aperture with a 40° diameter in Maxwellian view. Wavelength is governed by a Wratten 29 filter, while illuminance is controlled by neutral density filters.

Adaptation field. In order to reduce stray light, stabilize adaptation, reduce variability, and aid fixation, a 40° diameter continuous field with fixation crosshairs is provided in the optical system at the point labelled $A_{F + FIX}$ and F_L. This spectrally-unfiltered field provided $\overline{4}.6$ log scotopic trolands of illuminance, which was determined by neutral density filters. The fixation crosshairs were visible to the observer only when the illuminance level was considerably higher than the level used during data collection.

Head and eye position control. The observer's head and eye position is controlled by a Bausch and Lomb chin- and headrest which is mounted so that it can be accurately positioned in three planes. While light-adapted, the observer adjusted this device until he had a sharp and full view of the adaptation field 2.6 log trolands in illumination with the crosshairs in the center. The final filament image, approximately 0.5 x 2 mm, was centered in the pupil of each observer. Since the pupil was considerably larger than this during all phases of this study because of the low levels of illumination, pupil size should not reduce retinal illumination.

Chapter 4

Method

Observers. Three observers were used during the course of the experiment. The author, MCB, was a myopic (5/200 bilaterally) male 31 years of age, ARK was an emmetropic male 18 years of age, and DLG was an emmetropic female 17 years of age. No corrective lenses were worn by the observers during experimentation, but the final eye lens provided an adjustment for refractive error. The observers were screened for normal color vision with pseudo-isochromatic plates. Experimenters and observers alternated roles among sessions.

General procedure. At the beginning of each session, the observer aligned his right eye with the 40° diameter adaptation field at an illuminance of 2.6 log trolands. He adjusted the chin- and headrest and the final eye lens until he saw the full adaptation field and the fixation crosshairs in sharp focus. The observer then began to dark adapt. After 10 minutes of dark adaptation, the observer viewed the adaptation field at an illuminance of $\bar{2}.6$ log scotopic trolands. If the observer did not see the full adaptation field and the red fixation targets, he adapted an additional five minutes before viewing the fixation target again. (The observers always saw the full adaptation field after 15 minutes of dark adaptation.)

After 25 minutes of dark adaptation, the observer viewed the adaptation field at its experimental illuminance of $\bar{4}.6$ log scotopic trolands. The test flash (F_t) was then presented to the observer once every four seconds. Using the method of adjustment, the observer adjusted the variable wedge controlling F_t illuminance until he no longer detected the F_t. This procedure was repeated several times as a control measure to determine that dark adaptation was complete. This was indicated by stable threshold illuminance values. The procedure was then repeated with the adapting flash (F_a).

After determining these control threshold illuminance values, the F_ts and F_as appropriate to the experimental session were then presented at predetermined temporal onset intervals between the F_a and F_t (F_a - F_t intervals). Using the method of adjustment, the observer then adjusted the appropriate stimulus until he no longer detected the F_t. In Experiments 1 and 3, the observer varied F_t illuminance until he no longer detected the F_t. In Experiments 2 and 4, the observer adjusted the F_a until it masked the F_t.

A set of rules governed data collection. First, every threshold value determined with a specific set of stimulus parameters was repeated three times in a block within an experimental session. If the range of values exceeded 0.2 log units, one additional threshold value was determined. Second, every data point reported was based on observations obtained in at least two experimental sessions. Third, one determination of the threshold illuminance of the F_t presented alone was made after every block of trials. The daily mean of these determinations was plotted at the end of every session to determine whether long-term threshold trends were occurring over sessions. Fourth, no experimental session lasted more than 90 minutes after dark adaptation was complete. Finally, each observer was repetitively instructed to adjust the stimuli until the F_t was no longer detected. He was also instructed to use a blanking procedure when he was approaching threshold. That is, the observer pushed a button which cancelled the F_t for one presentation. Then he compared the appearance of the F_a presented alone with the next presentation where both flashes were presented together.

The general goal of this research was to determine whether the photopic system can influence the scotopic system in the metacontrast and paracontrast situations. This goal was acheived by using four strategies. Table 2 summarizes the stimulus parameters common to all the experimental strategies as well as the parameters specific to each strategy.

In the first and second experiments, thresholds are plotted in terms of log scotopic trolands, a photometric unit which expresses the illuminance at the retina. In the third and fourth experiments, thresholds are plotted in terms of log relative quanta incident at the cornea. This is because the C.I.E. standard relative spectral luminous efficiency functions for scotopic and photopic vision (scotopic and photopic luminosity functions) express the ratio of the luminous flux to the radiant flux at different wavelengths. This procedure accounts for quantal

Table 2

Parameters Common to All Experiments

	F_t	F_a
Duration	10 msec	10 msec
Diameter	2^{o}	2^{o} inner diameter 10^{o} outer diameter
Spatial location	7^{o} in the temporal visual field	7^{o} in the temporal visual field

Parameters Specific to Experiment 1

	F_t	F_a
Illuminance	Adjusted to threshold	Varied parametrically
Wavelength	512 nm	512 and 655 nm

F_a - F_t intervals (msec)

-100, -50, 0, +50, +100

Parameters Specific to Experiment 2

	F_t	F_a
Illuminance	Fixed at 0.5 log units above absolute threshold	Adjusted to mask the F_t
Wavelength	512 nm	512 nm and red-hued (Wratten 29 filter)

F_a - F_t intervals (msec)

Varied at 50 msec intervals between -200 and 450 msec

Table 2

(continued)

<u>Parameters Specific to Experiment 3</u>

	F_t	F_a
Log relative quanta	Adjusted to threshold	Fixed at values determined in Experiment 2
Wavelength	420, 472, 512, 577, 620 nm	512 nm and red-hued (Wratten 29 filter)

$F_a - F_t$ intervals (msec)

-150, 0, +150

<u>Parameters Specific to Experiment 4</u>

	F_t	F_a
Log relative quanta	Fixed at 0.5 log units above absolute threshold	Adjusted to mask the F_t
Wavelength	512 nm	Varied parametrically between 420 and 680 nm

$F_a - F_t$ intervals (msec)

-150, -50, +100, +200

absorption by the ocular media as well as by the photopigments. Consequently, the data must be presented in terms of log relative quanta to permit comparison with the C.I.E. scotopic and photopic luminosity functions corrected for quanta (Wyszecki and Stiles, 1967, pp 371-383).

Experiment 1. In the first experiment, threshold illuminance values of the 512 nm wavelength F_t were determined at five $F_a - F_t$ intervals (-100, -50, 0, +50, and +100 msec) with either a 512 or 655 nm wavelength F_a whose illuminance was parametrically varied. If the F_t threshold illuminance is determined by the scotopic system, and if the scotopic and photopic systems function independently, the results should be independent of F_a wavelength.

For each session, a single F_a wavelength was randomly selected. Two $F_a - F_t$ intervals for that wavelength were randomly selected without replacement from a table of intervals. For each $F_a - F_t$ interval, the experimenter used blocks of successively increasing F_a illuminance ranging in five equal steps from near F_a threshold illuminance to the limit of the apparatus.

Experiment 2. In the second experiment, threshold illuminance values of a 512 nm wavelength F_t were obtained four times in succession with no F_a present. The mean of these four determinations was computed. Then the F_t was presented at an illuminance value 0.5 log units above the mean threshold illuminance value. Next, an F_a with wavelength governed by either a 512 nm wavelength or a Wratten 29 filter was introduced at several $F_a - F_t$ intervals

(-200, -175, -150, -100, -50, 0, +50, +100, +150, +200, +250, +300, +350, +400, and +450 msec). The observer adjusted the illuminance of the F_a until it masked the F_t. If F_t threshold illuminance is determined by the scotopic system, and if the scotopic and photopic systems function independently, the results should be independent of F_a wavelength. The advantage of this strategy over that used in the first experiment is that it is unlikely that the F_t itself could appreciably influence the photopic system with a low illuminance at this wavelength.

In each experimental session, a single wavelength F_a was randomly selected. Within each session, threshold illuminance values were determined at seven or more F_a - F_t intervals, which were ordered randomly.

Experiment 3. The third experiment was conceptualized in the following manner. An F_a with its wavelength governed by either a 512 nm wavelength or Wratten 29 filter was presented to the observer at three F_a - F_t intervals (-150, 0, and +150 msec). Regardless of interval or wavelength, F_a illuminance was fixed at the level which masked the F_t in the second experiment. The log relative quanta of a variable wavelength F_t was adjusted by the observer until it was no longer detected. If the F_t threshold was mediated by only the scotopic system in the second experiment, the scotopic luminosity function corrected for quanta should describe F_t threshold log relative quanta.

In fact, the third experiment was performed the following way in order to insure continuity between the results of the second and third experiment and in order to account for intersession variability. At the beginning of each session, a 512 nm wavelength F_t was raised 0.5 log units above its average threshold illuminance value with no F_a present. This value had been determined over many previous sessions. An F_a of either wavelength was adjusted three times until the F_t was no longer detected. The mean F_a value was determined and held constant for the rest of the session. Then, a monochromatic filter governing F_t wavelength was selected. The F_t log relative quanta was adjusted until the F_t was masked. The experimenter recorded the log relative quanta value of this determination. Monochromatic filters 420, 472, 577, and 615 nm in wavelength were introduced in random order into the F_t channel at a F_a - F_t interval of 0 msec, while 472 and 577 nm wavelength monochromatic filters were used in random order when the F_a - F_t interval was -150 or +150 msec. These two intervals were selected because they were the longest intervals at which it was possible to obtain complete action spectra. At longer intervals, the apparatus did not provide sufficient illuminance to determine action spectra. The 0 msec F_a - F_t interval was selected because of its central location between these two intervals. The spatial alignment of the F_a was carefully checked with each change in F_t wavelength because of chromatic aberration which caused changes in the spatial position of the stimuli.

Experiment 4. In the fourth experiment, a 512 nm wavelength

F_t was presented at a constant illuminance of $\bar{1}.9$ log scotopic trolands, which was 0.5 log units above the average threshold illuminance with no F_a present. An F_a of a randomly-selected wavelength (either 420, 472, 495, 512, 525, 555, 577, 615, 630, 655, or 680 nm) was introduced at one of four F_a - F_t intervals (+200, +100, -50, and -150 msec). These intervals were selected to assess apparently crucial points in the data of Experiment 2. The observer then adjusted the F_a log relative quanta until it masked the F_t. If the influence of the F_a upon the F_t was due to the scotopic system alone for any given F_a - F_t interval, than F_a log relative quanta should be predicted by the scotopic luminosity function corrected for quanta.

Only one F_a - F_t interval was used in each experimental session, while at least five different wavelength filters were introduced into the F_t channel. Each wavelength change required realignment of the optical system because of chromatic aberration. Throughout each experimental session, the F_t threshold illuminance was determined with the F_a absent to insure that the observer's sensitivity had not changed during the course of the session.

Each of the functions resulting from the four different F_a - F_t intervals was obtained over two experimental sessions. Some of the same wavelength F_as were used in all experimental sessions to insure that intersession variability did not determine the results of this experiment.

Chapter 5

Results

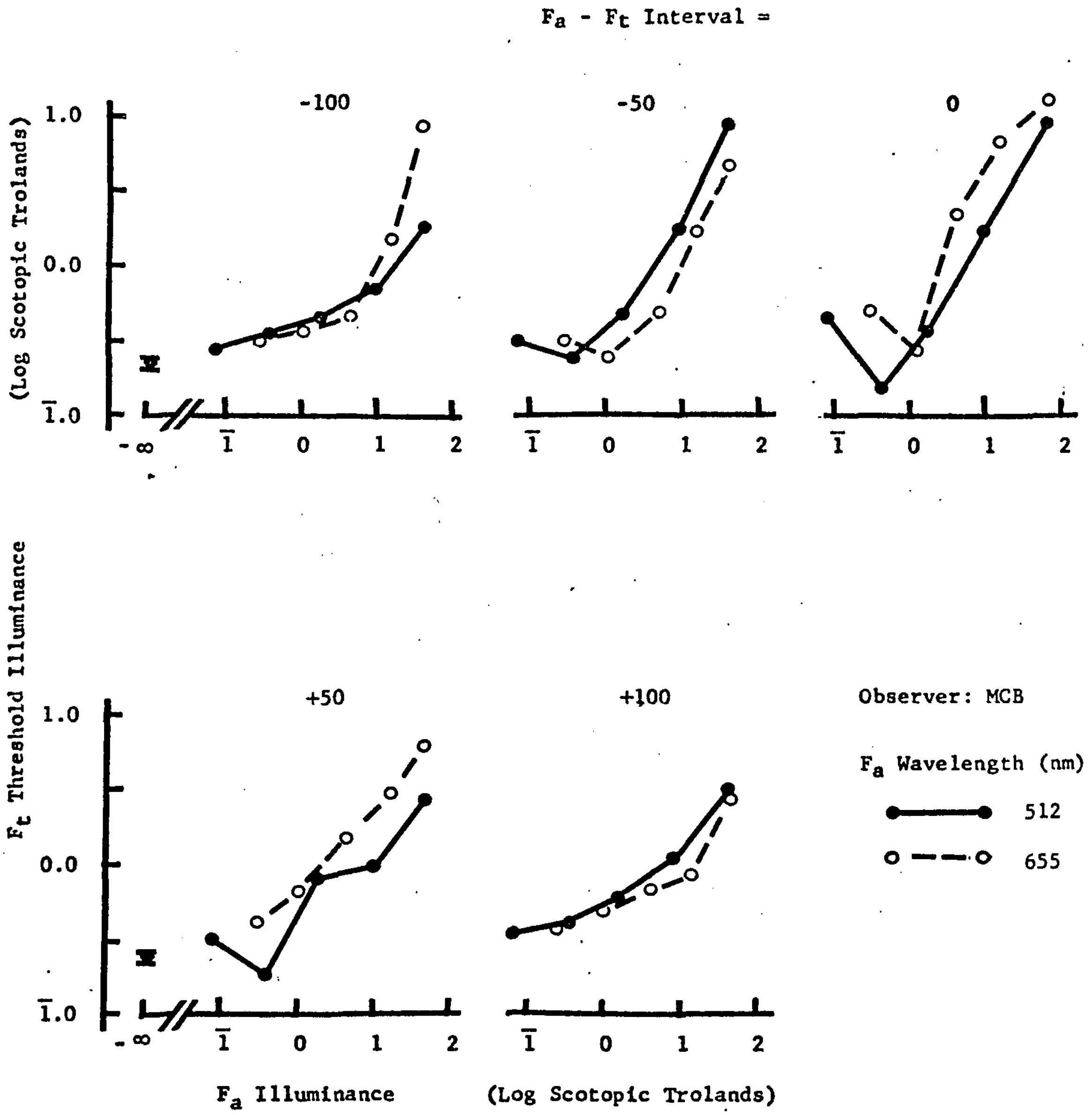
Experiment 1. In the first experiment, the observers adjusted the illuminance of a 512 nm wavelength test flash (F_t) until it was no longer detected in the presence of either a 512 or 655 nm wavelength adapting flash (F_a), whose illuminance was increased parametrically over the course of the session. These determinations were made at five temporal intervals between the onsets of the F_a and the F_t (F_a - F_t intervals) for F_as of either wavelength.

Fig. 5 for observer MCB and Fig. 6 for observer DLG present 512 nm wavelength F_t threshold illuminance as a function of scotopic illuminance for both a 512 and a 655 nm wavelength F_a. The specific F_a - F_t interval represented by each pair of functions is indicated above the functions. The threshold illuminance value of the F_t with no F_a present is indicated on the abscissa at the position labelled "minus infinity". The 95% fiducial limits are indicated by the crossbars. The 95% fiducial limits for the other data points throughout this study are generally less than 0.25 log units. Regardless of F_a wavelength, F_t threshold illuminance generally increase monotonically as a function of F_a illuminance.

If the influence of the F_a upon the F_t is due solely to the scotopic system, these functions should be independent of F_a wavelength at every F_a - F_t interval, i.e., they should be similar functions. This prediction is substantiated for the

Fig. 5. Results of Experiment 1. The F_t threshold illuminance as a function of F_a illuminance for five F_a - F_t intervals for observer MCB. Closed circles and solid lines indicate the function obtained when the F_a wavelength is 512 nm, while open circles and broken lines indicate the function obtained when the F_a wavelength is 655 nm. Threshold of the F_t presented alone is represented by the closed diamond symbol over the abscissa position marked "minus infinity". The crossbars indicate the 95% fiducial limits.

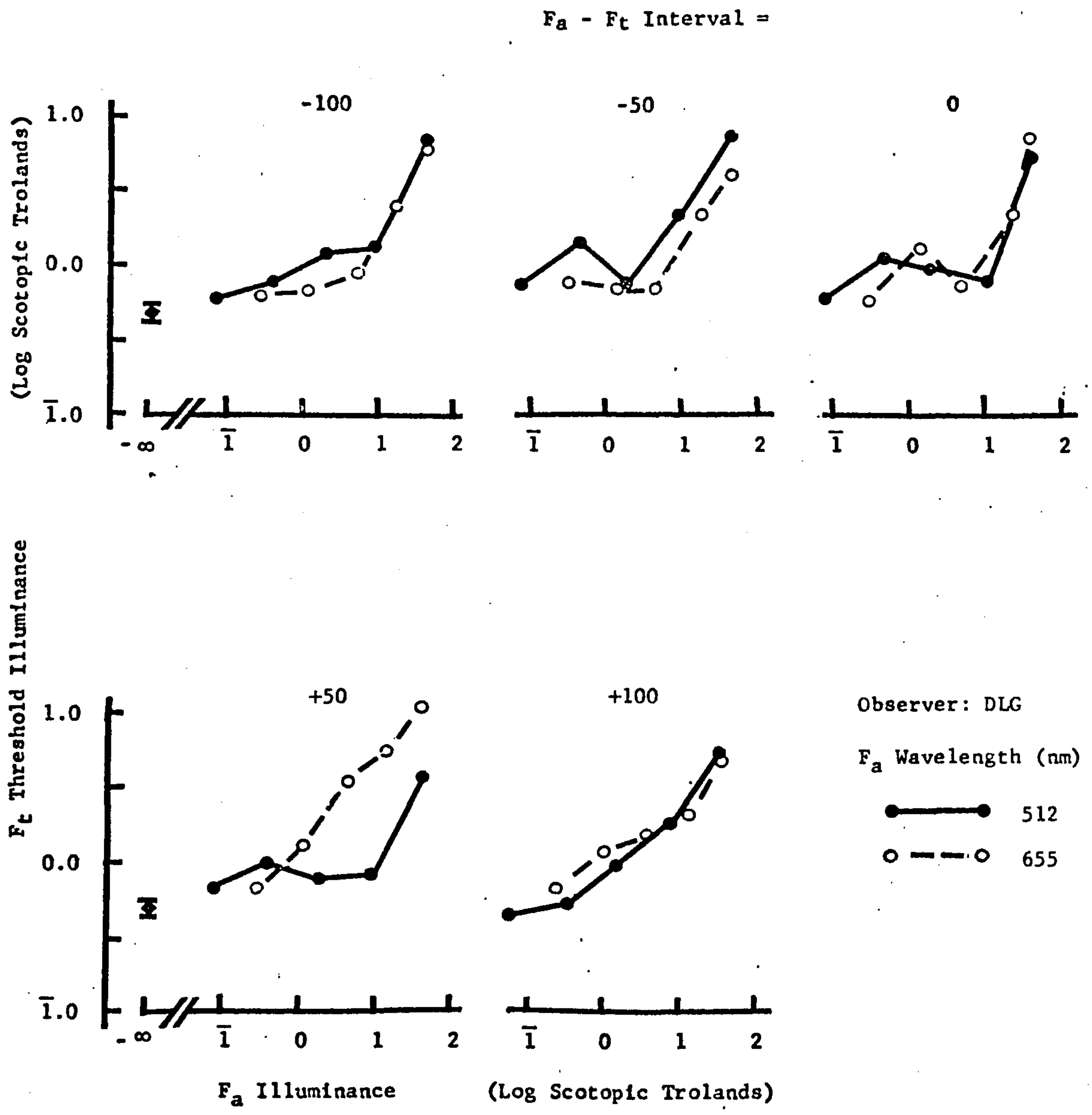
Fig. 5



Fa - Ft Interval =
-100
-50
0
+50
+100
1.0
0.0
$\bar{1}$.0
- ∞
$\bar{1}$
0
1
2
Ft Threshold Illuminance
(Log Scotopic Trolands)
Fa Illuminance
(Log Scotopic Trolands)
Observer: MCB
Fa Wavelength (nm)
512
655

Fig. 6. Results of Experiment 1. The F_t threshold illuminance as a function of F_a illuminance for observer DLG. See the legend of Fig. 5.

Fig. 6


F_a - F_t Interval =
-100
-50
0
+50
+100
F_t Threshold Illuminance
(Log Scotopic Trolands)
1.0
0.0
$\bar{1}$.0
- ∞
$\bar{1}$
0
1
2
F_a Illuminance
(Log Scotopic Trolands)
Observer: DLG
F_a Wavelength (nm)
● 512
○ 655

+100 and -100 msec F_a - F_t intervals for both observers and the 0 msec F_a - F_t interval for observer DLG. With the other intervals, however, F_t threshold illuminance seems to depend upon both F_a wavelength and illuminance. For example, at the +50 msec F_a - F_t interval, the F_a wavelength at low F_a illuminance does not seem to make a difference. However, at higher F_a illuminance, the 655 nm wavelength F_a causes a higher F_t threshold than the 512 nm wavelength F_a. At the -50 msec F_a - F_t interval the 512 nm wavelength F_a raises F_t threshold illuminance more than the 655 nm wavelength F_a, especially at the higher illuminance values. At the +50 msec F_a - F_t interval for observer DLG (Fig. 6), the 655 nm wavelength F_a raises the F_t threshold illuminance more than the 512 nm wavelength F_a. For observer MCB (Fig. 5), this trend is apparent at both the 0 and +50 msec F_a - F_t intervals. Apparently, at the -50 and +50 msec and perhaps at the 0 msec F_a - F_t intervals, F_t threshold illuminance does not increase as a simple function of increasing F_a illuminance. Since the wavelength of the F_a was the only other parameter that changed, the most probable explanation for the difference between the two functions is the activation of the photopic system by the 655 nm wavelength F_a.

Collectively, the results of the first experiment indicate that the effect of F_a illuminance upon F_t threshold illuminance is dependent upon F_a wavelength. Furthermore, this influence of wavelength is dependent upon F_a - F_t interval. The second experiment explores the influence of F_a wavelength and F_a - F_t interval on F_t threshold illuminance.

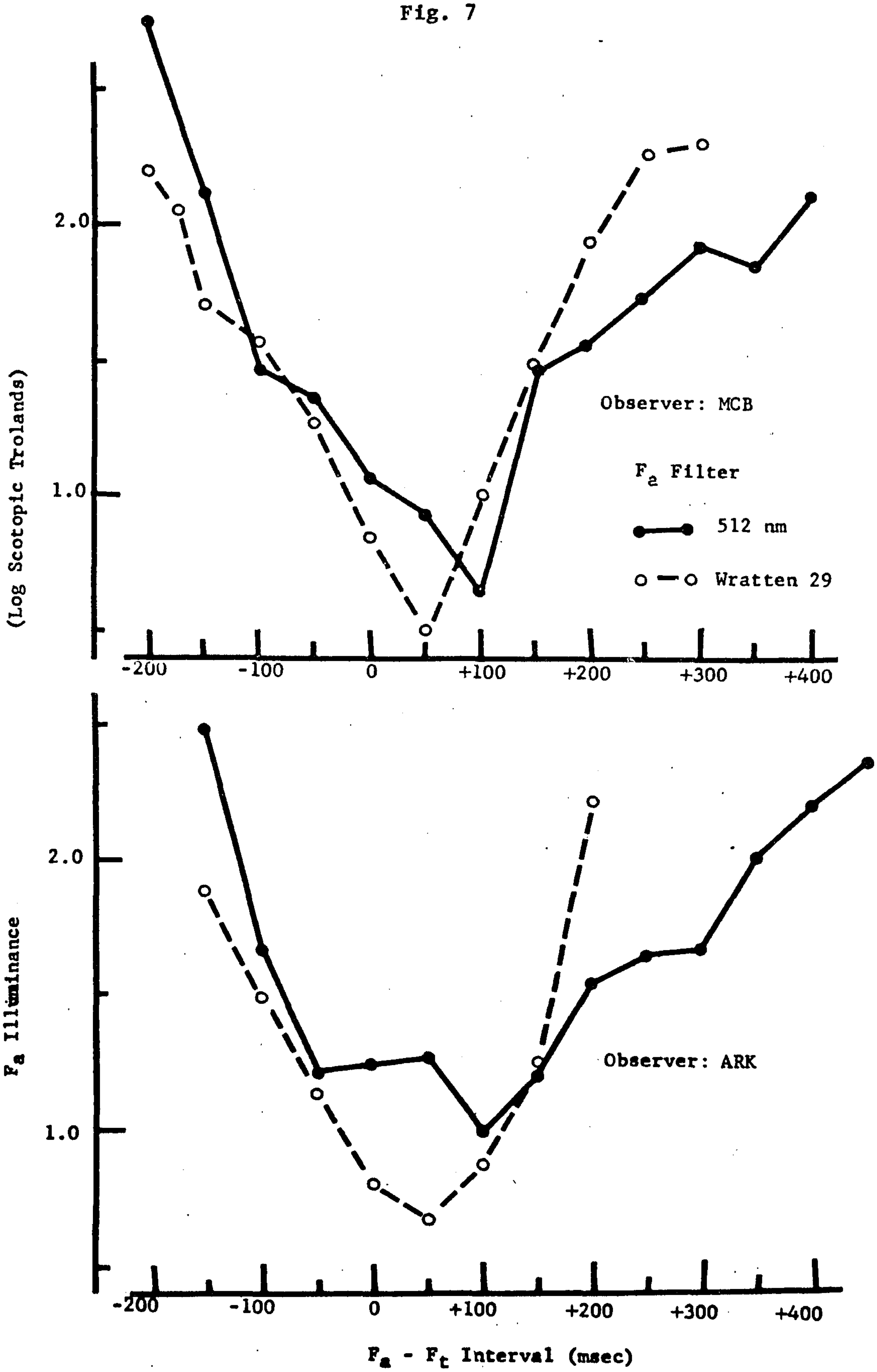
Experiment 2. In the second experiment, the observer adjusted the illuminance of a F_a until it masked a 512 nm wavelength F_t 0.5 log units above F_t threshold illuminance determined with no F_a present. The spectral composition of the F_a was determined by either a 512 nm wavelength or a Wratten 29 filter. Determinations were made at several F_a - F_t intervals with each filter.

Fig. 7 illustrates the F_a illuminance necessary to mask a 512 nm wavelength F_t 0.5 log units above F_t threshold illuminance with no F_a present as a function of F_a - F_t interval. Negative abscissa values indicate that the F_t onset precedes F_a onset, while positive abscissa values indicate that the F_a occurs first. One function was obtained with a 512 nm wavelength F_a, and the other function was obtained with a red-hued (Wratten 29 filter) F_a. The two sets of coordinates represent data obtained with two different observers. With both observers, the F_a illuminance necessary to mask the F_t first decreased, and then it increased as the F_a - F_t interval increased from negative to positive values.

The scotopic illuminance of the F_a indicates its influence on the scotopic system. If only the scotopic system influences the F_t threshold illuminance, the same U-shaped function should result, regardless of F_a wavelength. Fig. 7, however, indicates that the functions produced by the different wavelength F_as are dissimilar. Only at the -100, -50, and +150 msec F_a - F_t intervals do the different wavelength F_as have equivalent effects. The

Fig. 7. Results of Experiment 2. The F_a illuminance required to mask a F_t raised 0.5 log units above absolute threshold as a function of F_a - F_t interval for two observers. Closed circles and solid lines indicate the function obtained when the F_a wavelength is governed by a 512 nm wavelength filter, and open circles and broken lines indicate the function obtained when the F_a wavelength is governed by a Wratten 29 filter. The functions on the upper set of coordinates were obtained with observer MCB, and the functions on the lower set of coordinates indicate the functions obtained with observer ARK.

Fig. 7


2.0
1.0
-200
-100
0
+100
+200
+300
+400
Observer: MCB
F_a Filter
512 nm
Wratten 29
2.0
1.0
-200
-100
0
+100
+200
+300
+400
Observer: ARK
F_a Illuminance (Log Scotopic Trolands)
F_a - F_t Interval (msec)

functions obtained with the 512 nm wavelength filters differ unsystematically at the 0, +50, and +100 msec F_a - F_t intervals between the two observers. However, certain trends are still apparent. In general, the red-hued (Wratten 29 filter) F_a produces a function which is displaced towards more negative intervals than the function produced by the 512 nm wavelength F_a. The minima of these two functions are at the +50 and +100 msec F_a - F_t intervals respectively. Unreported data collected early during this study showed that F_a - F_t intervals spaced at 25 msec intervals conformed to the expected U-shaped function. Consequently, intervals more closely spaced than 50 msec appear unnecessary to acheive greater resolution in the function.

The effect of the F_a upon the scotopic system alone does not adequately explain the difference in F_t threshold illuminance at every F_a - F_t interval. To the extent that F_t threshold illuminance is mediated by the photopic system, these temporal shifts probably indicate scotopic-photopic interaction. The third experiment provides evidence that the scotopic system detected the F_t, regardless of the F_a - F_t interval and F_a wavelength.

Experiment 3. The third experiment is conceptually related to the second experiment in the following manner. At the -150, 0, and +150 msec F_a - F_t intervals, a determination was made of the illuminance value of either a 512 nm wavelength or red-hued (Wratten 29 filter) F_a that masked a 512 nm wavelength F_t $\bar{1}.9$ log scotopic trolands in illuminance. This illuminance was

0.5 log units above the average F_t threshold illuminance with no F_a present. Subsequently, F_ts of several different wavelengths were introduced while the F_a was maintained at the previously-determined illuminance level. The F_t threshold log relative quanta values were determined by adjusting the F_t log relative quanta until the F_t was no longer detected. The methods chapter describes the actual procedure, which was somewhat different from this conceptual description.

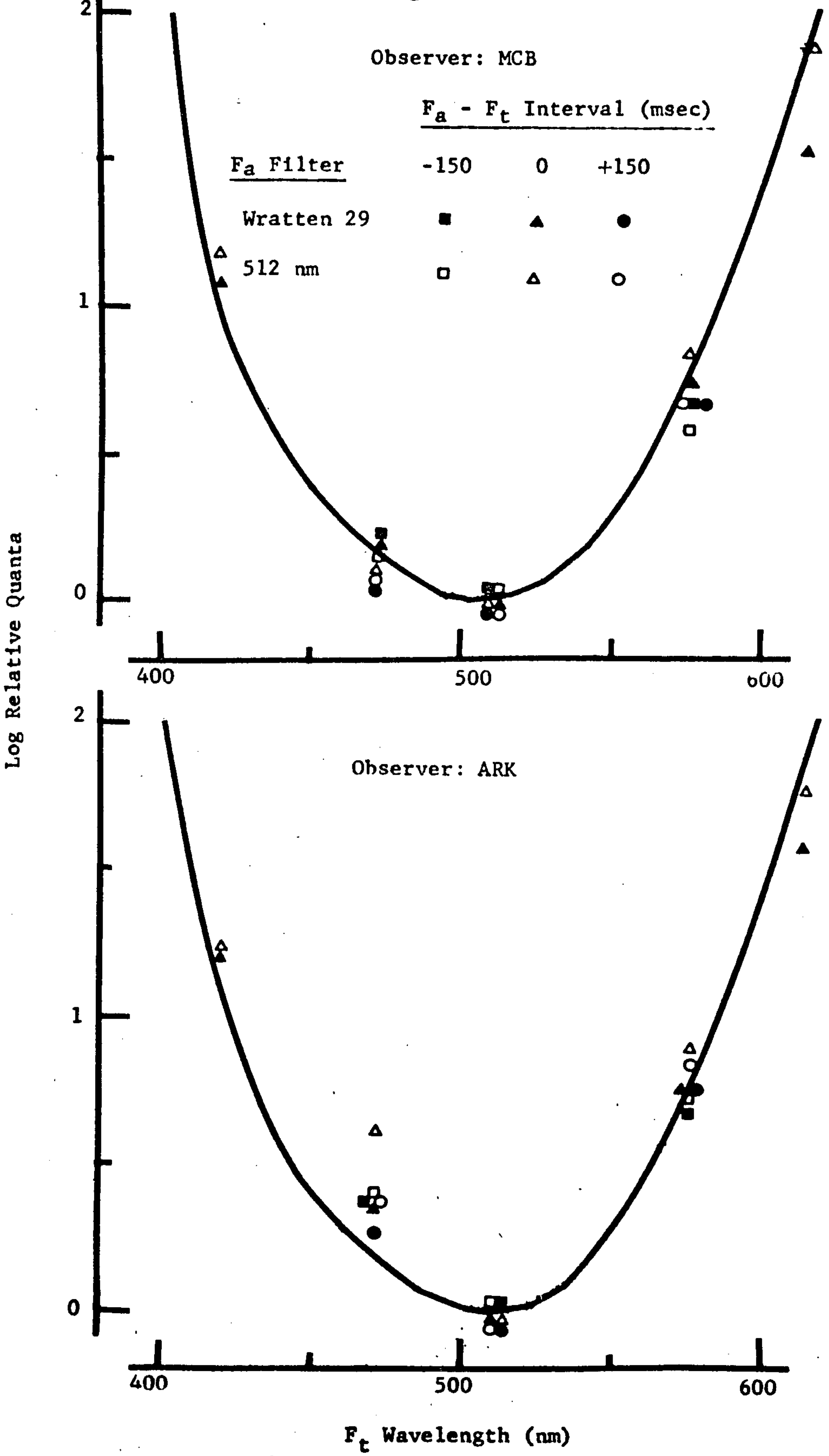
Fig. 8 shows F_t threshold log relative quanta as a function of F_t wavelength with F_a - F_t interval and F_a wavelength as parameters. For purposes of comparison, the plotted function is the C.I.E. scotopic luminosity function corrected for quanta (Wyszecki and Stiles, 1967, pp 378-383). The vertical position of each of the six sets of data points and the C.I.E. function was shifted vertically until their minima corresponded. This was the only curve-fitting manipulation.

Clearly, the six sets of data points do not deviate significantly from the data of the C.I.E. scotopic observer corrected for quanta. This finding strongly suggests that the F_t at threshold illuminance is detected by the scotopic system regardless of the F_a wavelength and F_a - F_t interval. The fourth experiment indicates the type of receptors stimulated by the F_a that is influencing the scotopic F_t threshold.

Experiment 4. The fourth experiment is conceptually related to the second experiment in the following manner. A 512 nm

Fig. 8. Results of Experiment 3. Log relative quanta of a F_t required to be masked by an F_a of an illuminance that masks a 512 nm wavelength F_t raised 0.5 log units above its absolute threshold as a function of F_t wavelength. Closed symbols indicate that the F_a wavelength is controlled by a Wratten 29 filter. Open symbols indicate that the F_a wavelength is controlled by a 512 nm wavelength filter. Squares indicate that the F_a - F_t interval is -150 msec, triangles indicate that the interval is 0 msec, and circles indicate that the interval is +150 msec. The solid line is the C.I.E. scotopic luminosity function corrected for quanta from Wyszecki and Stiles (1967, pp 378-383). The upper set of coordinates presents data obtained with observer MCB, and the lower set of coordinates presents data obtained with observer ARK.

Fig. 8


Observer: MCB
Fa - Ft Interval (msec)
Fa Filter
-150
0
+150
Wratten 29 ■ ▲ ●
512 nm □ △ ○
Observer: ARK
Log Relative Quanta
2
1
0
400
500
600
Ft Wavelength (nm)

wavelength F_t was presented at the same illuminance in both experiments. At the -150, -50, +100, and +200 msec F_a - F_t intervals, the log relative quanta of a variable wavelength F_a necessary to mask the F_t was determined.

Figs. 9 and 10 show the log relative quanta required to mask the F_t as a function of F_a wavelength. Each set of coordinates displays the results obtained at the indicated F_a - F_t interval with both observers. The solid and broken curves represent the C.I.E. scotopic and photopic luminosity functions respectively corrected for quanta (Wyszecki and Stiles, 1967, pp 378-383). The vertical position of each set of data points and the C.I.E. functions was shifted vertically until their minima corresponded. This was the only curve-fitting manipulation.

Fig. 11 shows the deviation of data points from the scotopic luminosity function corrected for quanta as a function of wavelength. Each set of coordinates displays the results obtained at the indicated F_a - F_t interval with both observers. This display emphasizes the deviations more than Figs. 9 and 10.

With a +100 msec F_a - F_t interval (Fig. 9 lower, Fig. 11 upper right), the data points generally correspond to the C.I.E. scotopic function. At this interval, it is reasonable to conclude that the scotopic system alone is influencing the F_t threshold illuminance. At the +200 msec F_a - F_t interval (Fig. 9 upper, Fig. 11 upper left), the data points do not correspond well to the scotopic luminosity function. At both the -50 (Fig. 10 upper, Fig. 11 lower left) and -150 (Fig. 10 lower, Fig. 11 lower right)

Fig. 9. Results of Experiment 4. Log relative quanta of an F_a required to mask a 512 nm wavelength F_t raised 0.5 log units above its absolute threshold as a function of F_a wavelength at positive F_a - F_t intervals. Closed circles indicate data obtained with observer MCB, while open circles indicate data obtained with observer ARK. The solid line indicates the C.I.E. scotopic luminosity function corrected for quanta, and the broken line indicates the C.I.E. photopic luminosity function corrected for quanta (Wyszecki & Stiles, 1967, pp 378-383). The upper set of coordinates presents data obtained when the F_a - F_t interval is +200 msec, and the lower set of coordinates presents data obtained when the F_a - F_t interval is +100 msec.

Fig. 9

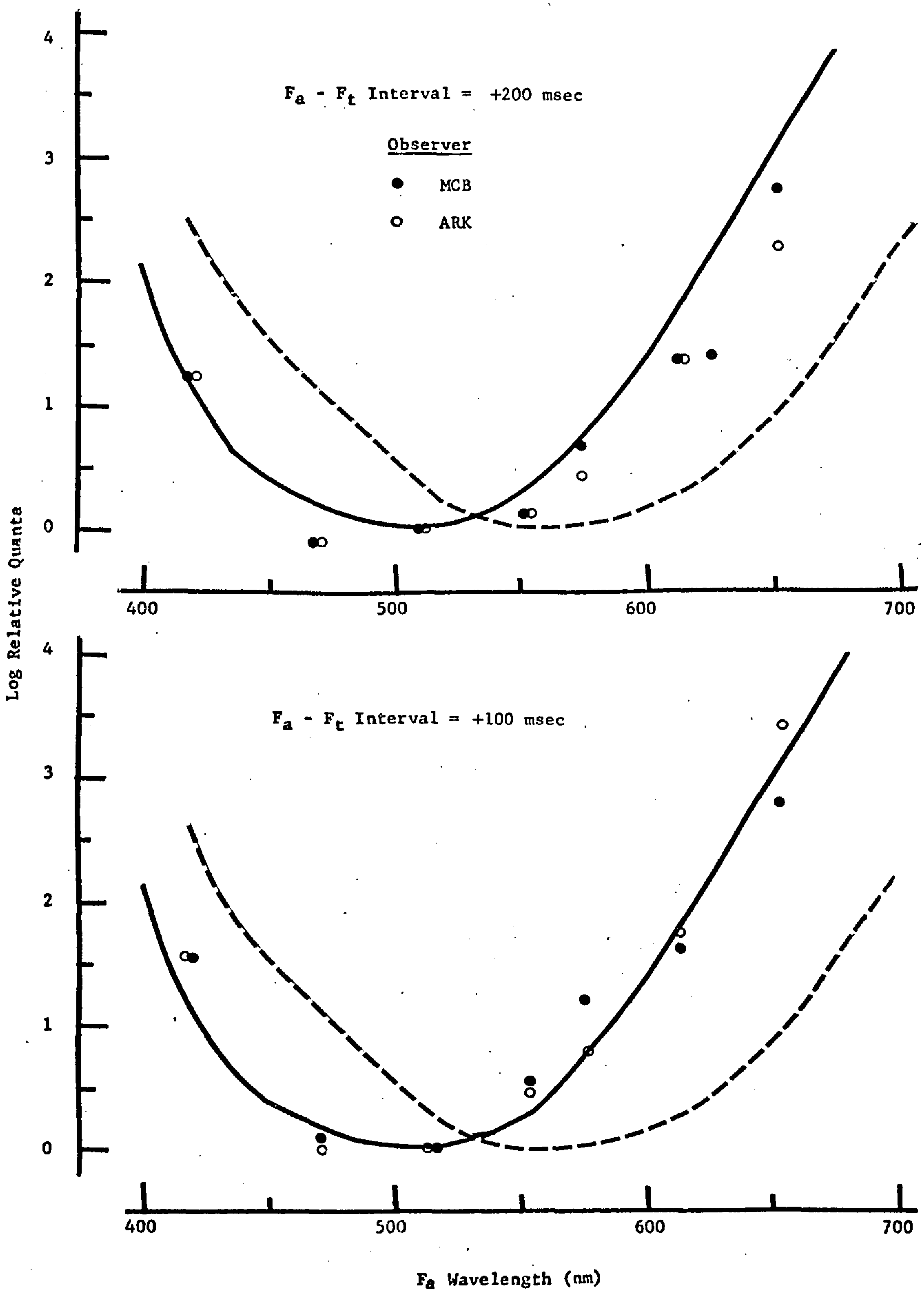

F_a - F_t Interval = +200 msec
Observer
● MCB
○ ARK
F_a - F_t Interval = +100 msec
Log Relative Quanta
0
1
2
3
4
400
500
600
700
F_a Wavelength (nm)

Fig. 10. Results of Experiment 4. Log relative quanta of an F_a required to mask a 512 nm wavelength F_t raised 0.5 log units above its absolute threshold as a function of F_a wavelength at negative F_a - F_t intervals. The upper set of coordinates presents data obtained when the F_a - F_t interval is -50 msec, and the lower set of coordinates presents data obtained when the F_a - F_t interval is -150 msec. See the legend of Fig. 9.

Fig. 10

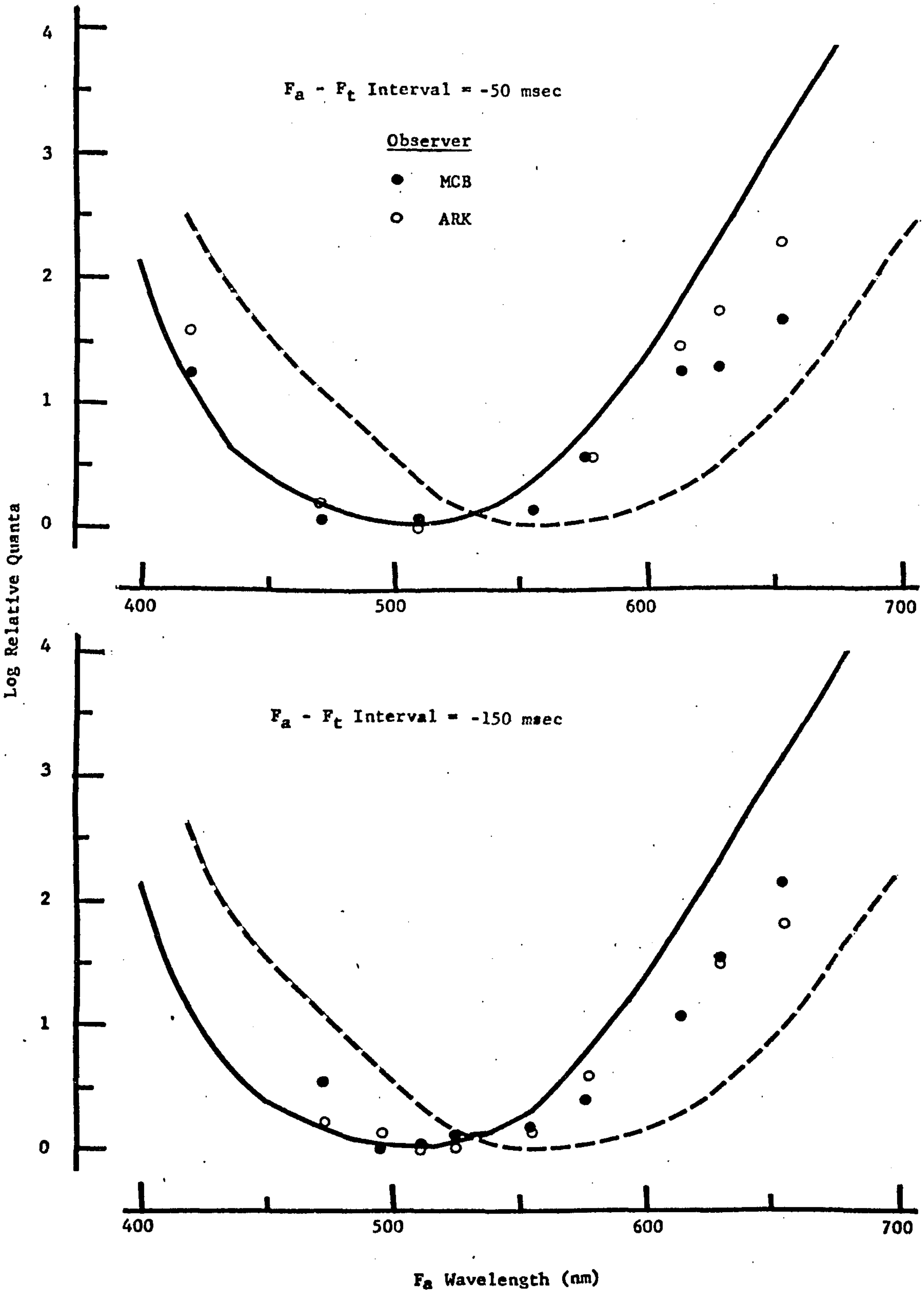
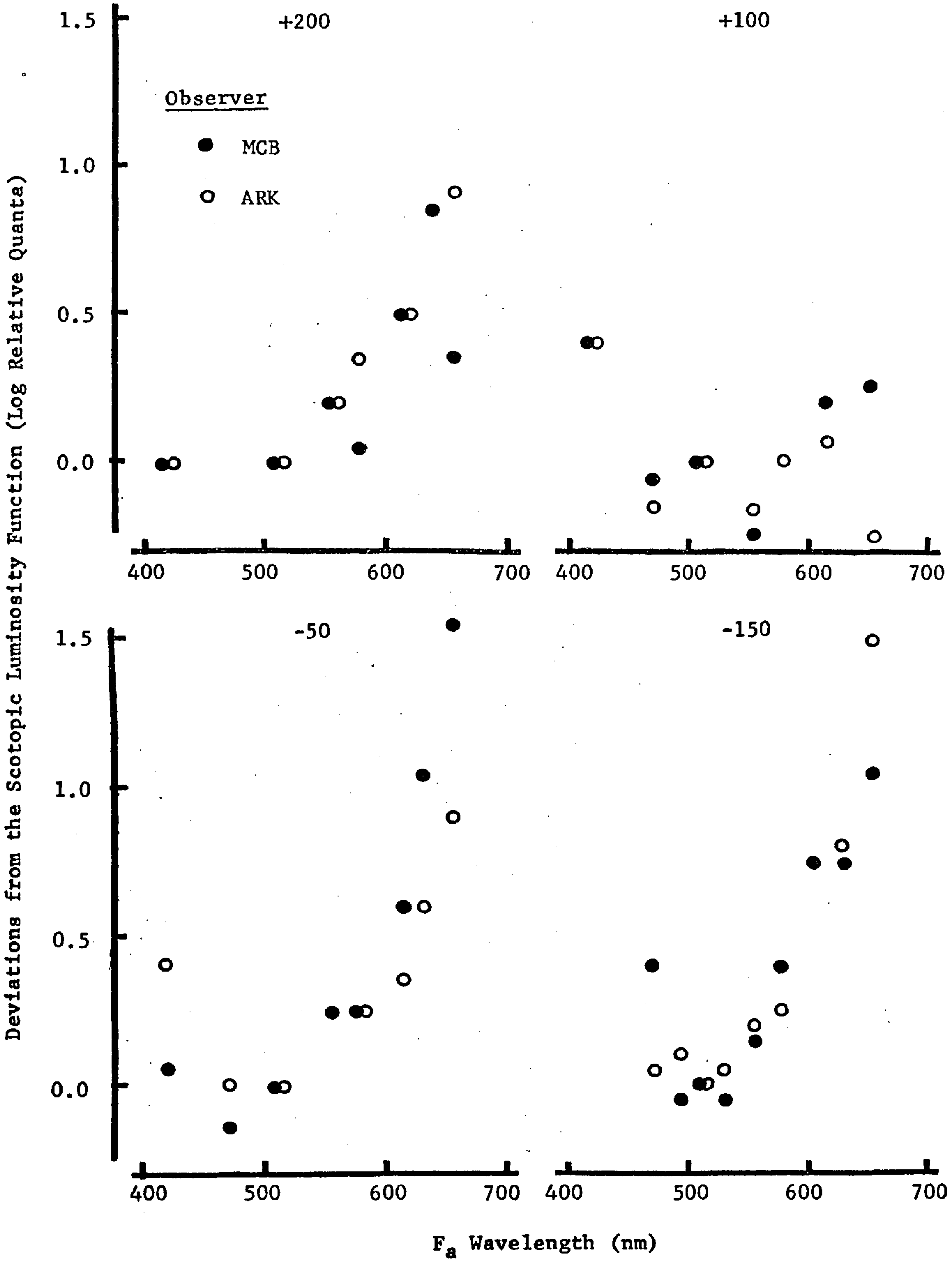

Fa - Ft Interval = -50 msec
Observer
● MCB
○ ARK
Fa - Ft Interval = -150 msec
Log Relative Quanta
0
1
2
3
4
400
500
600
700
Fa Wavelength (nm)

Fig. 11. Results of Experiment 4. Deviation of data points from the scotopic luminosity function corrected for quanta as a function of wavelength. Deviations for the +200 msec $F_a - F_t$ interval are plotted on the upper left set of coordinates, the +100 msec interval on the upper right set, the -50 msec interval on the lower left set, and the -150 msec interval on the lower right set. On each set of coordinates, observer MCB is represented by the closed circles and observer ARK by the open circles.

Fig. 11


+200
+100
-50
-150
Observer
● MCB
○ ARK
Deviations from the Scotopic Luminosity Function (Log Relative Quanta)
1.5
1.0
0.5
0.0
400
500
600
700
F_a Wavelength (nm)

msec $F_a - F_t$ intervals, close correspondence between the data points and the scotopic function corrected for quanta applies only for F_a wavelengths less than 512 nm. As the F_a wavelength increases, the F_a log relative quanta required to mask the F_t is considerably less than that predicted by the scotopic function while becoming closer to the photopic function. These data indicate that both the scotopic and photopic systems are influencing F_t threshold illuminance at the -50 and -150 msec $F_a - F_t$ intervals.

Chapter 6

Discussion

The first and second experiments of this study show that the influence of the adapting flash (F_a) on test flash (F_t) threshold is highly dependent on temporal onset interval between the F_a and F_t (F_a - F_t interval). The F_a is generally most effective in masking the F_t threshold when it precedes the F_t (Experiment 2) or perhaps when the stimuli are simultaneous in onset (Experiment 1). The effectiveness of the masking decreases as the F_a - F_t interval becomes longer. These findings are consistent with most metacontrast and paracontrast studies where the F_t threshold is the dependent variable (e.g., see Kahneman, 1968; Weisstein, 1972; Lefton, 1973; Matin, 1975; and Breitmeyer & Ganz, 1976). Furthermore, the first and second experiments show that the scotopic illuminance of the F_a required to mask a F_t is dependent on F_a wavelength. For example, Fig. 7 shows that flashes of the same scotopic illuminance but different wavelength are equivalent in their influence on F_t threshold at only three intervals. At intervals where the F_t precedes the F_a by more than 100 msec, the scotopic illuminance required to produce a given effect by the red-hued F_a is less than that of the 512 nm wavelength F_a. When the F_t follows the F_a by 150 msec or more, the scotopic illuminance required to produce a given effect by a red-hued F_a is more than that required by the 512 nm wavelength F_a. These results confirm other studies using metacontrast and paracontrast paradigms (Ingling, 1972;

Foster, 1976) or the Crawford (1947) adaptation paradigm (Frumkes et al., 1972, 1973). To the extent that the F_t is detected by the scotopic system alone in the first and second experiments, these results indicate a photopic influence on the scotopically-mediated threshold.

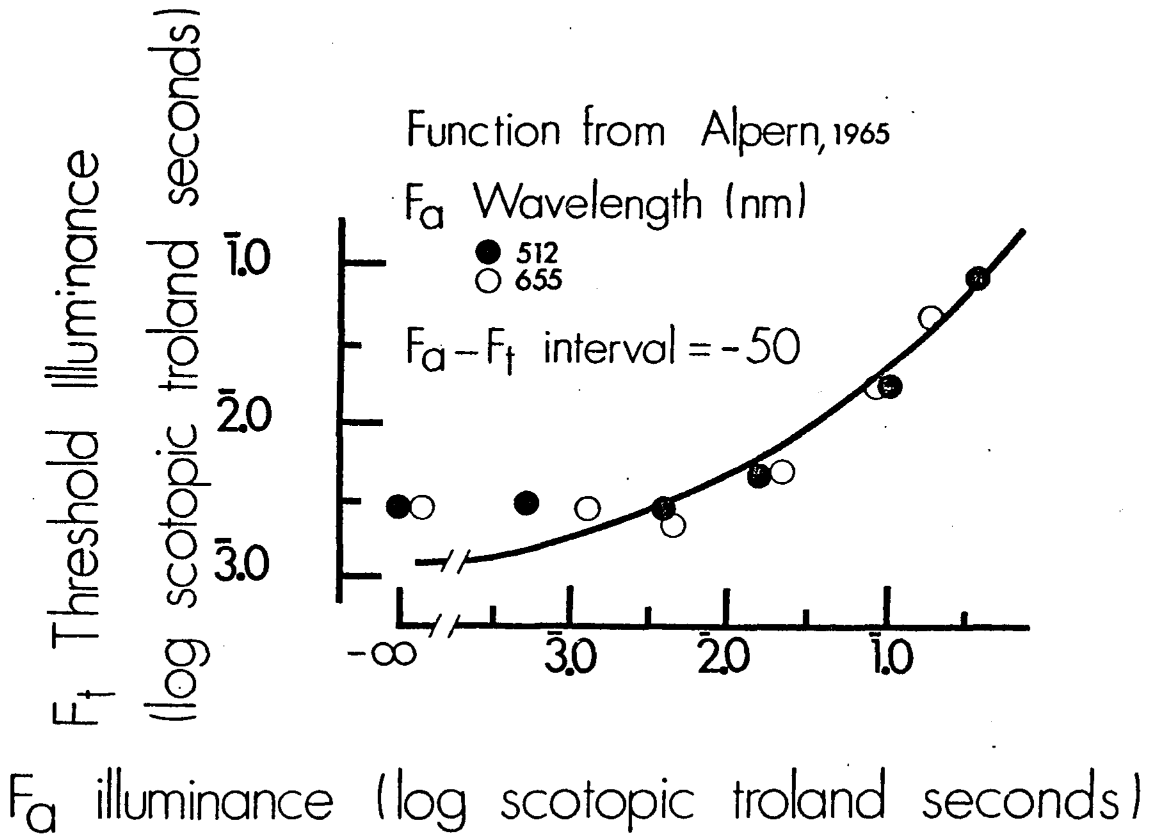
In order to interpret these data, it is important to consider whether the scotopic or photopic system is mediating the F_t threshold. In the first experiment, the only evidence of exclusive scotopic mediation of the F_t threshold is that the F_t was always within 1.5 log units of absolute threshold. Furthermore, it always appeared hueless to both observers. Therefore, given the classic spectral sensitivity data (Hecht & Hsia, 1945; Wald, 1945), the F_t is apparently mediated by the scotopic system alone. In the second and fourth experiments, however, the evidence for scotopic mediation of F_t threshold is much more compelling. First, the F_t was presented at a constant illuminance, which was 0.5 log units above absolute threshold. Second, the third experiment showed F_t threshold log relative quanta was always predictable from the scotopic luminosity function corrected for quanta regardless of the stimulus wavelength and F_a - F_t interval. Therefore, F_t threshold is certainly mediated by only the scotopic system in the second and fourth experiments.

Since F_t threshold is mediated by the scotopic system alone in the second experiment, and assuming that the illuminance calibration was correct, the influence of the F_a on the F_t threshold cannot be attributed solely to the scotopic system. If only the scotopic system influenced F_t threshold, the same scotopic illuminance would be required to mask the F_t regardless of F_a wavelength. This is obviously not the case. Moreover, a calibration error could not explain the data of the second experiment in terms of strict independence between the scotopic and photopic systems. If the scotopic system alone was influencing F_t threshold, the same masking function should be obtained, regardless of F_a wavelength. A calibration error would merely displace the different wavelength functions vertically with respect to each other. However, the second experiment clearly shows that the entire function was shifted in time as a function of F_a wavelength. In addition, there is a suggestion of a difference in shape between the two functions. That is, at $F_a - F_t$ intervals greater than +100, the limb of the function obtained with the 512 nm wavelength F_a was depressed with respect to the other function. Finally, the action spectra of the fourth experiment clearly show that the scotopic system alone cannot be influencing F_t threshold since an action spectrum of the fourth experiment clearly shows that an action spectrum much broader than the scotopic luminosity function corrected for quanta is obtained at negative $F_a - F_t$ intervals.

The present results apparently contradict those of Alpern (1965), but, in fact, they merely contradict his conclusions. Fig. 12 replots the data of Fig. 5 obtained at the -50 msec $F_a - F_t$ interval for observer MCB along with the empirical curve describing the data of Alpern (1965). The data points are the

Fig. 12. The F_t threshold illuminance in log scotopic troland seconds as a function of the illuminance in log scotopic troland seconds of F_as either 512 (closed circles) or 655 (open circles) nm in wavelength. The F_a - F_t interval is -50 msec, and the observer is MCB. One part of Fig. 5 presents the same data in terms of log scotopic trolands. The data is presented here in terms of log scotopic troland seconds to facilitate comparison with the function reported by Alpern (1965), which is represented by the solid curve. The increment threshold calibration procedure described on p 43 provided the basis for plotting the data of the present figure.

Fig. 12


Function from Alpern, 1965
F_a Wavelength (nm)
● 512
○ 655
$F_a - F_t$ interval = -50
$\bar{1}.0$
$\bar{2}.0$
$\bar{3}.0$
F_t Threshold Illuminance
(log scotopic troland seconds)
$-\infty$
$\bar{3}.0$
$\bar{2}.0$
$\bar{1}.0$
F_a illuminance (log scotopic troland seconds)

same in both Fig. 5 and Fig. 12. However, they appear different for three reasons. First, the function is considerably enlarged in Fig. 12. Second, the calibration used in plotting these data is based solely on the increment threshold technique described on p 43. The brightness matching and absolute threshold techniques described in the methods chapter were not used at all. This was done to conform with the procedure used by Alpern (1965). Third, the ordinate and abscissa values of Fig. 12 are plotted in log scotopic troland seconds to conform to the technique of Alpern (1965). The present data are consistent with those of Alpern (1965), despite the fact that the experiment was done with stimuli of a different shape and with a different observer.

The time course of contrast flash interaction. The results of the second and fourth experiments show that, at negative and short positive F_a - F_t intervals, the red-hued F_as are generally more effective in influencing F_t thresholds than the 512 nm wavelength F_a. As originally proposed by Frumkes et al. (1972) and later adopted by other investigators (Ingling, 1972; Frumkes et al., 1973; Foster, 1976), well-known latency differences between the scotopic and photopic systems easily explain this effect. These investigators assume that maximal interaction occurs when the neural signals originating from the F_a and F_t are at some fixed temporal relationship. As the neural signals become separated by increasing intervals, the masking effect decreases systematically. If both flashes stimulate only the scotopic system, a U-shaped function with its minimum centered at a 0 msec

$F_a - F_t$ interval should occur. A U-shaped function with its minimum centered at a negative $F_a - F_t$ interval should be obtained when the F_a stimulates both the scotopic system and the shorter-latency photopic system; specifically, more masking should occur at negative $F_a - F_t$ intervals. In fact, the data of the second experiment show that the red-hued F_a, which undoubtably influences the photopic as well as the scotopic system, is a more effective masking stimulus than the 512 nm wavelength F_a at the negative and short positive intervals. However, there are several flaws in such a latency difference hypothesis. First, the minimum of the function obtained when both flashes stimulate the scotopic system occurs at the +100 msec $F_a - F_t$ interval rather than the 0 msec interval, as predicted by the model. This additional latency might be attributed to a slow inhibitory signal generated by the annular surround. Second, if the different wavelength F_as of the second experiment are properly equated for scotopic illuminance, it would be difficult to explain why the red-hued F_a would ever be less effective than the 512 nm wavelength F_a in influencing F_t threshold. Yet the data of the second experiment clearly show (and the data for the +200 msec interval of Fig. 9 upper suggest) that the red-hued F_a is less effective than the 512 nm wavelength F_a in masking the F_t at intervals where the F_a precedes the F_t by 200 msec or more. Although no explanation is apparent, both observers noted at these intervals that the 512 nm wavelength F_a produced a definite and prolonged positive afterimage and the red-hued F_a did not. Whatever mechanism is responsible for the afterimage might account for this finding.

Mechanisms for scotopic-photopic interaction in the contrast flash situation. There are two general means by which the cones (or the photopic system) stimulated by the red-hued F_a could influence the rod- (or scotopic system) mediated F_t threshold. On the one hand, the data could be interpreted in terms of scotopic-photopic summation. That is, when the photopic system is stimulated by the F_a, it may summate with the scotopic system activity stimulated by the same F_a. This summed effect of the two systems would inhibit the scotopic system activity stimulated by the F_t.

On the other hand, this data could be interpreted in terms of scotopic-photopic inhibition. That is, when the photopic system is stimulated by the F_a, it may inhibit the scotopic system activity stimulated by the F_t.

At this time, it is difficult to discern which of these two possibilities describes the actual situation, since the mechanism of metacontrast and paracontrast is unknown. Alpern (1965) and Alpern and Rushton (1965, 1967) try to account for metacontrast in terms of purely retinal interactions. However, most metacontrast phenomena can be obtained both monocularly and dichoptically, suggesting that cortical interactions are occurring (for one review, see Ganz, 1975).

Before proposing a more detailed model, determination of whether the scotopic-photopic interaction reported here is retinal or cortical in origin would be valuable. A logical extension of the present study would modify the second experiment by presenting the F_t to one eye and the F_a to the other eye. If red-hued and 512 nm wavelength F_as are not equivalent in their influence on the F_t under these dichoptic conditions, this would suggest that the present scotopic-photopic interactions are cortical in origin. If the masking functions obtained with both wavelength F_as are identical, this would suggest that the scotopic-photopic interactions reported in this study are retinal in origin. Without further experimentation, the mechanisms underlying the photopic-scotopic interactions observed in this study remain obscure.

Chapter 7

Summary and Conclusions

The interrelationship between the scotopic and photopic systems was investigated in a series of metacontrast and paracontrast experiments. A Maxwellian view optical system was used to present all stimuli to three dark-adapted observers. A 2° diameter, 10-msec duration test flash (F_t) was presented at 7° on the horizontal meridian in the temporal visual field of the right eye. A 10-msec annular adapting flash (F_a) which had a 2° inner diameter and a 10° outer diameter was presented concentrically with the F_t. The temporal interval between the onsets of the stimuli (F_a - F_t interval) and the wavelength and illuminance of the flashes were systematically varied in the various phases of the study. (A negative F_a - F_t interval indicates that the F_t precedes the F_a; a positive interval indicates the opposite.)

In Experiment 1, the threshold of a 512 nm wavelength F_t was determined as a function of the scotopic illuminance of either a 512 nm or 655 nm wavelength F_a. With both F_as, the F_t threshold monotonically increased as the scotopic illuminance increased, regardless of the F_a - F_t interval. However, at certain F_a - F_t intervals, the scotopic illuminance of the F_a alone determined F_t threshold. At different F_a - F_t intervals, the 655 nm wavelength F_a was either more or less effective than the 512 nm wavelength F_a. These results are impossible to reconcile with the concept that only one type of receptor stimulated by the F_a is influencing F_t threshold.

In Experiment 2, a F_t 512 nm in wavelength was presented at a fixed illuminance of $\bar{1}.9$ log scotopic trolands (0.5 log units above absolute threshold). Because of its wavelength and illuminance, it was assumed to be detected solely by the scotopic system. The illuminance of either a 512 nm wavelength or a red-hued (Wratten 29 filter) F_a which masked the F_t was determined at many F_a - F_t intervals. Regardless of F_a wavelength, the F_a illuminance necessary to mask the F_t first decreased, and then increased as the F_a - F_t interval became longer. In general, however, the red-hued F_a was more effective in masking the F_t at negative F_a - F_t intervals, while the 512 nm wavelength F_a was more effective at positive F_a - F_t intervals. Only at the -100, -50, and +150 msec F_a - F_t intervals were the two different F_as equal in their effect on the F_t.

Experiment 3 was performed in order to ascertain that the scotopic system alone was detecting the F_t in Experiment 2. The illuminance of two F_as of different wavelength that masked the F_t was determined at three F_a - F_t intervals. With these six different conditions (three intervals at two F_a wavelengths), the threshold log relative quanta of a variable wavelength F_t was determined in the presence of the F_a. In all cases, the F_t log relative quanta described the sensitivity of the C.I.E. scotopic observer corrected for quanta. Therefore, in Experiment 2, the F_t must always be detected by the scotopic system.

In Experiment 4, a F_t, 512 nm in wavelength, was again presented at a fixed illuminance of $\bar{1}.9$ log scotopic trolands (0.5 log units above absolute threshold). The log relative quanta of a variable wavelength F_a which masked the F_t was determined at four F_a - F_t intervals. When the F_a preceded the F_t by 100 or 200 msec, the log relative quanta of the F_a necessary to mask the F_t was predictable by considering the F_a sensitivity to only the scotopic system. When the F_t preceded the F_a by 50 or 150 msec, however, the sensitivity of the scotopic system alone did not predict the log relative quanta of the F_a necessary to mask the F_t. With the red-hued F_as, the log relative quanta necessary to mask the F_t was considerably less than that predicted by scotopic sensitivity.

The results of these experiments show that, in metacontrast and paracontrast situations in which a F_t is detected only by the scotopic system, the type of receptor which influences F_t threshold is determined by the F_a - F_t interval. If the F_a precedes the F_t, the influence of the F_a on the scotopic system alone determines F_t threshold. These results are related to the difference in latency between the scotopic and photopic systems.

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