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THE TIME COURSE OF TEMPORAL SUMMATION AT VARIOUS BACKGROUND LUMINANCES

City University of New York PH.D. 1981

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THE TIME COURSE OF TEMPORAL SUMMATION AT VARIOUS BACKGROUND LUMINANCES

by

PRERNA M. SHAH

A dissertation submitted to the Graduate
Faculty in Psychology in partial fulfillment
of the requirements for the degree of
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of New York.

1981

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.

4/22/81
date

Mitchell L. Kietzman
Chairman of Examining Committee

4/29/81
date

Martin L. Hoffman
Executive Officer

Dr. William S. Battersby

Dr. Thomas E. Frumkes

Dr. Barbara J. Gillam

Dr. Harold Schuckman
Supervisory Committee

The City University of New York

Abstract

THE TIME COURSE OF TEMPORAL SUMMATION AT VARIOUS BACKGROUND LUMINANCES

by

Prerna M. Shah

Adviser: Professor Mitchell L. Kietzman

The present study evaluated changes in threshold luminance of a brief test flash superimposed spatially and temporally onto a subliminal conditioning flash. Parameters studied were background luminance, conditioning-flash duration and delay between the onsets of the conditioning and test flashes. The common purpose was to investigate excitatory effects within the visual system that were created by the subliminal conditioning flash, evaluated at various times during its exposure.

A four-channel Maxwellian view optical system was used to present the conditioning and test flashes, superimposed at 6° 30' along the right horizontal meridian of the right eye. The test flash was a 30' circular target of 5 msec duration; the conditioning flash was a 30' circular target with a duration of either 10 msec, 20 msec, 40 msec or 80 msec. All four conditioning flashes were equated for their energy content. The conditioning flash and test flash were spatially superimposed onto a 40° adapting field of either -3.0 log mL, 0.0 log mL or 2.0 log mL luminance. The test flash was temporally superimposed at five different delays from the onset of the conditioning flash; the temporal delays were either 0%, 25%, 50%, 75% or 100% of the respective conditioning-flash duration. A descending method of adjustment was used to obtain all threshold measurements. Two observers were tested extensively.

The data were analyzed to display the magnitude and time course of temporal summation. The magnitude of temporal summation was the difference in the test-flash thresholds presented with and without the conditioning flash. The time course of temporal summation was the change in the magnitude of temporal summation at various onset delays between the test and conditioning flashes.

The results were: (1) Increased background luminance and conditioning-flash duration decreased the magnitude of temporal summation, particularly at the shortest and longest delay intervals. (2) Increased background luminance and conditioning-flash duration also altered the time course of temporal summation such that lower background luminances and shorter conditioning flashes produced a flat function, while higher background luminances and longer conditioning flashes produced a non-monotonic function. (3) The non-monotonic function obtained at higher background luminances and longer conditioning flashes was symmetrical and "U"-shaped; maximum summation always occurred at the middle of the conditioning-flash duration (at 50% onset delay interval).

Results indicate that the temporal parameters of the visual system are altered by varying the level of adaptation. The neural mechanisms underlying the phenomenon of temporal summation and the effect of background luminance on temporal summation are discussed.

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Finally, I would like to thank my husband, Dr. Manoj R. Shah, for his moral support, understanding and patience.

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CHAPTER I

INTRODUCTION

The phenomenon of visual temporal summation, recognised since Bloch's report in 1885, is that the threshold sensation of a brief light stimulus depends on the total energy content of the stimulus, regardless of how that energy is distributed over time. With square-wave stimuli, summation means that the product of duration and luminance of a stimulus determine its effect up to a certain critical duration.[1] Beyond the critical duration, reciprocity between luminance and duration fails; however, a partial summation can still occur up to a utilization time. For stimuli with durations longer than utilization time, increasing the stimulus duration does not affect the visual response, and the response is a function of the level of stimulus luminance.

Visual temporal summation has been investigated for a number of different temporal waveforms (distribution of luminous flux with respect to time).

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[1] See page 7, Chapter II - RELATED LITERATURE - for an explanation of terminology.

An early study by Granit and Davis (1931) used a dual-flash technique in which two square-wave light flashes of equal duration were separated by various delay intervals of darkness. Assuming that there is some critical excitatory level in the visual system that must be reached before the observer can detect a flash, Granit and Davis measured the excitatory effect of the subliminal first flash (conditioning flash) by finding its influence upon the threshold of the second flash (test flash). In this technique, the onset of the conditioning flash is assumed to initiate excitation in the visual system which decays upon turning off the flash. The excitatory remainder of the conditioning flash, which is a sum total of excitatory and decay processes, is summated with the excitatory effect of the test flash. An increase in the delay between the onsets of the conditioning and test flashes reduces the available excitatory remainder of the conditioning flash because more of its excitation has decayed. As a result, at longer delay intervals, the energy of the test flash has to be increased for it to be detected. In effect, this two-flash technique investigates the excitability effect of the subliminal conditioning flash.

A variant of the dual-flash technique was used by

Battersby and Schuckman (1970) to study the magnitude and the time course of temporal summation. A brief test flash was superimposed onto a subliminal conditioning flash, during the exposure of the conditioning flash, at various delay intervals from its onset. The magnitude of temporal summation was measured as the difference between the threshold for the test flash presented alone and the threshold for the conditioning and test flashes presented together. The time course of temporal summation was measured as the change in the magnitude of summation at various delay intervals between conditioning-flash and test-flash onset. Battersby and Schuckman observed that as the conditioning-flash duration was increased, there was a gradual loss in temporal summation, which followed a definite time course. For longer conditioning flashes, temporal summation was maximum when the test flash was presented at the mid-duration of the conditioning flash, but was minimal at the earlier and later delay intervals. They postulated that there are two processes underlying this time course of temporal summation: first, an excitatory effect created by the onset of the conditioning flash and second, a decay of this excitatory effect, which either follows or overlaps the excitatory effect in time. A balance between these two processes is presumed to be determined by the conditioning-flash duration and its energy content.

Temporal summation has been shown to vary with numerous stimulus response characteristics and some organismic factors (see Chapter II - RELATED LITERATURE - for a complete review). A variation in the background luminance is also shown to influence temporal summation (for example, Barlow, 1958a; Biersdorf, 1955; van den Brink & Bouman, 1954; Graham & Kemp, 1938; Herrick, 1956; Roufs, 1972; Sperling & Jolliffe, 1965). The general finding is that an increase in the level of background luminance results in a decrease in the magnitude of temporal summation.

Although several psychophysical studies have demonstrated the effect of background luminance on the magnitude of temporal summation, there has been no attempt to study its effect on the time course of summation. There is growing evidence from electrophysiological studies that the level of background luminance alters the time course of excitation at the photoreceptor level (for example, Whitten & Brown, 1973). Since the excitation of photoreceptors is an essential condition for the excitation of the entire visual system, changes in the temporal parameters at the photoreceptor level might also have an effect behaviorally. A psychophysical investigation of the effect of background luminance on the time course of temporal summation would therefore be of great value.

The dual-flash technique used by Battersby and Schuckman is well suited for the investigation of the time course of temporal summation at various background luminances. It has certain advantages over the one used by Granit and Davis. First, it permits the investigation of the time course of both the excitatory and the decay effects of the conditioning flash, during the exposure of the conditioning flash. The effect of the background luminance on the postulated excitatory and decay processes can be investigated behaviorally, by determining the effect of background luminance on the magnitude and the time course of temporal summation at various conditioning flash - test flash onset delays. Secondly, this technique can be used to investigate the latency of the visual response. Frumkes, Sekuler, Barris, Reiss and Chalupa (1973) for instance, measured the time course of temporal summation for various conditioning-flash and test-flash wavelengths. They observed temporal shifts of the summation function, such that the delay interval associated with maximum summation varied, depending on the wavelengths of the conditioning-flash and the test-flash. The authors interpreted their results as a demonstration of the differences in latency responses of rods and cones. Alterations in the time course of temporal summation due to variation in the level of background luminance can also be interpreted to be due to the differences in latencies of rods and cones. This is based on the assumption that changes in the level of background luminance selectively stimulate rods and cones.

The purpose of the present study was to investigate the effect of background luminance on the magnitude and the time course of temporal summation by the dual-flash technique used by Battersby and Schuckman. Operationally, the magnitude of temporal summation was measured by the threshold luminance of the test flash in the dual-flash condition (subliminal conditioning flash + test flash), expressed as a percentage of the threshold luminance of the test flash in the single-flash condition (test flash alone). The time course of temporal summation was expressed by the changes in the magnitude of temporal summation at various conditioning flash - test flash onset delays, for several conditioning-flash durations. A detailed rationale of the study is presented in the next chapter (see page, 37).

CHAPTER II

RELATED LITERATURE

The Phenomenon of Temporal Summation

The Bunsen-Roscoe law of photochemistry states that the integral of luminous energy with respect to time determines the amount of a photochemical product. In 1885, Bloch first determined the applicability of the Bunsen-Roscoe law to the visual process by determining the threshold luminance of square-wave pulses of light of varying durations. For such a stimulus, the product of luminance (L) and duration (T) determines the total "luminous energy" of the stimulus.[2] Bloch's law states that the threshold of a brief flash of light is determined by the total energy content of the flash, as long as its duration does not exceed a certain critical duration.

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[2] Radiant energy corresponds to the product of the area, duration and radiance of the stimulus; luminous energy corresponds to the product of area, duration and luminance of the stimulus. Since in most psychophysical studies, including the present one, area is fixed, "energy" will be referred to as the product of luminance and duration.

Since that time, a large number of studies have investigated the extent of temporal summation in the visual system.[3] Figure 1 graphically illustrates typical results and enables us (see Kietzman, 1979) to introduce nomenclature used throughout the remainder of this presentation. The visual system completely summates the energy of light flash up to a critical duration (CD). Critical duration can be defined either as "initial critical duration" or "intercept critical duration". Initial critical duration is that stimulus duration beyond which there is a departure from complete summation. This is indicated in Figure 1 as the rise in the summation curve from zero slope. Intercept critical duration is indicated by the intercept obtained when the straight lines of complete summation (slope = 0) and no summation (slope = 1) are extended. Under some conditions, for stimulus flashes longer than critical duration, energy is only partially summated. Partial summation is indicated by the gradually rising curve. The longest duration of flash up to which partial summation occurs is known as the

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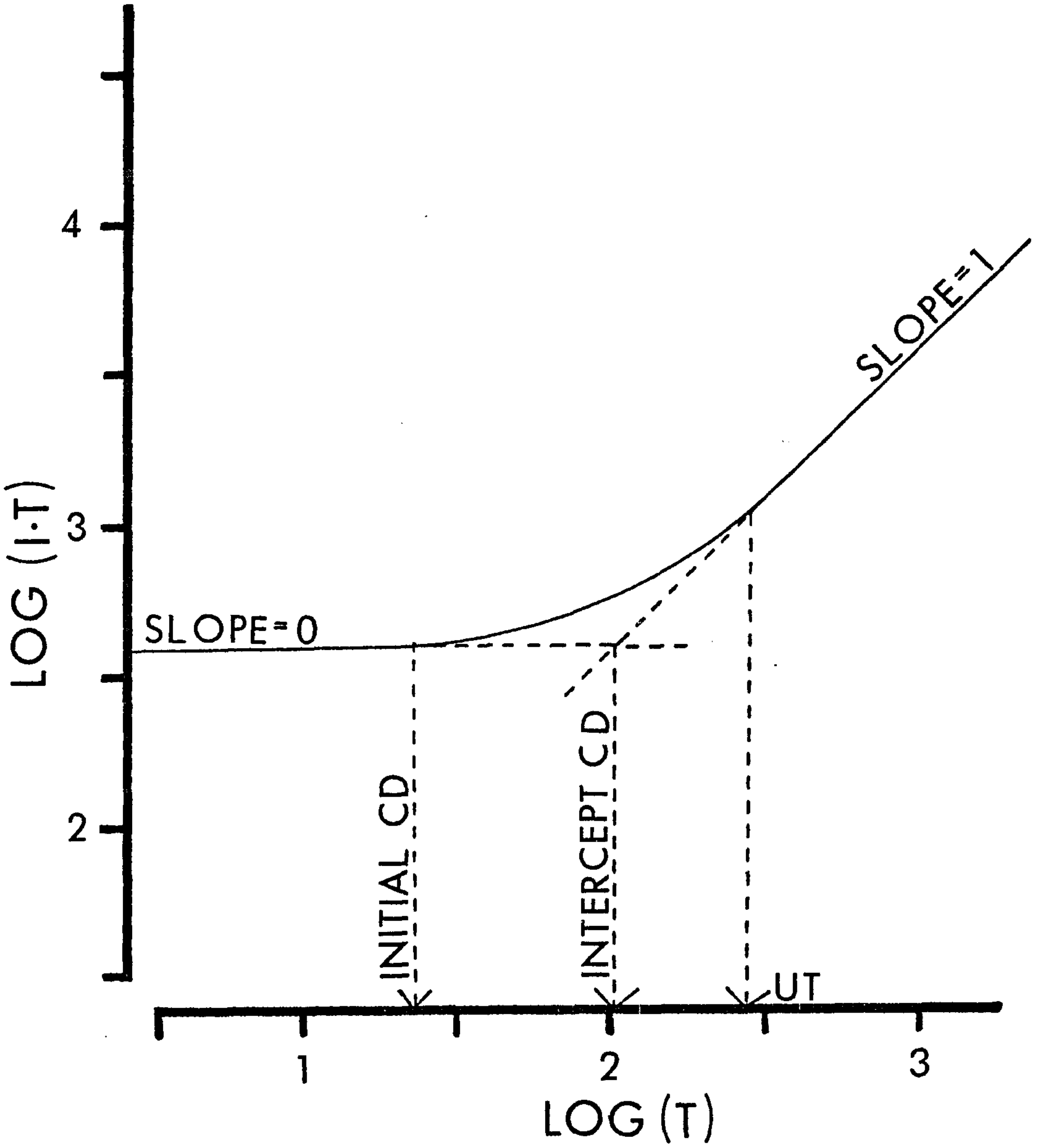
[3] In the literature, the terms temporal summation, temporal integration, luminance-duration reciprocity and intensity-time reciprocity have been used interchangeably.

Figure 1. An illustration of a single-flash temporal summation function. T = Stimulus duration. I = Luminance of the stimulus flash at threshold. I.T = Energy of the stimulus flash at threshold. CD = Critical duration. UT = Utilization time. The units of luminance and duration are arbitrarily selected.


LOG (I·T)
4
3
2
SLOPE=0
SLOPE=1
INITIAL CD
INTERCEPT CD
UT
1
2
3
LOG (T)

utilization time (after Pièron, 1952). With flashes longer than the utilization time, there is no further summation and threshold depends only on the luminance of the flash, which is demonstrated by a straight line of unit slope.

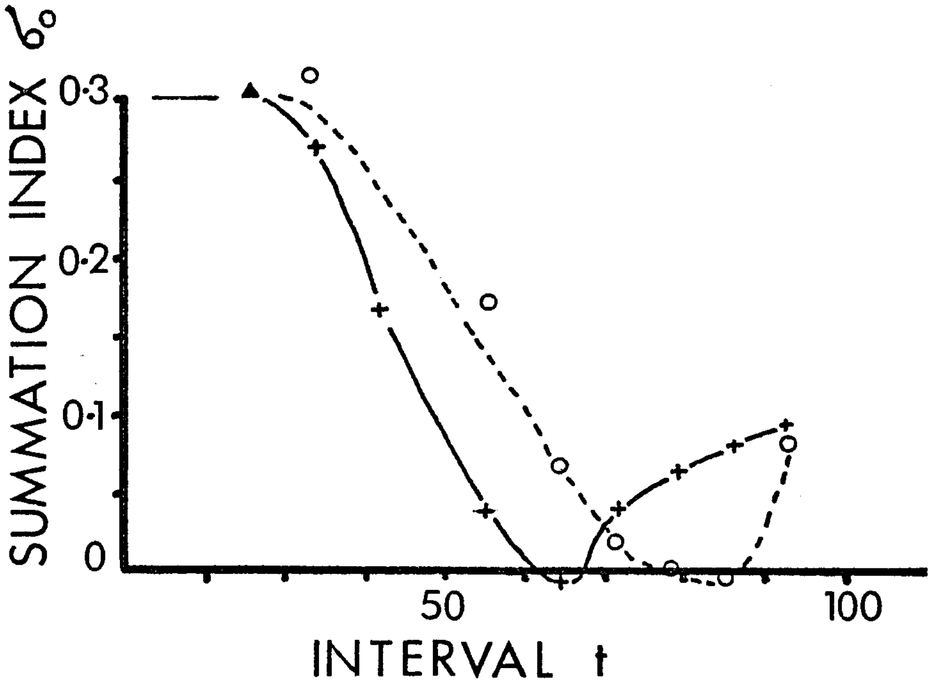
The region of partial summation is ignored by those investigators (for example, Biersdorf, 1955) who have measured intercept critical duration. Although critical duration is the upper limit of complete temporal summation, Bloch's law has not been shown to have a lower limit (Boynton, 1972). Beams (1935) investigated the lower limits of temporal summation and found that flashes as brief as 10^{-6} to 10^{-8} second were integrated. Gilmer (1937) also found complete summation of short flashes of 8×10^{-9} second duration.

The temporal summation function illustrated in Figure 1 has been obtained in many single-flash threshold studies (for example, Barlow, 1958a; Graham & Margaria, 1935; Karn, 1936; Sperling & Jolliffe, 1965). Temporal summation has also been studied using stimuli with temporal distributions other than square-waves. Long (1951) for instance, found that luminance-duration reciprocity was held for stimulus flashes of various waveforms. Davy (1952) studied temporal integration of flickering flashes. He varied the luminance and duration of the flashes but the cumulative energy of all flashes was held constant. Davy reported luminance-duration reciprocity for train durations of about 70 msec.

One fairly popular technique for studying temporal summation has been to employ two very brief (circa 5 msec) light flashes and vary the delay interval of darkness between them. Using such a paradigm for threshold response level, critical duration is defined as the total stimulus duration (onset of the first flash to the offset of the second flash) over which the threshold energy remains constant in order to obtain a constant level of responding. Beyond utilization time, response level is the same as for a single pulse, taking into account a correction for probability summation. This technique was initially employed by Granit and Davis (1931). They were influenced by the work of Eccles and Sherrington (1931) on the summation of successive subliminal stimuli in the spinal flexion reflex. In general, the temporal summation functions obtained with double-flash stimuli also show regions of complete summation, partial summation and no summation or probability summation (Battersby & Defabaugh, 1969; Bouman & van den Brink, 1952; Granit & Davis, 1931), but their absolute values may differ from those functions obtained for a single flash. Specifically, the critical duration for two flashes is briefer than the critical duration of a single flash (Berenhaus, 1980; Herrick, 1972; Roufs, 1973).

Other differences between temporal summation measured with double flashes have also been noted. For example, as shown in Figure 2, Ikeda (1965) found that temporal summation function contained regions of complete summation, partial summation, inhibition and probability summation. A summation index (σ) plotted on the ordinate is calculated by the following formula: $\sigma = 0.30 - \log(S_1 + S_2)$ where S_1 and S_2 are the threshold radiance of stimulus 1 and stimulus 2 respectively, when the two stimuli are combined, divided by the radiance of stimulus 1 and stimulus 2 respectively, when it is presented alone. A summation index value of 0.3 indicates complete summation, of 0.1 indicates probability summation, and a summation index value of less than 0.1 indicates inhibition. Prior to Ikeda's study, Clark and Blackwell (1958) also reported inhibition between two temporally separated light flashes. These results show that visual temporal summation is a complex phenomenon and that there are certain differences in the way the visual system processes a light stimulus that is continuous as

Figure 2. Summation index curves as a function of inter-flash intervals for "++case" from Ikeda (1965). $\sigma_{\bullet}$ = Summation index. T = Interval. The curve with crosses was obtained at 328 Trolands background luminance and the curve with open circles was obtained at 61.2 Trolands background luminance.


SUMMATION INDEX σ_0
0·3
0·2
0·1
0
50
100
INTERVAL t

compared to one that is interrupted by a dark interval.

Temporal summation has been demonstrated for psychophysical and physiological measures of visual response under many different stimulating conditions. Several studies have reported a value of 100 msec as the critical duration. However, it is shown that although the general shape of the temporal summation curve is similar in most of the studies, the absolute values of critical duration, utilization time and the extent of the partial summation region varies with the stimulus conditions and the response measures used. Stimulus variables such as the size of the test stimulus (Barlow, 1958a; Graham & Margaria, 1953; Karn, 1936), its wavelength (Sperling & Jolliffe, 1965) and its retinal position (Barlow, 1958a; Baumgardt & Hillman, 1961; Sperling & Jolliffe, 1965) alter the value of critical duration. The nature of the perceptual task involved is also considered to be significant. van den Brink (1957) found critical duration as high as 400 msec for the perception of movement. Kahneman and Norman (1964) reported critical duration to be about 100 msec for brightness discrimination but in the range of 200-350 msec for the task of identifying triads of digits. Bruder and Kietzman (1973) demonstrated that temporal summation also depends on the response measures used. For the same subjects, the critical duration for reaction time was shorter than the critical duration for measures of both response frequency and signal detectibility, with the critical duration for response frequency being longer than that for the signal detectibility. Organismic factors such as the age of the observer influence the value of critical duration (Eriksen, Hamlin & Brietmeyer, 1970).

Of primary importance in the present study is that background luminance has proved to be particularly important in affecting temporal summation (Barlow, 1958a; Graham & Kemp, 1938; Roufs, 1972; Stewart, 1972). However, before considering the specific influence of luminance on temporal summation, we must first consider the more general properties of visual adaptation.

The Mechanism of Visual Adaptation

The human observer is capable of seeing over a luminance range of thirteen log units (Riggs, 1971); yet under constant conditions of adaptation, electrophysiological studies show that the vertebrate visual system has a dynamic range of illuminance (that over which the response amplitude changes from 10% to 90% of maximum) of at most

2 or 3 log units. This apparent discrepency results from the fact that the dynamic range of operation over which the visual system operates changes as the prevailing level of illumination increases (light adaptation) or as the eye recovers from prior exposure to intense illumination (dark adaptation).

The mechanism underlying visual adaptation has been speculated on for at least one hundred years (see Pirenne, 1962). For example, as early as 1879, Kühne showed that light illumination reduces the concentration of visual purple in the retina. Taking such findings into consideration, Hecht and his colleagues conducted a systematic investigation of visual adaptation and the various factors that influence it, and developed a photochemical theory to explain the results (Hecht, 1934; Hecht, Haig & Wald, 1935; Hecht, Haig & Chase, 1937; Hecht & Hsia, 1945). According to this theory, light bleaches the available photopigments in the visual receptors. A decrease in sensitivity during light adaptation is due to the bleaching of visual pigments, and an increase in sensitivity during dark adaptation is a result of the regeneration of visual pigments. In other words, visual threshold depends on the availability of the unbleached photopigments.

Although such a photochemical theory can explain in at least a qualitative way some aspects of vision and specifically visual adaptation, it fails to encompass many visual facts. Psychophysical studies, such as that by Crawford (1947) and Baker (1953), have revealed that substantial changes in the visual threshold occur within a very short interval after the adapting light is turned on or off. These early threshold changes occur too soon to be explained by photochemical activity alone. Further evidence against the photochemical theory was received from electrophysiological studies on animals, dating back as early as the 1930's; these studies demonstrated that large changes of visual sensitivity occur without any significant changes in the visual pigment concentration (Granit, Holmberg & Zewi, 1938). This was later confirmed in humans by Rushton and his associates, who made direct comparisons between visual thresholds and rhodopsin concentration, as measured by retinal densitometry, during the course of light and dark adaptation (Rushton & Cohen, 1954; Rushton, Campbell, Hagins & Brindley, 1955; Rushton, 1961).

Several of the findings reported by Rushton and colleagues along with results of other investigators, bring into question a photochemical theory that claims that visual adaptation can be completely accounted for by the photolytic effect of the light adapting field. First, it has been reported that a light that bleaches trivial amounts of visual pigments (less than 2%) causes a substantial increase in the visual threshold (about three log units) (Dowling, 1967; Dowling & Ripps, 1972; Rushton & Cohen, 1954). Secondly, Rushton (1963b) and Baker (1963) discovered that the recovery of visual sensitivity was slower after a brief and intense flash illumination than after a prolonged light exposure, even though the quantity of rhodopsin bleached was identical under both conditions. Thirdly, the Bunsen-Roscoe photochemical law applies for the amount of bleached rhodopsin, but the "critical duration" is a matter of seconds, not milliseconds as in the case of visual threshold (Boynton, 1961; Campbell & Rushton, 1955; Rushton & Henry, 1968). Clearly, some non-photochemical factors must additionally limit temporal summation. Fourthly, contradicting the prediction of photochemical theory that the rods saturate when all the visual pigments are bleached, is the fact that the rod increment threshold reaches a saturation level when at most 5% to 10% of rhodopsin is bleached (Aguilar & Stiles, 1954). Finally, in recent years, several studies have observed various aspects of visual adaptation in isolated retinae separated from the pigment epithelium in which little or no pigment regeneration occurred (Dowling & Ripps, 1972; Hood, Hock & Grover, 1973; Kleinschmidt & Dowling, 1975; Sillman, Owen & Fernandez, 1973). Considered collectively, the investigations described above suggest that the photochemical factors are necessary but not sufficient to account for the phenomenon of visual adaptation. Certain neural mechanisms must also be involved.

Dowling (1963) has clarified the entire issue of photochemical versus neural mechanisms of visual adaptation. He has suggested that the rapid phase is neural in origin while the slow phase is related to the regeneration of rhodopsin. Physiological findings suggest that a significant portion of neural adaptation occur in the photoreceptors. Such a conclusion was reached by studies (see above) that have observed various aspects of adaptation in isolated retinae treated with aspartate. Aspartate isolates the photoreceptors by inactivating the bipolar and the horizontal cells and eliminating any influence from them. Other electrophysiological studies, such as that by Whitten and Brown (1973), have supported this view demonstrating that background luminance alters the temporal parameters of photoreceptors. The photoreceptors themselves are also equipped with certain inherent properties which enable them to respond differentially under varying conditions of illumination. For example, rods (which are stimulated under scotopic conditions of illumination) display different temporal parameters and sensitivity than cones (which are stimulated under photopic conditions of illumination) (Brown & Murakami, 1968; Brown & Watanabe, 1962; Fain & Dowling, 1973; Whitten & Brown, 1973).

Although a great deal of visual adaptation is observed at the photoreceptor level, there is growing evidence that neural structures beyond the photoreceptors also participate in adaptation. For example, Green, Dowling, Siegel and Ripps (1975) and Werblin and his colleagues (Normann & Werblin, 1974; Werblin, 1974; Werblin & Copenhagen, 1974) have studied the influence of both light and dark adaptation upon different levels of neural organization within the retina. Adaptation changes the dynamic range of operation and also compresses the operating range of voltage changes within the photoreceptors; in subsequent retinal neurons however, the effect of adaptation is largely restricted to the dynamic range of operation. But the effects of adaptation are much more diverse. Barlow, Fitzhugh and Küffler (1957) noted that the spatial characteristics of ganglion cell receptive fields changed dramatically as a function of light and dark adaptation. Since these neurons are the sole source of visual information to the brain, these more central changes in the neural organization must be reflected in psychophysical studies. There is evidence that adaptation also influences neural organization within the brain itself at the level of the lateral geniculate body (Poggio, Baker, Lamarre & Sanseverino, 1969) and perhaps also at the level of the visual cortex (Battersby & Wagman, 1962; Wagman & Battersby, 1959).

In summary, there is strong evidence that visual adaptation is primarily a retinal phenomenon involving both photochemical and neural mechanisms. In addition, higher visual centers also influence the process.

Influence of Light Adaptation upon Temporal Summation

Light adaptation changes temporal summation. For example, Graham and Kemp (1938) measured the threshold of different duration test flashes as a function of a steady background field. They found that the critical duration of the test flash decreased as the background luminance increased, although the shape of the temporal summation curve remained unaltered. Keller (1941) confirmed Graham and Kemp's findings. These findings have since been replicated and extended in many different ways. For example, Herrick (1956) extended Graham and Kemp's experiment by including increment and decrement threshold measures. He reported that as the background luminance is decreased, the critical duration is increased for both increment and decrement threshold measures. Biersdorf (1955) also demonstrated an inverse relation between critical duration and background luminance. He further reported that the level of background luminance does not alter the shape of the temporal summation function, that is, the sharpness of transition from complete summation to no summation. van den Brink and Bouman (1954) studied spatial and temporal summation of two flashes separated in time and space at various background luminances and retinal positions. They discovered that as the background luminance is increased, spatial summation decreases only in the periphery, while temporal summation decreases in both the fovea and the periphery. Since rods are predominant in the periphery and cones are concentrated in the fovea, background luminance seems to alter the temporal parameters of both rods and cones.

Barlow (1957; 1958a) investigated spatial and temporal summation of a test flash of varying size and duration, which was superimposed on a background of varying luminance. He found a decrease in spatial and temporal summation as the background luminance was increased. The range of background luminances employed by Barlow indicated that at high luminance levels the cones must be operating and at low luminance levels the rods must be stimulated. These results suggest that a decrease of temporal summation with an increase in background luminance apply to both rods and cones.

Background luminance was shown to affect temporal summation even with stimuli of different wavelengths (Sperling & Jolliffe, 1965). Although the critical duration varied for stimuli of different wavelengths, the effect of background luminance was the same on all of them, such that, as the background luminance was increased, the critical duration decreased. These results were true for both the fovea and periphery.

Roufs (1972) compared flicker, dual-flash and single-flash thresholds when the background luminance was varied. He demonstrated that the sensitivity to detect flicker and flash and the time integrating power of the visual system decreased as background luminance increased. The critical duration, which was used as a measure of temporal integration for flashes, decreased monotonically as the log of background luminance was increased. Therefore Roufs once again demonstrated the generality of the effect of background luminance on temporal summative power of the eye.

The studies discussed above illustrate how background luminance affects the summative properties of the eye. Ikeda (1965) demonstrated that background luminance also alters the inhibition obtained between two temporally separated light flashes, either positive or negative in luminance, with respect to the background. His results indicated that the level of background luminance does not alter the value of inter-flash interval up to which the two flashes were completely summated; however, it influenced the interval at which inhibition between the two flashes was observed (see Figure 2, page 15). Inhibition occurred for longer delay intervals under low levels of adaptation than under high levels. In a subsequent study, Uetsuki and Ikeda (1970) investigated the temporal summation function for two positive flashes under several background luminances. Results showed that the function changed dramatically as the background luminance varied from light to dark. Under a bright background, inhibition between the two flashes was strong and the inter-flash interval at which inhibition occurred was well defined. However, when the background luminance was reduced, inhibition between the two flashes was weakened and lasted even when they were separated by a long interval.

In summary, the results of psychophysical studies suggest that an increase in background luminance decreases visual temporal summation monotonically. Matin (1968) has attempted to quantify this relationship and has proposed that critical duration varies inversely and logarithmically with the level of adaptation. These findings suggest that in darkness the effect of light stimulus on the visual system lasts for a long time. This is significant when the response to successive light stimuli are considered, especially since the visual system is constantly bombarded by stimuli under normal conditions of responding.

Theoretical and Physiological Studies of Temporal Summation and Background Luminance

The mechanism underlying temporal summation are not understood. The similarity between Bloch's law of psychophysics and the Bunsen-Roscoe law of photochemistry suggests that photochemical factors limit temporal summation. Such a hypothesis can be exemplified by the photochemical theory of Hecht (1934) mentioned previously. Although this theory received support from some psychophysical studies (for example, Davy, 1952; Long, 1951) and some electrophysiological studies (for example, Hartline, 1934), it is not sufficient to account for all the features of temporal summation (see section: The Mechanism of Visual Adaptation).

Several objections have been raised against the photochemical explanation of temporal summation. First of all, a photochemically determined critical duration is found to be several orders of magnitude longer than that reported for psychophysical or neurophysiological measures. Secondly, temporal summation is shown to be dependent on the stimulus variables such as the size, wavelength and retinal position. Background luminance and response measures also alters temporal summation (see section: The Phenomenon of Temporal Summation). These findings cannot be explained by photochemistry alone. Thirdly, temporal summation is also observed in other sensory modalities (Zwislocki, 1960; 1969). Finally, some summation is shown to occur even when the two flashes of light are presented interocularly, that is, one flash in each eye (Battersby & Defabaugh, 1969; Matin, 1962). Although the magnitude of summation obtained interocularly is much less than that obtained monocularly, the fact that under these conditions there is summation bring into serious question the photochemical interpretation and suggests that peripheral and/or central neural processes must also be responsible for temporal summation.

Barlow (1958; 1964) proposed a signal to noise theory to explain the influence of background luminance on temporal summation. According to this theory, a stimulus produces a "signal" that has to be discriminated from the "noise" within the visual system. This noise consists in part of "dark noise" which is unrelated to background luminance and is possibly the result of spontaneous processes within the photoreceptors. The other component of "noise" is dependent on the quantum fluctuations of light. This component is directly related to the background luminance. As the level of background luminance is raised, there is an increase in the quantum fluctuation of light which results in an elevation of the noise level. This leads to an increase in the stimulus increment threshold. An increase in stimulus duration and size, beyond the limits of complete temporal and spatial summation, respectively, and an increase in background luminance, all lead to a breakdown in the quantum fluctuation hypothesis. Barlow proposed that retinal mechanisms, such as lateral inhibition which increases under light adaptation, are responsible for reducing spatial and temporal summation. Barlow's conjecture which pushes the limiting process in vision from photopigment to the nervous system, led to a new look at the whole issue of background luminance and its effect on vision. As a consequence there have been a number of theories in vision which have either emphasized physiological mechanisms (for example, Brown & Murakami, 1968; Whitten & Brown, 1973) or Fourier analysis (for example, Kelly, 1971a, b; Matin, 1968; Sperling & Sondhi, 1968).

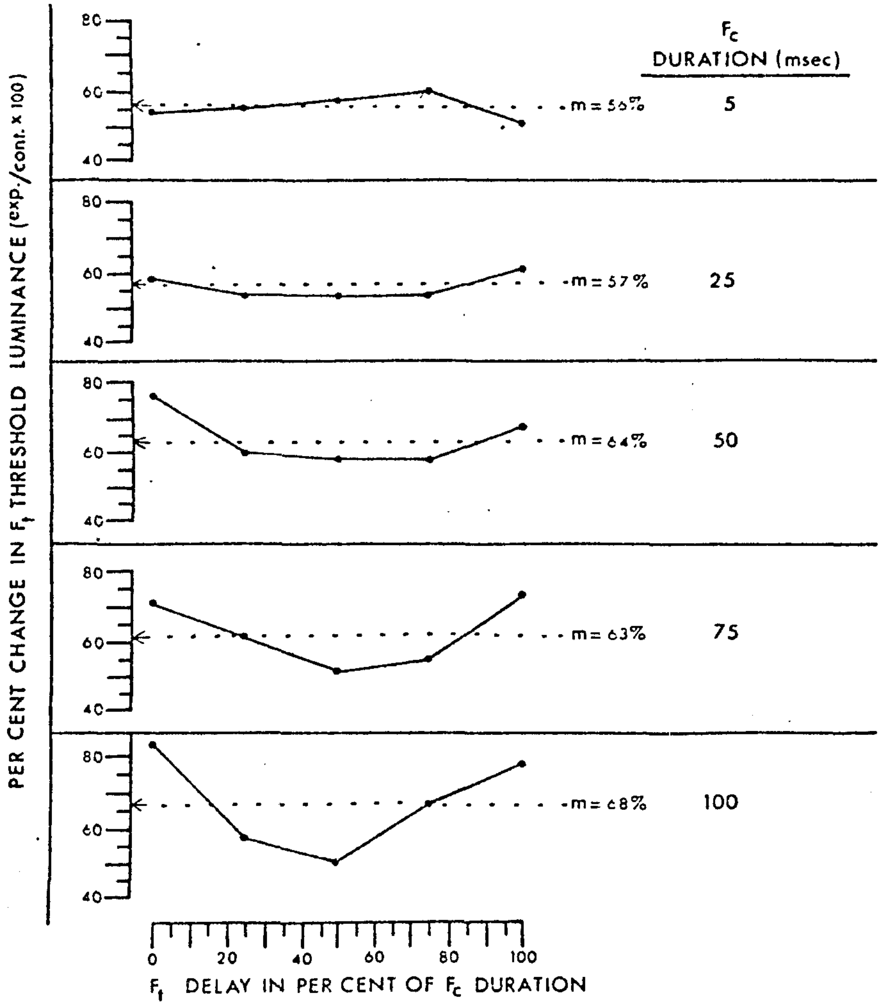
One such theory of particular interest is that of Uetsuki and Ikeda (1970) who have postulated a mechanism responsible for the variation in temporal summation and inhibition under different conditions of background luminance. According to their model, somewhere in the visual system the response to a flash of light is biphasic, that is, it has a positive and a negative component. The ganglion cells are the likely site at which a biphasic response may be obtained. The negative component of the biphasic response is altered by a change in the background luminance such that at high luminance level the negative component is very pronounced, and at low luminance level it is very shallow but prolonged. When the two flashes are separated by a brief interval, various response components of the first flash coincide in time with that of the second flash. As the interval is increased there is a gradual decrease in the overlapping of responses until finally the two responses are totally independent. There is a linear summation between overlapping response component and the resultant response determines the temporal summation function. Since the biphasic response of the visual system to a flash of light changes with the background luminance, the resultant temporal summation function also changes. Uetsuki and Ikeda's theory is important since it attempts to incorporate the data on both temporal summation and inhibition as it is affected by the level of light adaptation.

Uetsuki and Ikeda's conjecture that more than one process is involved in temporal summation is not unique. As early as 1931, Granit and Davis postulated a mechanism of temporal summation of two subliminal flashes (see Chapter I - INTRODUCTION). They assumed that a critical excitatory level in the visual system must be reached before the observer can detect a flash. In their experiment the onset of the initial subliminal conditioning flash was said to set off some excitatory effect in the visual system, which decays away when the flash is turned off. Since temporal summation between two subliminal flashes occurs only when they are separated by a very brief interval, Granit and Davis suggested that the decay of the excitatory effect of the conditioning flash must be very rapid.

More recently, Battersby and Schuckman (1970) have proposed that such short-term decay effects are not only demonstrated by two temporally separated light flashes, but also by a single sustained flash. They studied the magnitude and time course of temporal summation of subliminal conditioning flashes of various durations. A brief test flash was superimposed on the conditioning flash at various temporal delays from its onset (see Chapter I - INTRODUCTION - page 3). The test-flash luminance was measured at various temporal delays, so that the summated energy of the two flashes reached threshold. The results indicated that complete temporal summation, or luminance-duration reciprocity, was limited to conditioning-flash duration of 10 msec or less. For longer durations, there was a gradual loss of summation which followed a definite time course, such that summation was maximal when the test flash was presented near the middle of the conditioning flash and was minimal at the two extreme ends of the conditioning flash. When the percent change in test-flash threshold luminance was plotted as a function of the conditioning flash-test flash onset delays (in percent of conditioning-flash duration), a "U"-shaped function was obtained. Figure 3 illustrates the time course of temporal summation for various conditioning-flash durations as obtained by Battersby and Schuckman. It is evident that as the conditioning-flash duration increases, the maximal and the minimal changes in summation also increase in magnitude.

Non-monotonic responses of the visual system are not unique to threshold detection measures. Similar results have also been obtained by studies investigating other visual phenomena. Shickman (unpublished dissertation) for example, studied the temporal resolving power of the eye, by measuring the separation threshold of two brief flashes of light that were superimposed on a longer conditioning flash (one second duration), at various delays from its onset. Results indicated that the resolving power of the eye varied non-monotonically during the exposure of the conditioning flash. Maximum resolution occurred at about 150 msec delay from the onset of the conditioning flash, while resolution was reduced prior to and following this delay.

Figure 3. Temporal summation data from Battersby and Schuckman (1970). On the ordinate is plotted the percent change in the luminance of the test-flash threshold (experimental/control x 100). On the abscissa is expressed the temporal delay between conditioning-flash and test-flash onsets (in percent of conditioning-flash duration). Curves for five different conditioning-flash durations are illustrated. Horizontal dashed lines represent the mean test-flash threshold change for each conditioning-flash duration. F_t = Test flash. F_c = Conditioning flash.


PER CENT CHANGE IN F_t THRESHOLD LUMINANCE (exp./cont. × 100)
F_c
DURATION (msec)
80
60
40
m = 56%
5
80
60
40
m = 57%
25
80
60
40
m = 64%
50
80
60
40
m = 63%
75
80
60
40
m = 68%
100
0
20
40
60
80
100
F_t DELAY IN PER CENT OF F_c DURATION

Although several psychophysical studies have demonstrated the differential effect of background luminance on the magnitude of temporal summation, there has been no attempt to investigate its effect on the time course of temporal summation. Battersby and Schuckman (1970) have proposed two hypothetical processes that determine the time course, namely, the excitatory effect created by the energy of the conditioning flash and the decay of this excitatory effect. If the background luminance influences the rate at which these two processes occur, it should be reflected in the time course of temporal summation obtained under various conditions of background luminance.

Although the mechanisms postulated by Battersby and Schuckman are hypothetical and there is no knowledge regarding their location, there is growing evidence that background luminance alters the temporal parameters of the visual system at various physiological levels (see section: <u>Influence of Light Adaptation upon Temporal Summation</u>). More significant is the finding that background luminance alters the time course of the photoreceptors themselves. Whitten and Brown (1973) showed that the decay of the receptor potential is much slower under dark-adapted than under light-adapted conditions. Another important finding is that rods and cones, which are differentially active under scotopic and photopic conditions of illumination, respectively, also differ in their time constants and their sensitivity (Fain & Dowling, 1973; Whitten & Brown, 1973). The cones seem to have faster temporal parameters, as illustrated by rapid rise and fall times of the late receptor potential; they are also known to be less sensitive than rods. Therefore, during light adaptation, not only are the fast reacting cones more active, but the temporal parameters of rods and cones are hastened too. Although photoreceptor activity alone does not determine visual perception, it does provide the building blocks for more central information processing. Alterations in the photoreceptor temporal parameters associated with changing background luminance may be reflected in the time course of brightness sensation during and following a stimulus flash.

Rationale for the Present Study

The present psychophysical study measures the time course of temporal summation using the procedure employed by Battersby and Schuckman (1970). For this technique, threholds of a short duration test flash are determined during the time course of different duration conditioning flashes of subliminal luminance. Battersby and Schuckman used conditioning flashes of various durations that were equated for threshold sensation. However, they reported that their longer conditioning flashes were not completely summated, a fact that obscures the interpretation of their results. Accordingly, they suggest that future studies might use conditioning flashes equated for energy, as that would enable an investigation of the effect of temporal dispersion of conditioning-flash energy simply by varying its duration. In the present study, this suggested procedure is followed and in addition the level of background luminance is varied in order to assess its influence on the magnitude and the time course of temporal summation.

In summary, the goals of the present study were twofold: first, to investigate the time course of temporal summation of conditioning flashes equated in energy but varied in duration; second, to compare the magnitude and the time course of temporal summation at different levels of background luminances.

CHAPTER III

METHOD

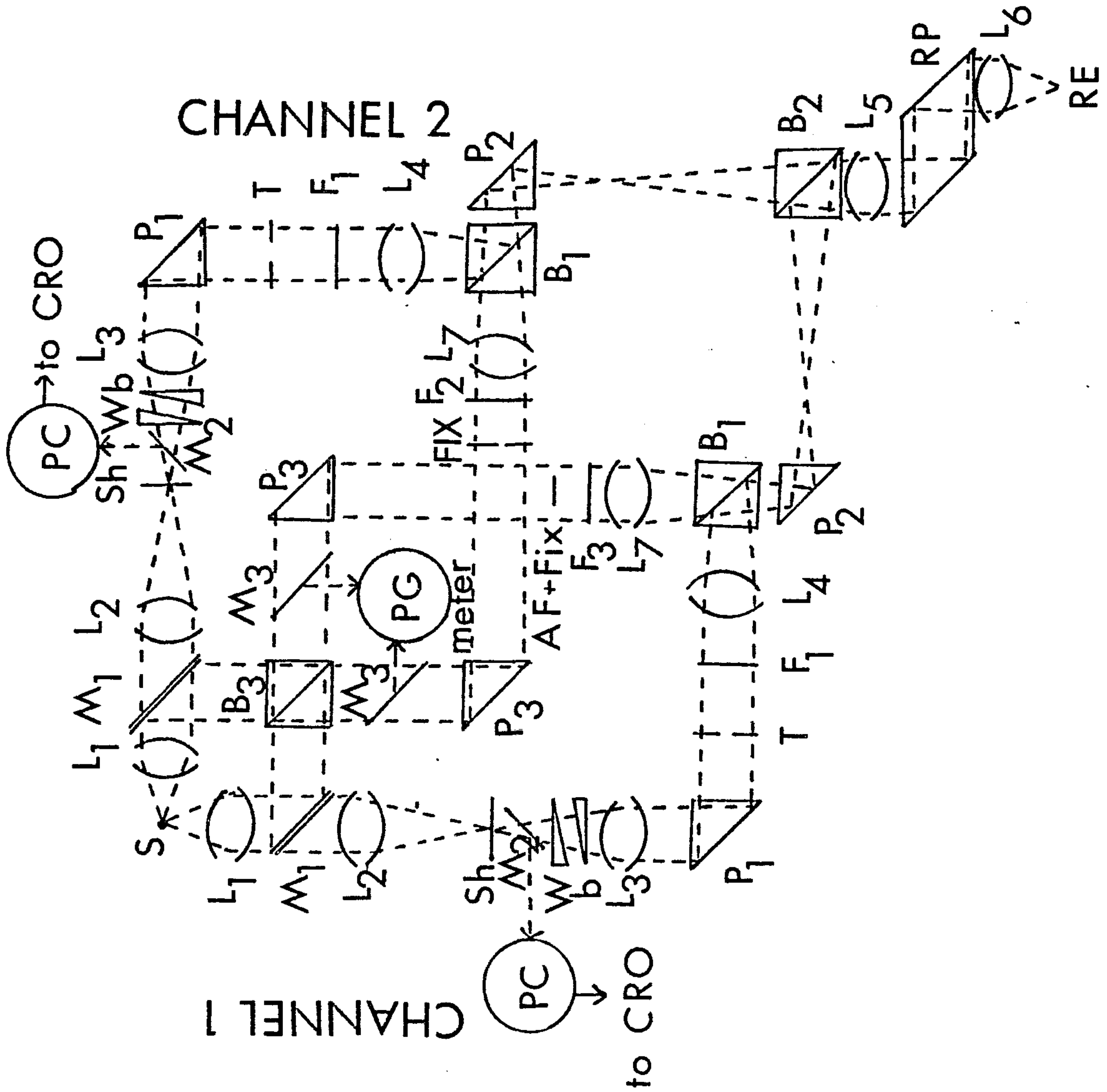
Apparatus

Optical System

A four-channel Maxwellian view optical system was used to present all the stimuli. Frumkes and Sturr (1968) and Battersby and Schuckman (1970) have described the optics and the electronic controls of this system. It had two major channels and two minor channels. The major channels were used to present the stimuli and the minor channels were used to present the adapting field and the fixation targets. Figure 4 is a schematic diagram of the optical system.

Major Channels. Figure 4 shows the two symmetric major channels. The light source indicated by S, was a tungsten filament lamp of 18 amperes current (General Electric CPR Projection lamp). However, the lamp was powered at about 16.5 amperes in order to increase its life. The same lamp was used throughout the entire experiment. The lamp was powered by a 6-volt power supply, whose output was controlled by a rheostat, and its current was monitored by an ammeter. This source

Figure 4. Schematic diagram of the Maxwellian view optical system. The light beams used in this study are indicated by dotted lines. For further explanation, see text.


CHANNEL 2
PC
to CRO
Sh
Wb
M_2
L_3
P_1
T
F_1
L_4
P_2
B_1
B_2
L_5
RP
L_6
RE
FIX
F_2
L_7
P_3
M_3
PG
meter
A F+Fix
F_3
L_7
B_1
P_2
L_4
F_1
T
L_1
M_1
L_2
B_3
M_3
P_3
S
L_1
M_1
L_2
Sh
M_2
W
b
L_3
P_1
PC
to CRO
CHANNEL 1

provided a light beam for all the four channels. As shown in Figure 4, lens L_1 was a collimating lens that was placed one focal distance away from the source. M_1 was a mirror that allowed some light to pass through it and deflected approximately 20% to the minor channel. L_2 was a lens that focused the image of a source in the plane of the shutter, Sh. The shutter, which was attached to a D.C. oscillograph drive unit (which in turn was electronically controlled by Tektronix pulse and waveform generators), controlled the duration of stimuli produced by the major channels.

In Figure 4, W indicates a neutral density wedge which was balanced by a balancing wedge, b. These were 4 log unit circular neutral density wedges that were mounted on a shaft of a two-way stepper and geared to a read-out dial, and they controlled the luminance of the major channels. A two-way lever switch was provided, which by moving the wedge, increased or decreased stimulus luminance by 0.01 log mL per press. Fixed neutral density filters placed in filter rack F_1 provided further luminance control. M_2 indicated a mirror which was inserted between the shutter and the wedge. This mirror reflected some light to the photocell, which monitored the temporal parameters of all light flashes, which was in turn displayed on the oscilloscope, CRO. Therefore, all flash durations and intervals were continuously monitored.

Lens L_3 recollimated the light. P_1 was a right-angle prism that diverted the path of light. T indicates the target rack that held a target plate of 2"x2". The size of the stimulus was determined by the size of an aperture in the target plate. A micromanipulator permitted adjustment of the horizontal and vertical positions of the target plate, thus providing the control of the retinal position of the stimulus.

L_4 was a focusing lens that was placed at its focal distance away from the target plate. B_1 was a beam splitter that combined a major and a minor channel. P_2 was a right-angle prism that diverted the path of light beam to the beam splitter B_2. B_2 combined all four channels and permitted the presentation of all major and minor channels to one eye. L_5 was a collimating lens. Rp was a rhomboid prism which could be rotated to displace the light beam laterally, which allowed for the adjustment of varying interpupillary distances for the observers. L_6 was the final focusing lens that focused the image on the crystalline lens of the eye indicated by RE in Figure 4.

In summary, the optical system provided two major channels, the luminance and duration of which could be varied. The two major channels were used to produce the conditioning flash and the test flash.[4]

Minor Channels. There were two minor channels which provided the adaptation field and the fixation targets. These channels also monitored the source current. As indicated in Figure 4, M_1 was a mirror that deflected approximately 20% of the light from the major channels to the minor channels. B_3 was a beam splitter that combined the two minor channels. M_3 was a mirror that reflected some light to the photocell PC. The photocell was connected to a milliammeter, thus permitting continuous monitoring of the source. P_3 was a right-angle prism that changed the course of the light beam. AF+Fix indicates the adapting field slide with a fixation target and FIX indicates the rack where the slide with the fixation target alone was placed. F_2 and F_3 were the filter racks in which were placed the filters that controlled the luminance of the adapting field and the fixation targets. L_7 was a focusing lens that converged the light beam on the beam splitter B_1. B_1 combined one minor channel with one

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[4] As indicated in Figure 4, major channel 1 provided the test flash and major channel 2 provided the conditioning flash.

major channel.

Time Control

Tektronix 160 series pulse and waveform generators permitted precise control of the duration of all pulsed stimuli, interstimulus intervals and the recycling rate. In addition, stimulus duration and interstimulus intervals were continuously monitored on an oscilloscope (Tektronix 360 indicator). In the present experiment, the recycling rate was always once every four seconds.

Luminance Calibration

A brightness match was made between one major channel and a standard source, which had an illuminance of 11.3 mL. By this means, the dial setting of this channel which corresponds to 11.3 mL was obtained. Brightness matches were obtained to calibrate the other three channels. A chart of the dial readings and its corresponding luminance in log mL was then obtained for both major channels for easy reference.

Stimulus Size and its Retinal Position

A projection procedure showed that a 1 mm aperture corresponded to a 1.8° stimulus. This information made it easy to calibrate both retinal position and stimulus diameter. Throughout the study, 30' diameter stimuli were used for both test and conditioning flashes. These were superimposed 6° 30' from the fixation, in the right temporal field, along the horizontal meridian.

Fixation Target

A photographic film with the fixation target was inserted in one of the minor channels at the point indicated by FIX in Figure 4. Four red dots (Wratten 29 filter) served as the fixation target. Each dot was approximately 15' in diameter and they formed a 3° square. The observers were asked to fixate in the center of the square. Neutral density filters, which controlled the luminance of the fixation target, were inserted in the filter rack F_2 in front of the fixation target. The luminance of the fixation target was varied for different background luminances so that the fixation target appeared to be equally bright under all background luminances.

Adaptation Field

The other minor channel provided the adapting field. The AF+Fix in Figure 4 indicates the adapting field with the fixation crosshairs. The adapting field was 40° in diameter and was exposed continuously. The adapting field provided the background luminance, which was varied by inserting neutral density filters in the filter rack F_3 (Figure 4). Three different background luminances of -3.0 log mL, 0.0 log mL and 2.0 log mL were used in the experiment. The conditioning flash and the test flash were concentrically superimposed on the adapting field in the Maxwellian view, such that it appeared in the parafovea at 6° 30' along the right horizontal meridian of the right eye. The crosshairs aided fixation under photopic conditions of adaptation.

Head and Eye Position

The position of the observer's head and eye were controlled by a chin and head-rest, which was mounted in front of the optical bench and could be moved in all three planes. Before each experimental session, the observer adjusted the chin and head-rest until he had a full view of the 40° adapting field and the fixation crosshairs were sharply in focus. Since the stimuli were to be presented at a fixed retinal position, it was essential to control the head and eye position.

Observers

Two undergraduate male students were paid for their services as observers. JH was 20 years old and

FC was 18 years old. Both had normal, uncorrected, 20/20 vision as indicated by recent optometric eye examination. Both observers had previous experience in psychophysical experiments, but were naive regarding the purpose of the experiment. Both were right-handed.

Procedure

General Procedure

The entire experiment was conducted monocularly with the observer using his right eye. The left eye was occluded by means of an eye patch. At the begining of each session, the observer adjusted the chin and head-rest until he could view the entire 40° adapting field and the fixation crosshairs. These adjustments were made under the background luminance of 0.0 log mL. One of the three background luminances (-3.0 log mL, 0.0 log mL or 2.0 log mL) for that particular session was then selected based on a predetermined table, where the order of presenting the background luminance was block randomized. Appropriate neutral density filters were then inserted in the filter rack F_3 of the adapting channel as indicated in Figure 4. The observer adapted to the background luminance for 10 minutes prior to threshold measurements.

The conditioning flash was presented by Channel 2 and the test flash was presented by Channel 1 (see Figure 4). After the observer adapted to the appropriate background luminance for 10 minutes, five threshold luminance measurements were obtained for the 5 msec conditioning flash.[5] The mean threshold luminance of these five measurements was calculated. The conditioning-flash channel was then set at one of the four conditioning-flash durations (10 msec, 20 msec, 40 msec or 80 msec) as determined from a table, where the order of presenting the conditioning-flash duration was counterbalanced across sessions. The luminance of the conditioning-flash channel was set at a value such that the total energy (luminance x duration) of the conditioning flash was equal to that of the 5 msec conditioning flash, whose mean threshold was just determined. To present a subliminal conditioning flash, a 55% transmission filter was inserted in the conditioning-flash channel. The test-flash channel

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[5] If there were no significant variations in these five threshold readings, it was assumed that the observer was completely adapted to the background luminance. If variations did occur, the observer was adapted to the background for an additional 5 minutes. Such a check was particularly useful at the low background luminance level.

was set at 5 msec duration and was presented at any one of the five delays, from the onset of the conditioning flash. The onset delays were expressed as a percentage of the conditioning-flash duration and were either 0%, 25%, 50%, 75% or 100% of the respective conditioning-flash duration. The order of the five stimulus onset delays was randomized within a session. To obtain a threshold measure, the luminance of the test flash was varied by the observer in small steps (by the two-way lever switch). The specific procedure used to obtain all threshold measurements is described in the next section. For each stimulus onset delay, two test-flash threshold readings were taken. One was the dual-flash condition, where both the test flash and the conditioning flash were presented; this was the experimental condition. The other was the single-flash condition, where the test flash was presented alone; this was the control condition. The order of the single-flash and dual-flash conditions was randomized. Table 1 summarizes all the stimulus parameters used in this experiment.

This procedure produced a total of 15 threshold readings in each session. Five threshold readings were taken of the 5 msec conditioning flash, 5 readings were taken of the test flash alone, and 5 readings were

TABLE 1

Stimulus Parameters

	Conditioning Flash
Size:	30' diameter.
Duration:	10 msec, 20 msec, 40 msec and 80 msec.
Luminance:	Set at a value that maintained a constant energy content (luminance x duration) at 55% of threshold energy, as measured with the 5 msec conditioning flash.
	Test flash
Size:	30' diameter.
Duration:	5 msec.
Luminance:	Varied to reach a threshold value.
	Stimulus onset delay interval
0%, 25%, 50%, 75% and 100% of the respective conditioning-flash duration.	
	Retinal Position
Both the test flash and the conditioning flash were presented 6° 30' away from the fixation, along the right horizontal meridian of the right eye.	
	Adapting Field
Size:	40° diameter.
Duration:	Exposed continuously.
Luminance:	-3.0 log mL, 0.0 log mL and 2.0 log mL.

taken of the test flash when it was presented with the subliminal conditioning flash of a particular duration, at each of the five different onset delays. In the subsequent sessions, these 15 threshold readings were taken five times for each of the four conditioning-flash durations and the three background luminances, yeilding a total of 60 sessions and 900 threshold readings per observer.

The conditioning flashes were equated for their energy content and not for their sensitivity. In order to determine whether the conditioning flashes were temporally summated, it was essential to find out how the threshold luminance varied as the conditioning-flash duration was increased. These were the control data and were obtained at all three background luminances. The control data were obtained in three sessions - once at the begining of the experiment, next at the middle of the experiment and finally at the end of the experiment. The averaged threshold luminances of the three sessions were plotted as a function of conditioning flash durations to obtain the luminance-duration reciprocity functions. Thus the control data refers to the threshold measurements of the conditioning flash of varying durations, while the control condition described earlier, refers to the threshold measurement of the 5 msec test flash.

Specific Procedure to obtain the Threshold

The descending method of adjustment was used to determine all the threshold measurements. Stimuli were presented once every four seconds. The stimulus luminance was decreased from a high but unknown level, well above the observer's threshold. The observer himself manipulated the two-way lever switch that controlled the stimulus luminance. As soon as the flash was presented, the observer responded whether or not he saw the flash. If the flash was detected, the luminance was decreased to a desired amount by the observer himself in small steps of 0.01 log mL. If the flash was not seen, the luminance was held constant. Initially, when the luminance was considerably above threshold, the observer decreased the luminance in large steps. As he approached the threshold, the luminance was decreased in very small steps (1 or 2 lever presses). The luminance value for which five consecutive "no" responses were obtained was considered to be the observer's threshold. This criterion was used to obtain all the threshold measurements. For each threshold run, a minimum of six blanks were presented. Most of the blanks were presented in the range of uncertainty, that is, at or near threshold. The observer could also call for a blank at any time. Feedback was given after the observer responded to the blank, This procedure helped stabilize the observer's criterion and decreased the variability. There were two types of blanks - one in which no stimulus was presented, and the other in which a subliminal conditioning flash at 55% of its threshold value was presented. The two types of blanks appeared equally often and the observers were not able to tell them apart.

Design of the Experiment

A complete within-subjects design was used in the experiment. In this design, each observer was given all the levels of independent variables. Since each observer underwent all different experimental conditions, the potential confounding subject variables were eliminated. Any differences in the observer's behaviour would only be due to the differences in the experimental conditions. The order of the three background luminances was randomized, but with the restriction that each one occurred once in blocks of three. The progressive errors, which are the errors in performance due to successive trials on a task, were minimized by counterbalancing the order of each interval and each duration over the five threshold readings taken for each combination. Counterbalancing was done using a predetermined table.

Treatment of the Data

The raw data consisted of the test-flash threshold luminances obtained in the dual-flash condition (experimental condition) and the single-flash condition (control condition) for all combinations of background luminances, conditioning-flash durations and conditioning flash-test flash onset delays. The test-flash luminance in the dual-flash condition (conditioning flash + test flash) was expressed as a percentage of the test-flash luminance in the single-flash condition (test flash alone). These percentages are referred to in the text as the percent change in test-flash threshold luminance, which reflects the magnitude of temporal summation. These percentages were averaged over all the sessions and the means were plotted as a function of the conditioning flash-test flash onset delays (expressed as percentage of the conditioning-flash duration).

The functions generated thereby gave the time course of temporal summation. The background luminance and the duration of the conditioning flash was varied as a parameter.

In the dual-flash condition, the luminance of the conditioning flash was set at 55% of its threshold value (as measured by the 5-msec conditioning flash). In order to obtain complete summation, the test-flash luminance is required to be set at a value so that when it is expressed as a percentage of the test-flash luminance in the single-flash condition, it will be equivalent to 45%. Percentages higher than this value reflects a breakdown in temporal summation, that is, relatively more test-flash luminance is required to reach threshold.

Analyzing the data in such a manner enables one to display and evaluate the differences in temporal summation as the background luminance, the conditioning-flash duration, and the stimulus onset delays are varied.

CHAPTER IV

RESULTS

Figures 5 and 6 show all the experimental data and Figures 15 and 16 show all the control data obtained for observers JH and FC in this study. The remainder of the figures are derived plots.

In Figures 5 and 6, the ordinate shows the mean percent change in test-flash threshold luminance (test-flash luminance in the dual-flash condition expressed as a percentage of the test-flash luminance in the single-flash condition). The delay interval between the conditioning-flash and test-flash onsets (expressed as a percentage of the conditioning-flash duration) is plotted on the abscissa. The four different conditioning-flash durations are represented by the four different sets of co-ordinates as indicated. The three different symbols indicate the three different background luminance levels. If perfect temporal summation occurred between the test flash and the conditioning flash, all data would adhere to the 45% ordinate position, regardless of the levels of the three independent variables, of background luminance, conditioning-flash duration or onset delay interval.

Figure 5. The time course of temporal summation for observer JH. The four different sets of co-ordinates represent data obtained with different conditioning-flash durations (as indicated). The different symbols correspond to the background luminances (as indicated). For each set of co-ordinates, the percent change in test-flash threshold luminance is plotted as a function of the delay interval between conditioning-flash and test-flash onsets. The abscissa is expressed in terms of the percent of conditioning-flash duration. For further explanation, see text.

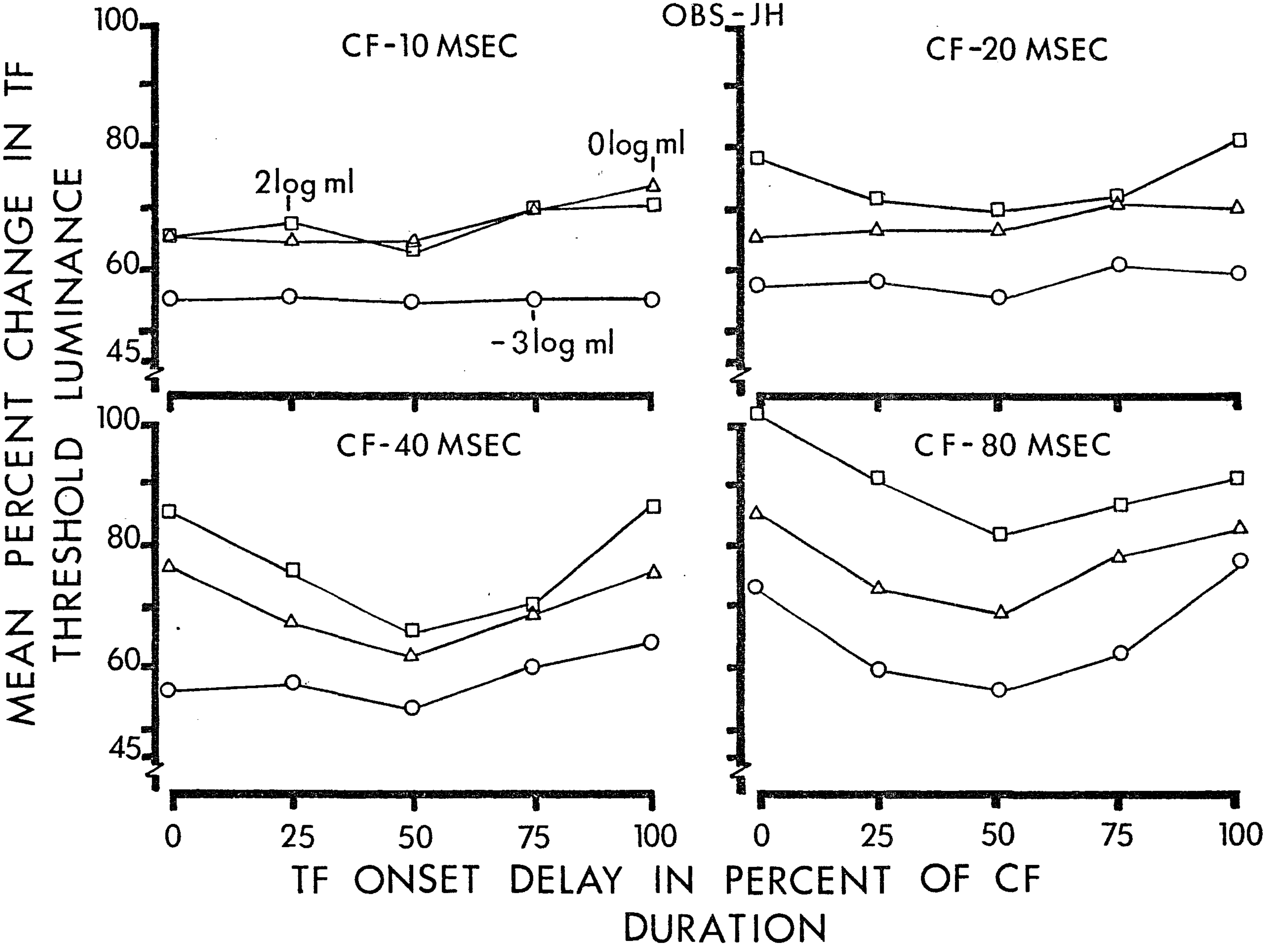
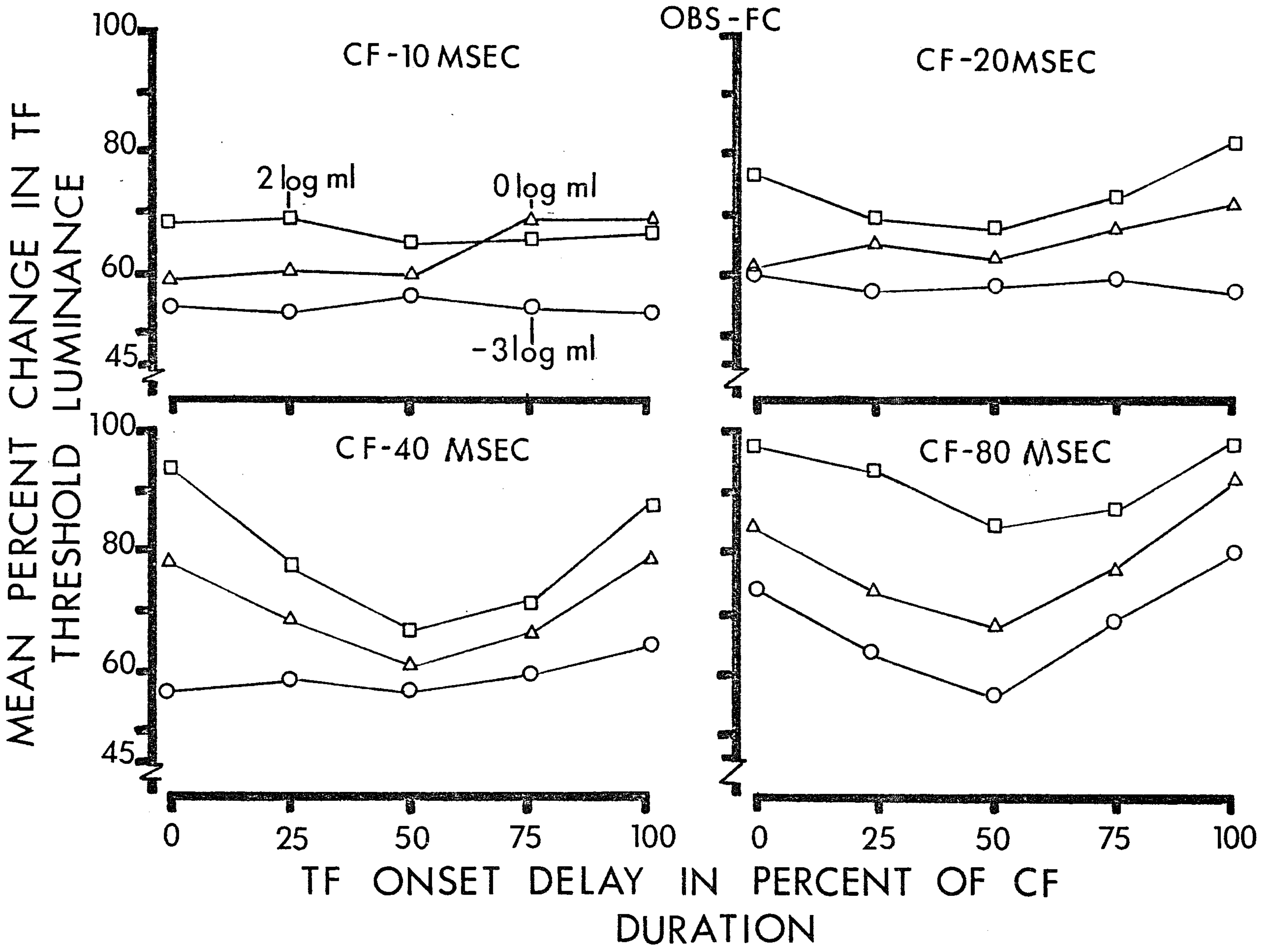

OBS-JH
CF-10 MSEC
CF-20 MSEC
CF-40 MSEC
CF-80 MSEC
2 log ml
0 log ml
-3 log ml
100
80
60
45
100
80
60
45
0
25
50
75
100
0
25
50
75
100
MEAN PERCENT CHANGE IN TF THRESHOLD LUMINANCE
TF ONSET DELAY IN PERCENT OF CF DURATION

Figure 6. The time course of temporal summation for observer FC. The four different sets of co-ordinates represent data obtained with different conditioning-flash durations (as indicated). The different symbols correspond to the background luminances (as indicated). For each set of co-ordinates, the percent change in test-flash threshold luminance is plotted as a function of the delay interval between conditioning-flash and test-flash onsets. The abscissa is expressed in terms of the percent of conditioning-flash duration. For further explanation, see text.


OBS-FC
CF-10 MSEC
CF-20MSEC
CF-40 MSEC
CF-80 MSEC
2 log ml
0 log ml
-3 log ml
MEAN PERCENT CHANGE IN TF THRESHOLD LUMINANCE
100
80
60
45
0
25
50
75
100
TF ONSET DELAY IN PERCENT OF CF DURATION

Clearly, this is not the case. Temporal summation is always less than 45% but it is maximum with dim background luminance, short conditioning-flash duration and at 50% delay interval.

The effect of each independent variable on the magnitude and the time course of temporal summation is as follows:

Delay Interval

Figures 5 and 6 indicate that as the conditioning flash-test flash onset delay is systematically increased, the percent change in test-flash threshold follows a definite time course at a particular conditioning-flash duration and background luminance level. For the shortest conditioning flash (10 msec) and at the dimmest background luminance (-3.0 log mL), the percent change in test-flash threshold luminance remains essentially constant at about 55% level for both observers, indicating complete summation.[6] However, as

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[6] A 55% transmission was used to obtain a subliminal conditioning flash. Theoretically, 45% of the control threshold indicates complete summation; however, 55% is still considered to be in the range of complete summation. The 10% loss in summation can be explained as the error in the calibration or the quality of the filter of the optical system.

the background luminance and the conditioning-flash duration increases, there is an increase in the percent change in test-flash threshold luminance at longer delay intervals, indicating a loss of summation. At still higher background luminances and longer conditioning-flash durations, the percent change in test-flash threshold luminance varies non-monotonically as a function of the delay intervals, such that summation is minimum at the earliest delay interval, reaches a maximum value at the 50% delay interval, and decreases to a secondary minimum at the longest delay interval. As a result, there is a symmetrical "U"-shaped function of the time course of temporal summation at higher adaptation levels and for the longer conditioning flashes.

Battersby and Schuckman (1970) also obtained a "U"-shaped function of the time course of temporal summation when the duration of the conditioning flash was increased (see Figure 3, page 35). Since Battersby and Schuckman conducted their study at 0.0 log mL background luminance level, the experimental data obtained in this study at 0.0 log mL background luminance is replotted (Figures 7 and 8), in order to aid comparisions between the two studies. Comparing Figures 7 and 8 with Figure 3, it is clear that the

Figure 7. The time course of temporal summation at 0.0 log mL background luminance, for observer JH. The four different sets of co-ordinates represent the data obtained with different conditioning-flash durations (as indicated). For each set of co-ordinates, the percent change in test-flash threshold luminance is plotted as a function of the delay interval between conditioning-flash and test-flash onsets. The abscissa is expressed in terms of the percent of conditioning-flash duration.

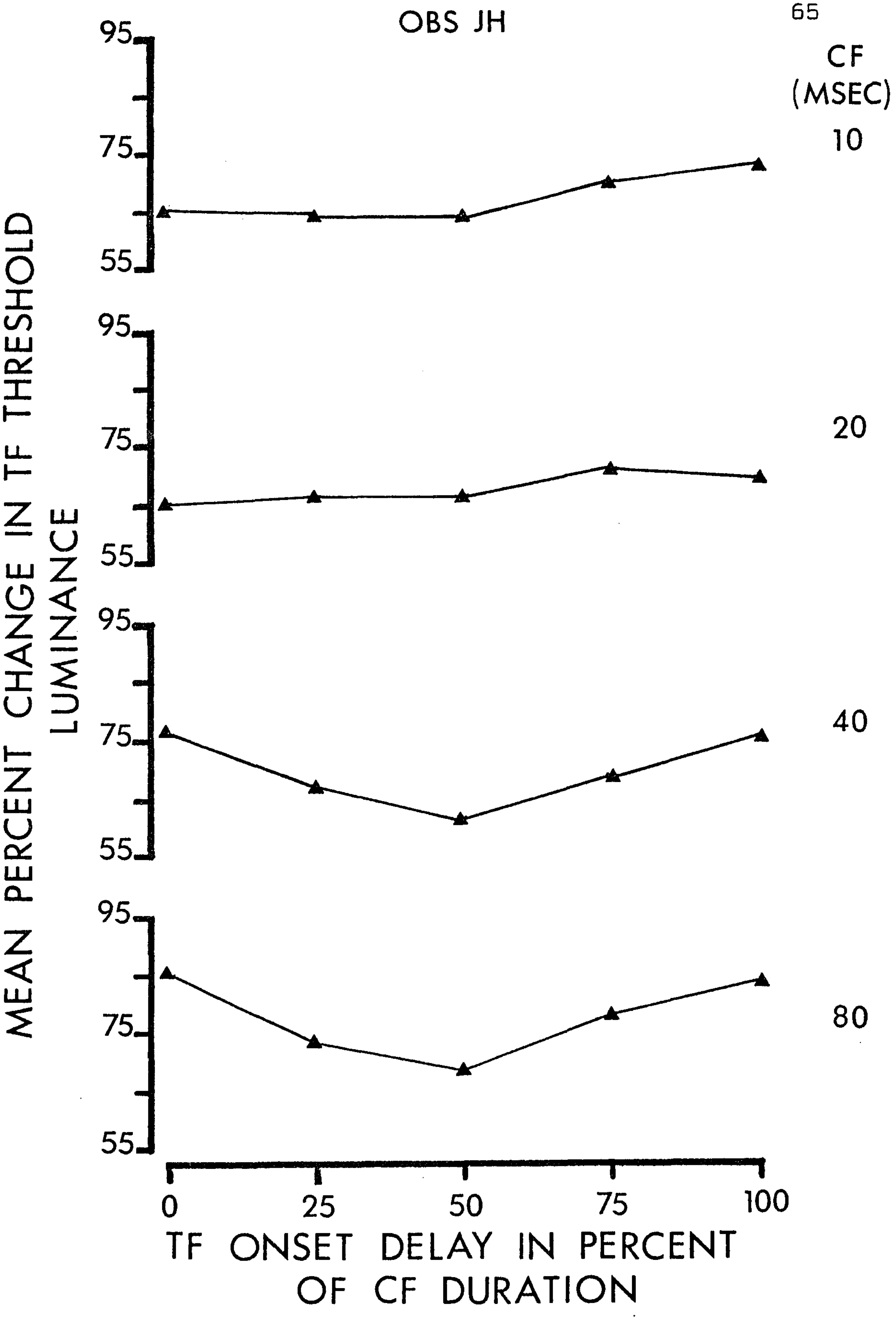
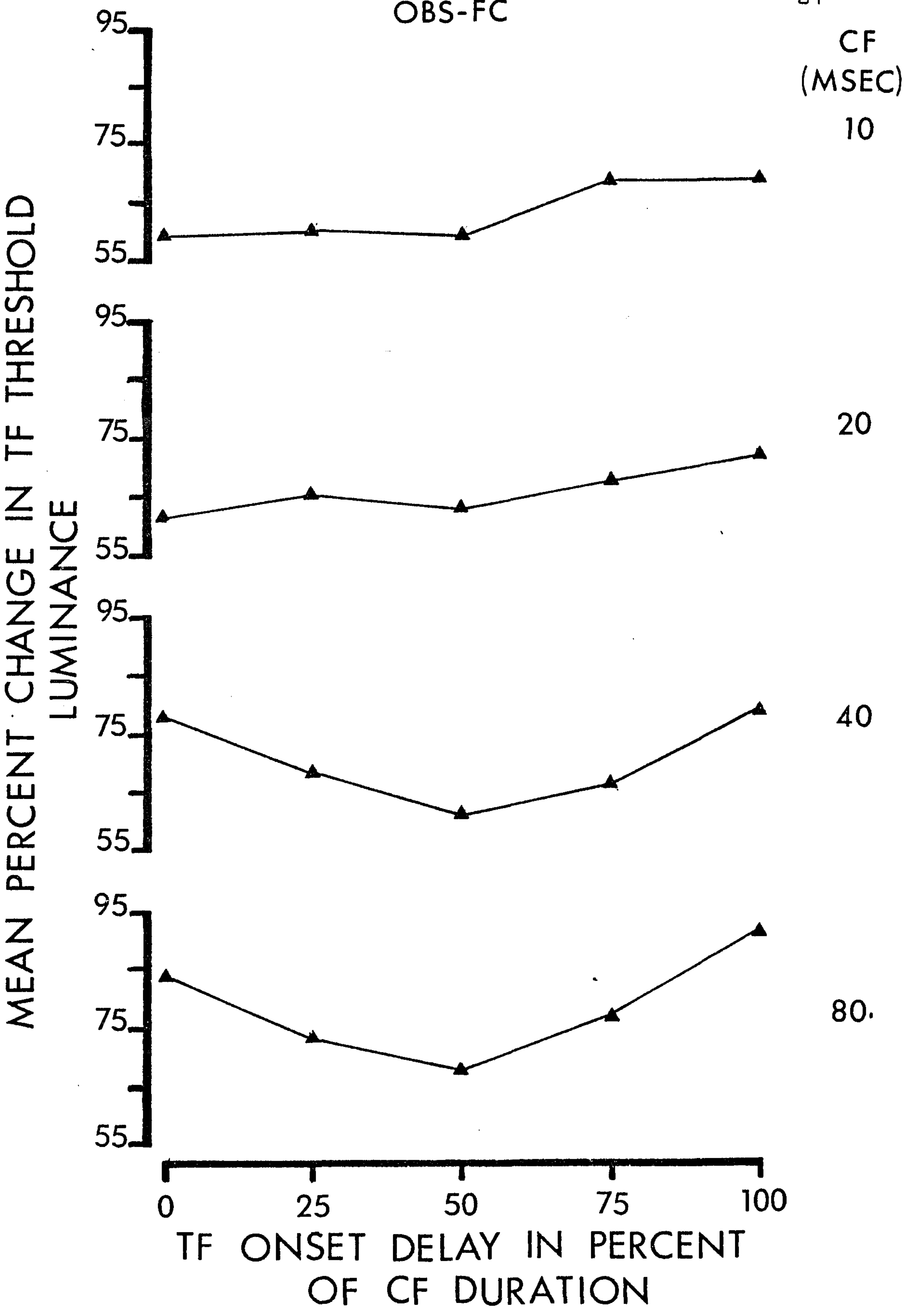

OBS JH
CF (MSEC)
10
20
40
80
95
75
55
MEAN PERCENT CHANGE IN TF THRESHOLD LUMINANCE
0
25
50
75
100
TF ONSET DELAY IN PERCENT OF CF DURATION

Figure 8. The time course of temporal summation at 0.0 log mL background luminance, for observer FC. The four different sets of co-ordinates represent the data obtained with different conditioning-flash durations (as indicated). For each set of co-ordinates, the percent change in test-flash threshold luminance is plotted as a function of the delay interval between conditioning-flash and test-flash onsets. The abscissa is expressed in terms of the percent of conditioning-flash duration.


OBS-FC
CF
(MSEC)
10
20
40
80.
MEAN PERCENT CHANGE IN TF THRESHOLD
LUMINANCE
95
75
55
0
25
50
75
100
TF ONSET DELAY IN PERCENT
OF CF DURATION

general shape of the time course of temporal summation is similar in both studies.

Background Luminance

Figures 5 and 6 show that as the level of background luminance increases, the percent change in test-flash threshold luminance increases at all conditioning-flash durations and also at all conditioning flash-test flash onset delays. This means that an increase in background luminance results in a decrease in magnitude of temporal summation, as has been reported previously (for eample, Barlow, 1958a).

Figures 5 and 6 also show that an increase in background luminance alters the time course of temporal summation. At any conditioning-flash duration, when the level of background luminance is increased, the time course of temporal summation approaches a "U"-shaped function. This is particularly evident at longer conditioning flashes. The "U"-shaped function is symmetrical, maximum summation always occurring at the 50% delay interval. Alteration in the background luminance does not cause any asymmetry (that is, temporal shifts) of the summation function.

At the lowest background luminance (-3.0 log mL) the rods must be primarily stimulated since the

threshold of cones is higher than that level (-1.0 log mL); while at the highest background luminance (2.0 log mL) the cones must be predominantly stimulated, since most of the rods are saturated by that level of luminance. Both the rods and the cones must be active at the 0.0 log mL background luminance. Comparing the results obtained at the three background luminance levels, the following suggestions can be made:
(1) The magnitude of temporal summation is greater for rods than cones. (2) For shorter conditioning-flash durations, the function of the time course of temporal summation, for both rods and cones, is flat. (3) At longer conditioning-flash duration, the function of the time course of temporal summation, for both rods and cones, is non-monotonic. These observations indicate that the time course of temporal summation for both rods and cones is similar. However, the non-monotonic function is established at shorter conditioning-flash durations for cones than for rods.

Conditioning-Flash Duration

Figures 5 and 6 demonstrate that as the conditioning flash increases in duration, the percent change in test-flash threshold luminance increases at all background luminances and at all conditioning flash-test flash onset delays.

At any background luminance level, when the conditioning-flash duration is increased, the time course of temporal summation approaches a "U"-shaped function.

Inter-relationship between the Independent Variables

The general findings of this study are (as indicated in Figures 5 and 6) that an increase in background luminance and conditioning-flash duration decreases the magnitude of temporal summation and alters its time course, which is particularly evident at the two extreme delay intervals. The effect of each independent variable on temporal summation is enhanced when all the three variables are varied simultaneously. The inter-relationship between the three variables is evident from the following observations: (1) The effect of background luminance, in decreasing the magnitude of temporal summation and altering its time course, is enhanced at longer conditioning-flash durations. This is exemplified by the increased separation of the summation curves at longer conditioning flashes. (2) The conditioning-flash duration, at which the "U"-shaped function of the time course of temporal summation is established, is altered by a change in the background luminance level. An increase in the background luminance establishes the "U"-shaped pattern at shorter conditioning-flash durations. (3) The difference between the maximum summation (obtained at 50% delay interval) and the minimum summation (obtained at 100% delay interval) increases as the conditioning-flash duration and adaptation level increases.

A set of derived plots (Figures 9 through 14) for both observers further clarify the general findings discussed above.

In Figures 9 and 10, the ordinate shows the grand mean of the percent change in test-flash threshold luminance. This is obtained by taking an average of the data obtained at all delay intervals. On the abscissa is plotted the conditioning-flash duration. The background luminance level is the parameter. The results show that as the conditioning-flash duration and the level of background luminance increase, the magnitude of temporal summation decreases, irrespective of the delay interval.

The effect of background luminance and conditioning-flash duration on the magnitude of temporal summation is further verified by Figures 11 and 12, where the data are plotted only for the 100% delay interval. The 100% delay is selected because a

(Text continued on page 80)

Figure 9. The grand mean of the percent change in test-flash threshold at all conditioning flash-test flash onset delay intervals, as a function of the conditioning-flash duration. The background luminance (BL) is the parameter. Observer: JH

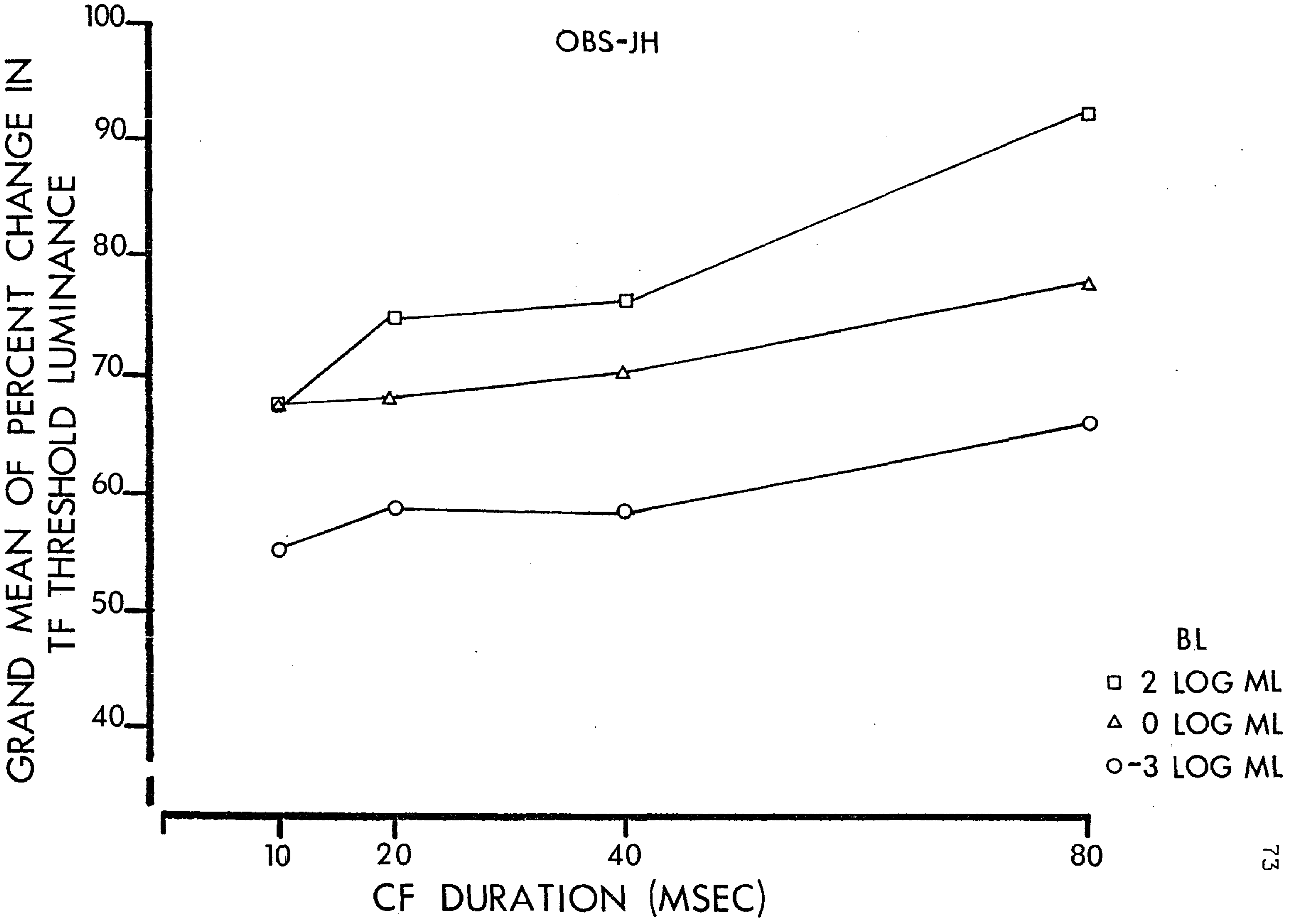

OBS-JH
GRAND MEAN OF PERCENT CHANGE IN TF THRESHOLD LUMINANCE
100
90
80
70
60
50
40
10
20
40
80
CF DURATION (MSEC)
BL
□ 2 LOG ML
△ 0 LOG ML
○ -3 LOG ML

Figure 10. The grand mean of the percent change in test-flash threshold at all conditioning flash-test flash onset delay intervals, as a function of the conditioning-flash duration. The background luminance (BL) is the parameter. Observer: FC

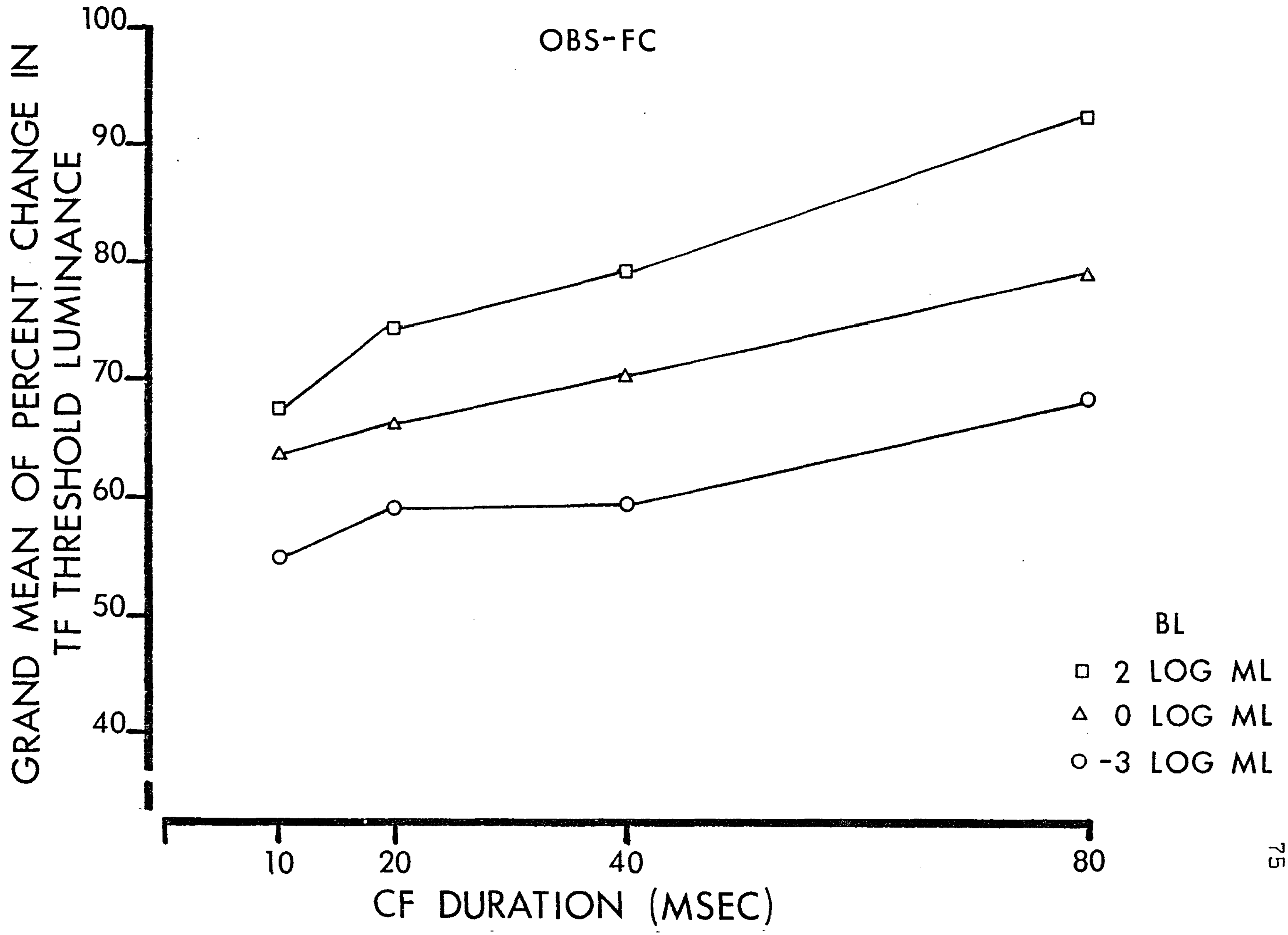

OBS-FC
GRAND MEAN OF PERCENT CHANGE IN TF THRESHOLD LUMINANCE
100
90
80
70
60
50
40
10
20
40
80
CF DURATION (MSEC)
BL
□ 2 LOG ML
△ 0 LOG ML
○ -3 LOG ML

Figure 11. The mean percent change in test-flash threshold luminance at 100% delay interval, as a function of the conditioning-flash duration. The different symbols correspond to the background luminances (BL) as indicated in the key. Observer: JH

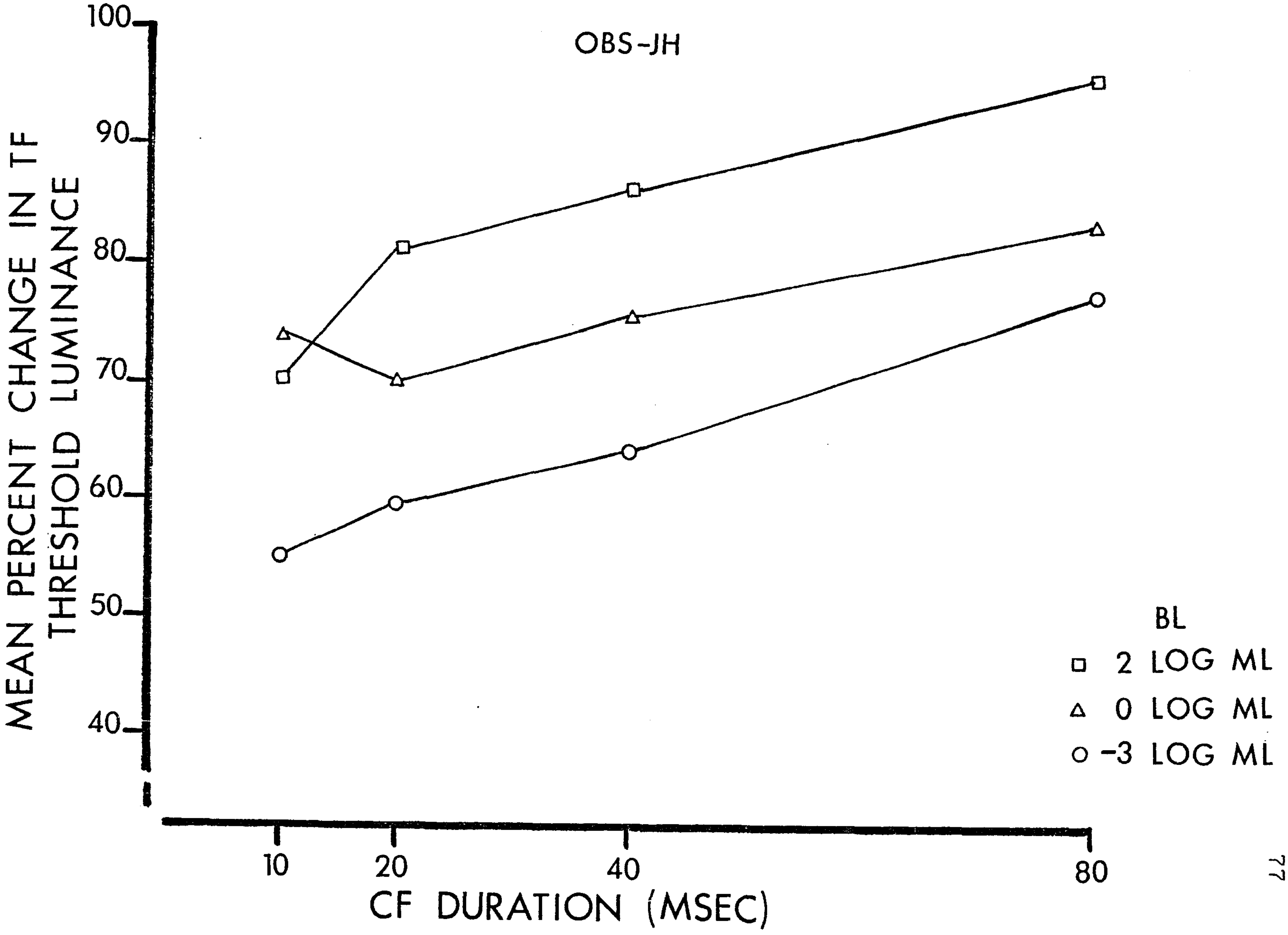
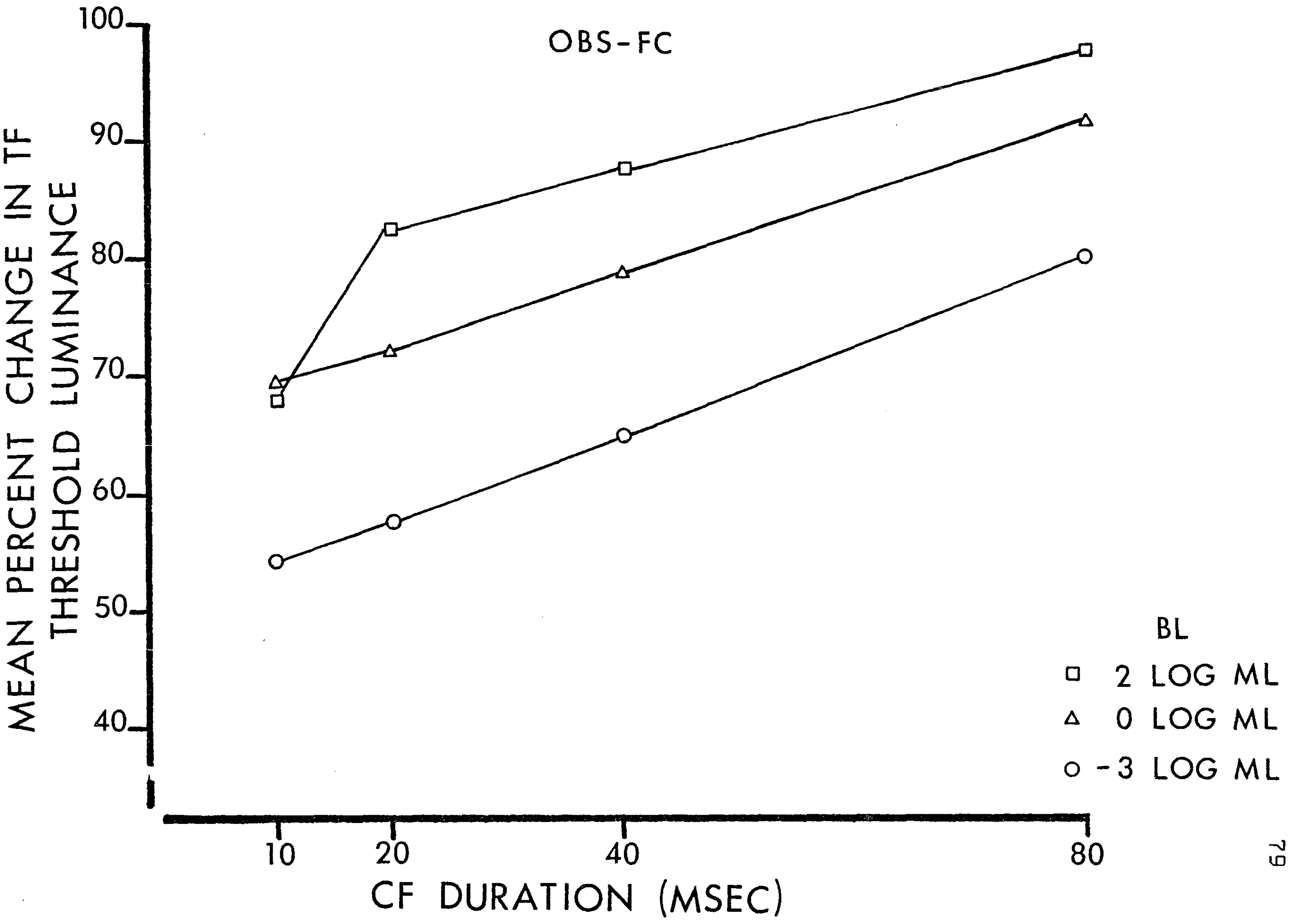

OBS-JH
MEAN PERCENT CHANGE IN TF THRESHOLD LUMINANCE
100
90
80
70
60
50
40
10
20
40
80
CF DURATION (MSEC)
BL
□ 2 LOG ML
△ 0 LOG ML
○ -3 LOG ML

Figure 12. The mean percent change in test-flash threshold luminance at 100% delay interval, as a function of the conditioning-flash duration. The different symbols correspond to the background luminances (BL) as indicated in the key. Observer: FC


OBS-FC
MEAN PERCENT CHANGE IN TF THRESHOLD LUMINANCE
100
90
80
70
60
50
40
10
20
40
80
CF DURATION (MSEC)
BL
□ 2 LOG ML
△ 0 LOG ML
○ -3 LOG ML

change in test-flash threshold luminance is observed at this interval even at shorter conditioning flashes and lower levels of background luminance. The data displayed in these figures once again confirm the general tendencies of the results, that the magnitude of temporal summation decreases as the background luminance and conditioning flash duration increases.

The data plotted in Figures 13 and 14 are also derived from the experimental data displayed in Figures 5 and 6. The percent change in test-flash threshold luminance is plotted as a function of the delay interval in milliseconds, for all conditioning-flash durations. Some of the delay intervals overlap, when the data obtained for all conditioning-flash durations are plotted. An average of the percent change in test-flash threshold luminance is obtained at each delay interval when there is more than one measurement. A single function is plotted through these averaged values. The three co-ordinates display the data obtained at three background luminance levels. The results show that as the delay interval in msec increases, there is an initial increase in temporal summation followed by a gradual decrease in summation. The non-linearity of the summation function is clearly evident at higher background luminances. At the

Figure 13. The mean percent change in test-flash threshold luminance as a function of the conditioning flash-test flash onset delay in msec, for all four conditioning-flash durations. The three different sets of co-ordinates represent the data obtained at different background luminances (BL). The different symbols correspond to the different conditioning-flash durations, as indicated in the key. Observer: JH

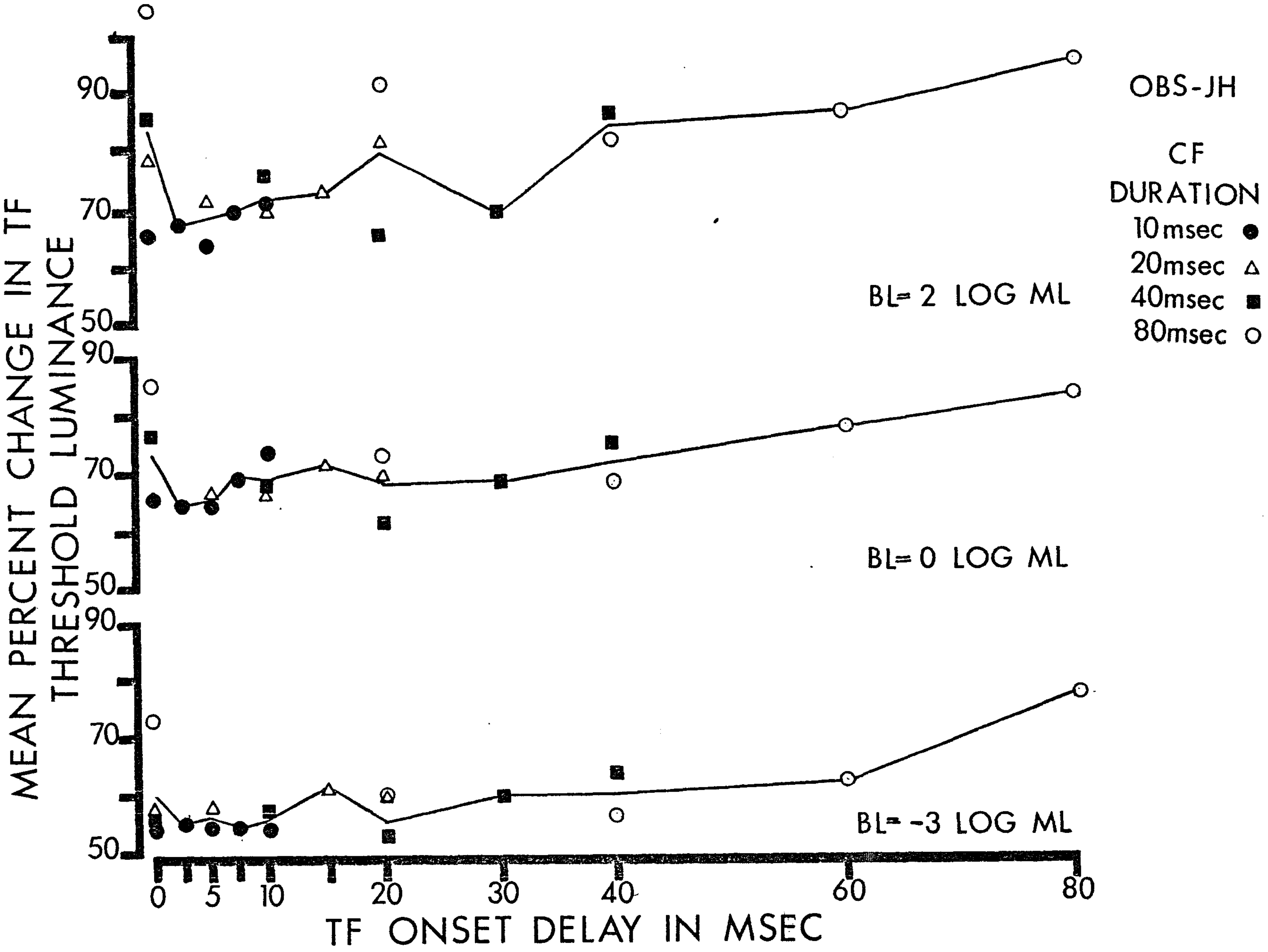
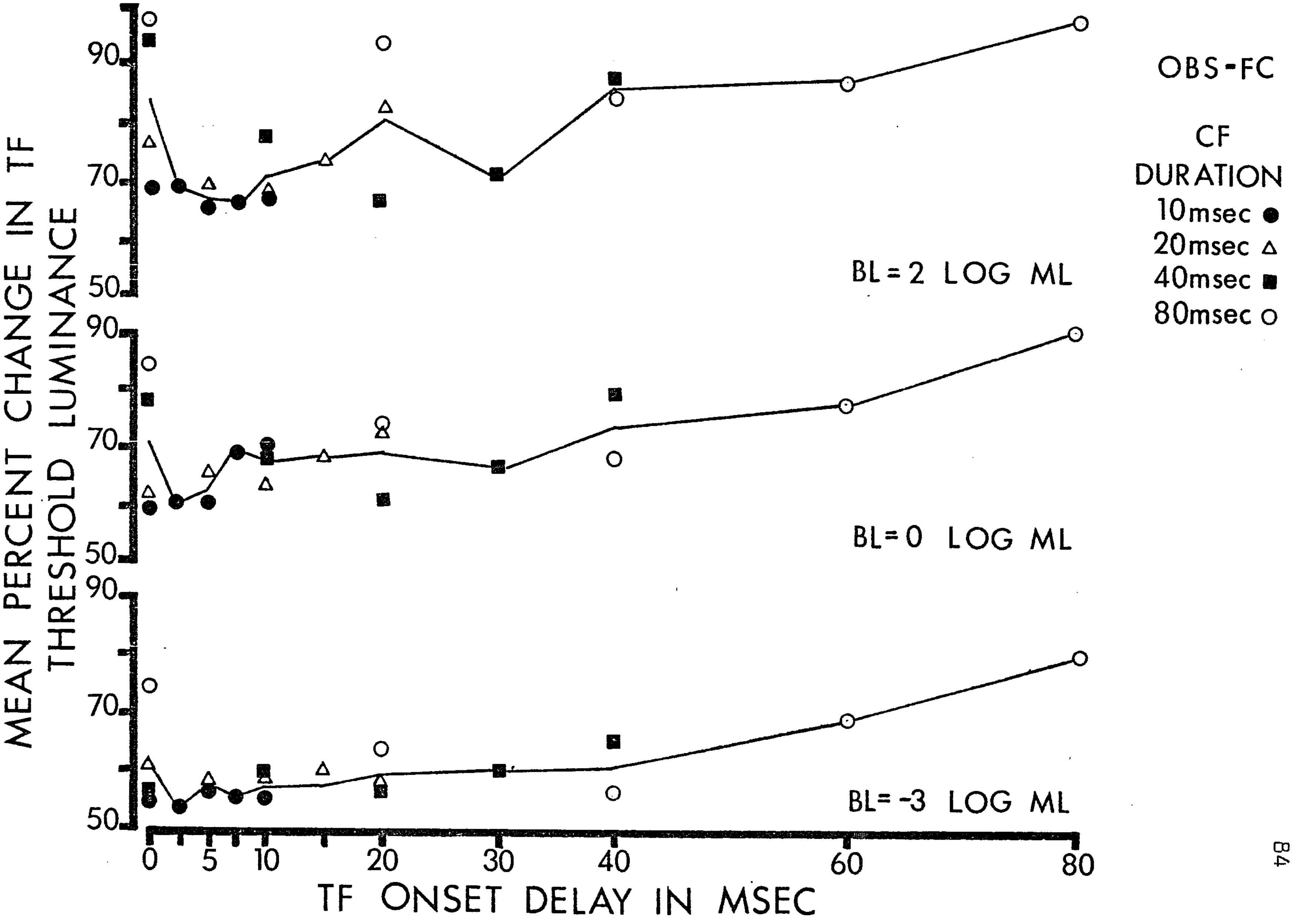

OBS-JH
CF DURATION
10msec ●
20msec △
40msec ■
80msec ○
BL= 2 LOG ML
BL= 0 LOG ML
BL= -3 LOG ML
MEAN PERCENT CHANGE IN TF THRESHOLD LUMINANCE
90
70
50
90
70
50
90
70
50
0
5
10
20
30
40
60
80
TF ONSET DELAY IN MSEC

Figure 14. The mean percent change in test-flash threshold luminance as a function of the conditioning flash-test flash onset delay in msec, for all four conditioning-flash durations. The three different sets of co-ordinates represent the data obtained at different background luminances (BL). The different symbols correspond to the different conditioning-flash durations, as indicated in the key. Observer: FC


MEAN PERCENT CHANGE IN TF THRESHOLD LUMINANCE
90
70
50
BL = 2 LOG ML
90
70
50
BL = 0 LOG ML
90
70
50
BL = -3 LOG ML
0
5
10
20
30
40
60
80
TF ONSET DELAY IN MSEC
OBS-FC
CF DURATION
10msec ●
20msec △
40msec ■
80msec ○

highest background luminance, there is an initial "dip" (indicating an increase in summation) in the summation function, followed by a gradual decrease in summation presumably leading to an asymptotic level.

Single-Flash Temporal Summation Data

The four conditioning flashes used in this study were equated for their luminous energy and not with reference to the observer's sensitivity to the flashes (that is, the sensation level). In order to find out whether these conditioning flashes were completely summated, it was necessary to obtain single-flash threshold data. Figures 15 and 16 display these single-flash control data obtained for both observers. In Figures 15 and 16, the log of the threshold luminance of the conditioning flash is plotted as a function of the log of the duration of the conditioning flash. The data are obtained at all three background luminance levels. An additional flash of 5 msec duration is included, based on the assumption that such a brief flash should be completely summated at all background luminances. Lines of -1.0 slope, indicating complete temporal summation, are drawn from the 5 msec data points in order to evaluate the rest of the data.

Results show that as the conditioning-flash

Figure 15. Single-flash luminance-duration reciprocity functions for observer JH. On the ordinate is expressed the log of conditioning-flash threshold luminance. On the abscissa is shown the conditioning-flash duration. The different symbols represent the different background luminance levels (BL), as indicated in the key.

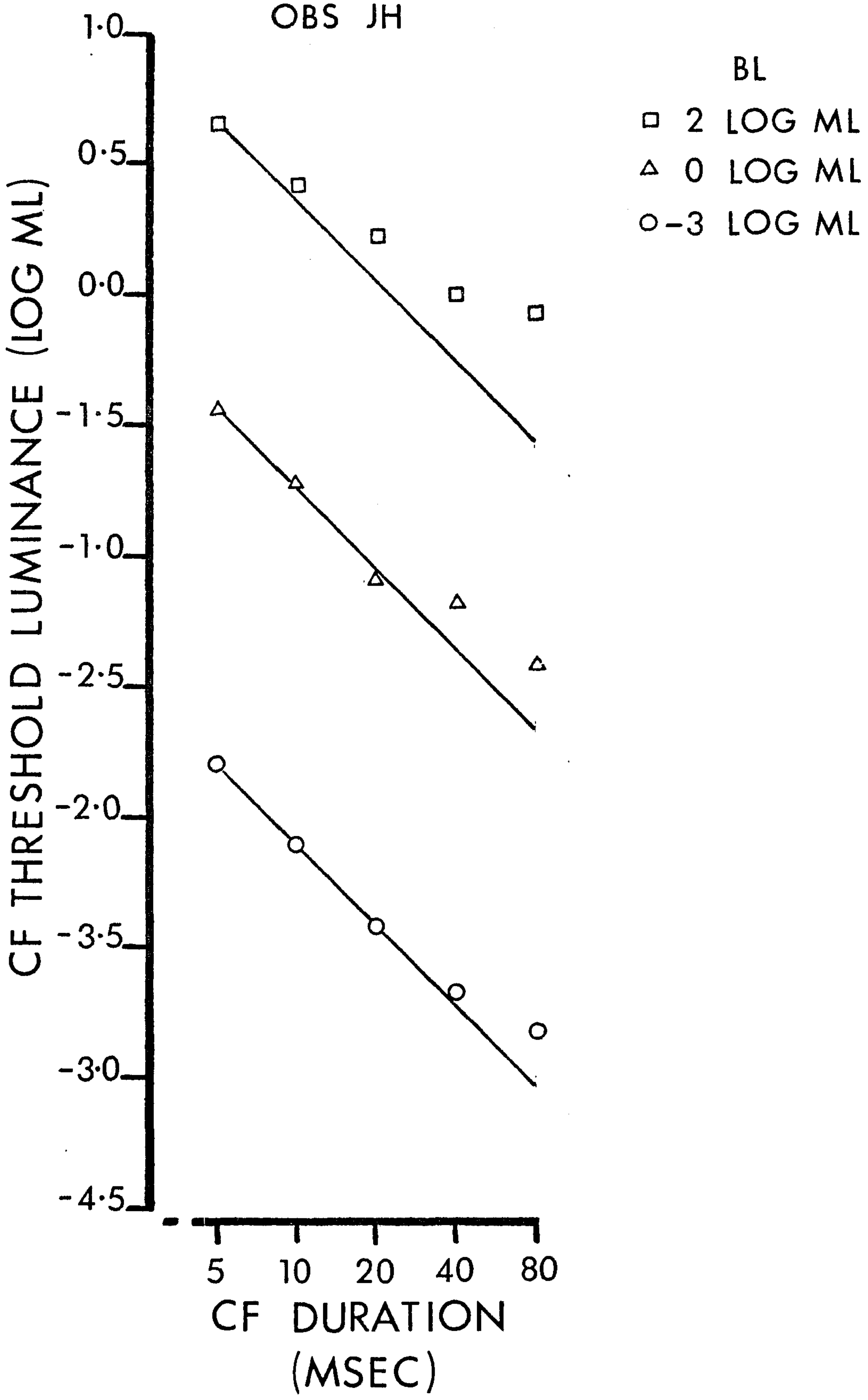
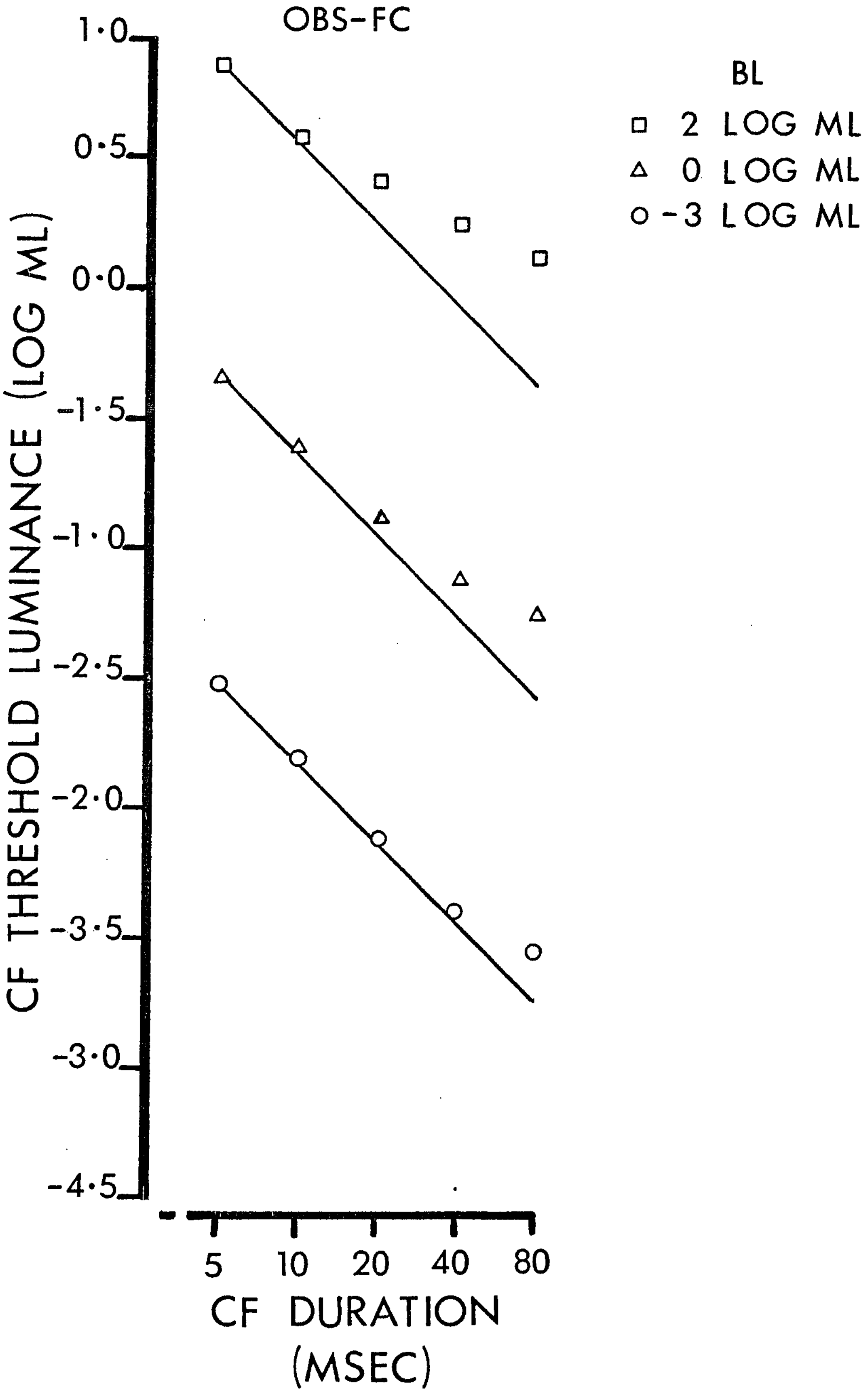

OBS JH
BL
□ 2 LOG ML
△ 0 LOG ML
○ −3 LOG ML
CF THRESHOLD LUMINANCE (LOG ML)
1·0
0·5
0·0
-1·5
-1·0
-2·5
-2·0
-3·5
-3·0
-4·5
5
10
20
40
80
CF DURATION
(MSEC)

Figure 16. Single-flash luminance-duration reciprocity functions for observer FC. On the ordinate is expressed the log of conditioning-flash threshold luminance. On the abscissa is shown the conditioning-flash duration. The different symbols represent the different background luminance levels (BL), as indicated in the key.


OBS-FC
BL
□ 2 LOG ML
△ 0 LOG ML
○ -3 LOG ML
CF THRESHOLD LUMINANCE (LOG ML)
1·0
0·5
0·0
-1·5
-1·0
-2·5
-2·0
-3·5
-3·0
-4·5
5
10
20
40
80
CF DURATION
(MSEC)

duration increases, its threshold luminance decreases at all background luminances. If perfect luminance-duration reciprocity were demonstrated, all data would adhere to the lines of -1.0 slope, regardless of the value of conditioning-flash duration and background luminance. Clearly, this is not the case. The data points tend to scatter away from the lines of -1.0 slope as the conditioning-flash duration and the background luminance increases.

In summary, the single-flash data presented in Figures 15 and 16 indicate that complete temporal summation is demonstrated for shorter conditioning-flash durations as the background luminance is increased. This finding is in agreement with the dual-flash data discussed previously. Since the rods are primarily stimulated at -3.0 log mL background luminance and the cones are primarily stimulated at 2.0 log mL background luminance, the single-flash data obtained at these background luminances are essentially demonstrating the differences in the magnitude of temporal summation between rods and cones.

Table 2 displays the single-flash threshold data obtained for both observers, for the 5 msec test flash, at all three background luminances. In each session, this was the control condition, which was compared with

TABLE 2

Test-Flash Threshold Luminance (log mL)
in the Single-Flash Condition

Observer	Background luminance (log mL)		
	-3.0	0.0	2.0
JH	-2.4	-1.57	0.97
FC	-2.68	-1.78	1.13

the test-flash threshold obtained in the dual-flash condition (conditioning flash + test flash), at all five delay intervals. The data presented in Table 2 indicate that the test-flash threshold luminance decreases as the background luminance increases. These results are in agreement with the experimental data (Figures 5 & 6) and the control data (Figures 15 & 16).

CHAPTER V

DISCUSSION

The results of the study demonstrate the effect of background luminance, conditioning-flash duration, and the stimulus-onset delay on the magnitude and the time course of temporal summation. The data reveal that an increase in background luminance and conditioning-flash duration decrease the magnitude of temporal summation, which is particularly evident at the shortest and at the longest delay intervals. These results are in agreement with previous studies that have investigated the effect of background luminance on temporal summation (for example, Barlow, 1958a; Graham & Kemp, 1938; Roufs, 1972a. See Chapter II - RELATED LITERATURE - for a more detailed review).

The magnitude of temporal summation measured at various delay intervals from the onset of the conditioning flash, gave the time course of temporal summation. The results indicate that an increase in background luminance and conditioning-flash duration alter the time course of temporal summation. At low background luminances and shorter conditioning flashes, the time course of temporal summation is a flat function. However, as the background luminance and the conditioning-flash duration increase, the time course of temporal summation approaches a "U"-shaped, non-monotonic function. In other words, at higher background luminances and longer conditioning flashes, summation is maximum at the middle of the conditioning-flash duration (50% delay interval), but is reduced at earlier and later delay intervals. Such a "U"-shaped function of the time course of temporal summation was also obtained by Battersby and Schuckman (1970), upon varying the conditioning-flash duration. The results obtained in this study are in agreement with their conclusion that visual temporal summation is non-linear.

Changes in background luminance do not cause any temporal shifts of the summation function. The time course of temporal summation function is very symmetrical, maximum summation always occurring at the 50% onset delay interval, regardless of the value of the conditioning-flash duration. The level of background luminance however, determines the conditioning-flash duration at which the "U"-shaped function is established. As the level of adaptation increases, the "U"-shaped function of the time course of temporal summation is established at shorter conditioning flashes.

The mechanism by which the background luminance influences the magnitude and the time course of temporal summation is not completely understood. Several theories have been put forward and mechanisms have been postulated to explain the effect. Some years ago Barlow (1958a; 1965) observed the inter-related effects of background luminance, stimulus size, and stimulus duration on the increment threshold, in that an increase in any of them resulted in an increase in the value of the increment threshold. A common factor underlying all three conditions is an increase in the amount of light to be transmitted to the higher visual system. Barlow also observed that an increase in the level of adaptation decreased the temporal and spatial summation. He suggested that a physiological mechanism such as lateral inhibition, which increases with an increase in the level of adaptation, may be responsible for the decrease in temporal and spatial summation. The results of the present study agree with Barlow's findings that either an increase in the background luminance or an increase in the stimulus duration results in a decrease in temporal summation. However, it does not provide any further evidence as to whether or not lateral inhibition is the underlying mechanism.

More recently, the idea that the level of background luminance influences temporal summation by altering the spatial properties of the retina, has been proposed by Uetsuki and Ikeda (1970). They have suggested that the temporal response to a brief flash of light is biphasic, that is, it has a positive and a negative component. The ganglion cells were considered to be the likely site at which such a response is obtained. They postulated that responses from the central excitatory region and the surrounding inhibitory region of the ganglion cell receptive field, temporally summate to give a biphasic response. Previous studies have shown that an alteration in the adaptation level changes the receptive field organization of the ganglion cells (Barlow, Fitzhugh & Küffler, 1957; Rodieck & Stone, 1965). Based on these findings, Uetsuki and Ikeda further suggested that the changes in the ganglion cell receptive field organization due to variations in the background luminance resulted in an alteration of the temporal response obtained at that level. Such changes in the temporal response were presumed to determine the variations in the shape of the temporal summation luminances.

Although Uetsuki and Ikeda's proposal is a very convincing one, it lacks empirical evidence.

Appropriate electrophysiological studies need to be conducted in order to investigate the temporal response to a flash of light at various levels of the visual system. However, until proper electrophysiological studies are conducted, systematic psychophysical studies can provide some answers. The present study can be considered a step towards providing some initial answers. The function of the time course of temporal summation obtained in this study is essentially a behavioral measurement of the temporal response to a light stimulus, during the exposure of the stimulus. Uetsuki and Ikeda have proposed that variations in the background luminance changes the temporal response of the visual system, which in turn alters the summation function. The present study supports this suggestion, based on the observation that changes in background luminance alters the shape of the time course of temporal summation.

Uetsuki and Ikeda, however, observed inhibition between the two temporally separated light flashes. A decrease in background luminance prolonged the stimulus onset interval at which inhibition between the two flashes was observed. No such inhibition was reported in the present study. The discrepency between the results obtained in this study and that obtained by

Uetsuki and Ikeda can be explained by the differences in the stimulus conditions. They used two brief flashes of equal duration, separated by a delay interval. In the present study, a brief test flash was presented during the exposure of the conditioning flash of varying durations. There was no dark interval between the two flashes. It is possible that the visual system responds differentially to two temporally separated light flashes as compared to two temporally superimposed light flashes.

The dual-flash technique used in this study permits the investigation of the changes exhibited by the visual system as the conditioning flash is in progress, from its onset to its offset. An extension of the present study would be of great value, where the test flash is presented at various delays, preceding and following the conditioning-flash exposure. Such a study would bridge the gap between the present study and that of Uetsuki and Ikeda.

Battersby and Schuckman (1970) have suggested a mechanism underlying the time course of temporal summation. They have postulated that there are two processes that can account for this phenomenon. One is the initial excitatory effect of the light flash, which takes some time to build up; and the other is the decay of this excitatory effect, which follows or overlaps the excitatory effect in time. A balance between these two processes determine the time course of temporal summation (see Chapter II - RELATED LITERATURE - for a complete discussion of these mechanisms). A hypothesis was forwarded that if changes in background luminance alter these two processes, it should also be reflected in the time course of temporal summation obtained at these background luminances (see Chapter I - INTRODUCTION). A corollary to this hypothesis is that changes in the time course of temporal summation observed at various background luminances is a reflection of the effect of background luminances on the underlying processes.

Results obtained in this study lead to the following suggestions regarding the effects of background luminance on the mechanisms underlying the time course of temporal summation: (1) Changes in background luminance might influence the two hypothetical processes of excitation and decay (as postulated by Battersby & Schuckman). This is reflected in the alteration of the time course of temporal summation from a flat function to a non-monotonic, "U"-shaped function. (2) The effect of background luminance on the two hypothetical processes of excitation and decay must be equal and symmetrical. This conclusion is supported by the symmetrical "U"-shaped functions of the time course of temporal summation that were obtained at higher background luminances. (3) The effect of background luminance on the two hypothetical processes of excitation and decay might be that of limiting its temporal parameters. An increase in background luminance might accelerate the rate of excitatory and decay effects of the stimulus flash. This is reflected in a breakdown in complete summation and establishment of the "U"-shaped summation function at shorter conditioning-flash durations, as the background luminance is increased.

There is no evidence of the existence of these postulated mechanisms by which the background luminance influences the time course of temporal summation. However, electrophysiological studies provide some evidence regarding the existence of similar mechanisms. Whitten and Brown (1973) for example, recorded the cone receptor potentials from the monkey retina and reported that an increase in the background luminance accelerates the decay of the receptor potentials. This means that the changes in time constants due to variation in the level of background luminance obtained behaviorally is already evident at the photoreceptor level.

The results of the present study therefore support Battersby and Schuckman's postulation, that there is a balance between the excitatory and the decay effects of the light flash on the visual system which determines the time course of temporal summation. A more critical test of this hypothesis would be an experimental separation of the excitatory and the decay processes. The two independent variables utilized in this study, namely, the conditioning-flash duration and the background luminance, when used with square-wave stimuli, were not able to obtain this separation. Varying the waveform of the conditioning flash may attain this goal. A recent study (Krauskopf, 1980) has noted that extensive viewing of a visual field whose luminance was varied as a sawtooth function in time, selectively raised the increment and decrement threshold, depending on the sign of the sawtooth. One can similarly vary the luminance of a conditioning flash as a sawtooth function of time and investigate its effect on the visual system by measuring the threshold of a test flash presented at various delays during the exposure of the conditioning flash, which gives the time course of temporal summation. It is suggested that by varying the sign of the sawtooth and its rise time, one can vary the rate at which the excitatory and the decay processes occur, which would also be reflected in the time course of temporal summation. Such an experiment would further substantiate the hypothesis forwarded by Battersby and Schuckman.

Frumkes, Sekular, Barris, Reiss and Chalupa (1973) have used the dual-flash technique, similar to the one used here, to investigate the interaction between rods and cones (see Chapter I - INTRODUCTION). They varied the wavelengths of the conditioning flash and the test flash so as to stimulate either the rods or the cones. They obtained "U"-shaped functions of the time course of temporal summation similar to that observed in this study. When the conditioning flash and the test flash were homochromatic, maximum summation occurred at the middle of the conditioning-flash duration; however, when the two flashes were heterochromatic, temporal shifts of the summation functions were observed. The direction of the temporal shift depended on the wavelength of the conditioning flash and the test flash. The authors interpreted their results to be a reflection of the differences in latencies between rods and cones.

Although the two extreme background luminances used in this study maximized the conditions under which either rods or cones were active, no temporal shifts in the time course of temporal summation were observed. One possible explanation is that conditioning and test flashes used in this study were achromatic and previous studies have not observed temporal shifts of summation functions under these conditions. Future studies may investigate the time course of temporal summation at various background luminances using conditioning and test flashes of various wavelengths, so as to selectively stimulate either rods or cones. Based on the finding that the level of background luminance alters the latency of the visual response (for example, Hartline, 1940), it is suggested that variations in the background luminance may further influence the temporal shift of the summation function produced by the heterochromatic conditioning and test flashes. Such a study would provide information regarding the latencies of rods and cones and the manner in which they interact with each other under different conditions of adaptation.

A comparision between the magnitude and the time course of temporal summation obtained at the two extreme luminances in this study could reveal the differences in the summative capacity of rods and cones. This suggestion is based on the assumption that the rods must be primarily active under -3.0 log mL background luminance and the cones must be predominantly stimulated at 2.0 log mL background luminance (see Chapter IV - RESULTS - page 69). The obtained results indicate that the magnitude of temporal summation of rods is greater than that of cones. The time course of temporal summation is similar for rods and cones. However, the temporal parameters of rods are slower than that of cones. These suggestions are in agreement with the electrophysiological findings discussed previously (Fain & Dowling, 1973; Whitten & Brown, 1973).

Variation in the level of adaptation alter the two fundamental visual functions, namely, detection and discrimination. Parallel to such changes in functions are the changes in the summative and the resolving capacity of the eye. Under low levels of adaptation, the summative capacity increases, which enhances detection; while at higher levels of adaptation, the resolving power of the eye increases which aids in discrimination. The similarity between the time course of temporal summation obtained in this study and the time course of temporal resolution obtained by Shickman (see Chapter II - RELATED LITERATURE - page 33) suggests that although temporal summation and temporal resolution seem to be two opposite functions, there is a basic similarity between the mechanisms underlying the two functions. Future studies may investigate these phenomena using other techniques of stimulation and response measurements. Such studies would provide information as to whether or not the non-monotonic behaviour of the visual system is specific for the conditions of stimulation (used in this study), or whether it is a property of the visual system in general.

BIBLIOGRAPHY

Aguilar, M., & Stiles, W. S. Saturation of the rod mechanism of the retina at high levels of stimulation. Optica Acta, 1954, 1, 59-65.

Baker, H. D. The instantaneous threshold and early dark adaptation. Journal of the Optical Society of America, 1953, 43, 798-803.

Baker, H. D. Initial stages of light and dark adaptation. Journal of the Optical Society of America, 1963, 53, 98-103.

Barlow, H. B. Increment thresholds at low intensities considered as signal/noise discriminations. Journal of Physiology, 1957, 136, 469-488.

Barlow, H. B. Temporal and spatial summation in human vision at different background intensities. Journal of Physiology, 1958, 141, 337-350.

Barlow, H. B. Dark-adaptation: A new hypothesis. Vision Research, 1964, 4, 47-58.

Barlow, H. B. Optic nerve impulses and Weber's law. Cold Spring Harbor Symposium of Quantitative Biology, 1965, 30, 539-546.

Barlow, H. B., Fitzhugh, R., & Küffler, S. W. Change of organization in the receptive fields of the cat's retina during dark adaptation. Journal of Physiology, 1957, 137, 338-354.

Battersby, W. S., & Defabaugh, G. L. Neural limitations of visual excitability: After-effects of subliminal stimulation. Vision Research, 1969, 9, 757-768.

Battersby, W. S., & Schuckman, H. The time course of temporal summation. Vision Research, 1970, 10, 263-273.

Battersby, W. S., & Wagman, I. H. Neural limitations of visual excitability. IV: Spatial determinants of retrochiasmal interaction. American Journal of Physiology, 1962, 203, 359-365.

Baumgardt, E., & Hillmann, B. Duration and size as determinants of peripheral retinal response. Journal of the Optical Society of America, 1961, 51, 340-344.

Beams, J. W. The eye as an integrator of short light flashes. Journal of the Optical Society of America, 1935, 25, 48.

Berenhaus, I. One-pulse and two-pulse measures of visual temporal integration. Unpublished doctoral dissertation, City University of New York, 1980.

Biersdorf, W. R. Critical duration in visual brightness discrimination for retinal areas of various sizes. Journal of the Optical Society of America, 1955, 45, 920-925.

Bloch, A. M. Experiences sur la vision. C. R. Soc. Biol., Paris, 1885, 37, 493-495.

Bouman, M. A., & van den Brink, G. On the integrate capacity in time and space of the human peripheral retina. Journal of the Optical Society of America, 1952, 42, 617-620.

Boynton, R. M. Some temporal factors in vision. In W. A. Rosenblith (Ed.), Sensory communication. New York: Wiley, 1961.

Boynton, R. M. Discrimination of homogenous double pulses of light. In D. Jameson & L. M. Hurvich (Eds.), Handbook of sensory physiology, Vol. VII/4, Visual psychophysics. Berlin: Springer-Verlag, 1972.

Brown, K. T., & Murakami, M. Rapid effects of light and dark adaptation upon the receptive field organization of S-potentials and late receptor potentials. Vision Research, 1968, 8, 1145-1171.

Brown, K. T., & Watanabe, K. Isolation and identification of a receptor potential from the pure cone fovea of the monkey retina. Nature, 1962, 193, 958-960.

Bruder, G. E., & Kietzman, M. L. Visual temporal integration for threshold, signal detectibility, and reaction time measures. Perception and Psychophysics, 1973, 13, 293-300.

Campbell, F. W., & Rushton, W. A. H. Measurement of the scotopic pigment in the living human eye. Journal of Physiology, 1955, 130, 131-147.

Clark, W. C., & Blackwell, H. R. Visual detection thresholds of single and double light pulses, and the temporal element contribution hypothesis. University of Michigan, Engineering Research Institute Report, 1958, 2144-343-T.

Crawford, B. H. Visual adaptation in relation to brief conditioning stimuli. Proceedings of the Royal Society (London), Ser. B, 1947, 134B, 283-300.

Davy, E. The intensity-time relation for multiple flashes of light in the peripheral retina. Journal of the Optical Society of America, 1952, 42, 937-941.

Dowling, J. E. Neural and photochemical mechanisms of visual adaptation in the rat. Journal of General Physiology, 1963, 46, 1287-1300.

Dowling, J. E. The site of visual adaptation. Science, 1967, 155, 273-279.

Dowling, J. E., & Ripps, H. Adaptation in skate photoreceptors. Journal of General Physiology, 1972, 60, 698-719.

Eccles, J. C., & Sherrington, C. S. Studies on the flexor reflex. I Latent period. Proceedings of the Royal Society (London), 1931, B107, 511-534.

Eriksen, C. W., Hamlin, R. M., & Breitmeyer, R. J. Temporal factors in visual perception as related to aging. Perception and Psychophysics, 1970, 7, 354-356.

Fain, G. L., & Dowling, J. E. Intracellular recordings from single rods and cones in the mudpuppy retina. Science, 1973, 180, 1178-1181.

Frumkes, T. E., & Sturr, J. F. Spatial and luminance factors determining visual excitability. Journal of the Optical Society of America, 1968, 58, 1657-1662.

Frumkes, T. E., Sekuler, M. D., Barris, M. C., Reiss, E. H., & Chalupa, L. M. Rod-cone interaction in human scotopic vision - I. Temporal analysis. Vision Research, 1973, 13, 1269- 1282.

Gilmer, T. E. The integrating power of the eye for short flashes of light. Journal of the Optical Society of America, 1937, 27, 386-388.

Graham, C. H., & Kemp, E. H. Brightness discrimination as a function of the duration of the increment in intensity. Journal of General Physiology, 1938, 21, 635-650.

Graham, C. H., & Margaria, R. Area and the intensity-time relation in the peripheral retina. American Journal of Physiology, 1935, 113, 299-305.

Granit, R., & Davis, W. A. Comparative studies on the peripheral and the central retina. IV. Temporal summation of subliminal visual stimuli and the time course of the excitatory after-effect. Vision Research, 1931, 10, 644-653.

Granit, R., Holmberg, T., & Zewi, M. On the mode of action of visual purple on the rod cell. Journal of Physiology, 1938, 94, 430-440.

Green, D. G., Dowling, J. E., Siegel, I. M., & Ripps, H. Retinal mechanisms of visual adaptation in the skate. Journal of General Physiology, 1975, 65, 483-502.

Hartline, H. K. Intensity and duration in the excitation of single photoreceptor units. Journal of Cellular and Comparative Physiology, 1934, 5, 229-247.

Hartline, H. K. The nerve messages in the fibers of the visual pathway. Journal of the Optical Society of America, 1940, 30, 239-247.

Hecht, S. Vision: II. The nature of the photoreceptor process. In C. Murchison (Ed.), A handbook of general experimental psychology. Worchester, Mass.: Clark University Press, 1934.

Hecht, S., & Hsia, Y. Dark adaptation following light adaptation to red and white lights. Journal of the Optical Society of America, 1945, 35, 261-267.

Hecht, S., Haig, C., & Chase, A. M. The influence of light adaptation on subsequent dark adaptation of the eye. Journal of General Physiology, 1937, 20, 831-850.

Hecht, S., Haig, C., & Wald, J. Dark adaptation of retinal fields of different size and location. Journal of General Physiology, 1935, 19, 321-337.

Herrick, R. M. Foveal luminance discrimination as a function of the duration of the decrement or increment in luminance. Journal of Comparative Physiological Psychology, 1956, 49, 437-443.

Herrick, R. M. Increment thresholds for two identical flashes. Journal of the Optical Society of America, 1972, 62, 104-110.

Hood, D. C., Hock, P. A., & Grover, B. G. Dark adaptation of the frog's rods. Vision Research, 1973, 13, 1953-1963.

Ikeda, M. Temporal summation of positive and negative flashes in the visual system. Journal of the Optical Society of America, 1965, 55, 1527-1534.

Kahneman, D., & Norman, J. The time-intensity relation in visual perception as a function of observer's task. Journal of Experimental Psychology, 1964, 68, 215-220.

Karn, H. W. Area and the intensity-time relation in the fovea. Journal of General Psychology, 1936, 14, 360-369.

Keller, M. The relation between the critical duration and intensity in brightness discrimination. Journal of Experimental Psychology, 1941, 28, 407-418.

Kelly, D. H. Theory of flicker and transient responses. I. Uniform fields. Journal of the Optical Society of America, 1971a, 61, 537-546.

Kelly, D. H. Theory of flicker and transient responses. II. Counterphase gratings. Journal of the Optical Society of America, 1971b, 61, 632-640.

Kietzman, M. L. How many characteristics of temporal summation? The Behavioral and Brain Sciences, 1979, 2, 266-268.

Kleinschmidt, J., & Dowling, J. E. Intracellular recordings from gecko photoreceptors during light and dark adaptation. Journal of General Physiology, 1975, 66, 617-648.

Krauskopf, J. Discrimination and detection of changes in luminance. Vision Research, 1980, 20, 671-677.

Long, G. E. The effect of duration of onset and cessation of light flash on the intensity-time relation in the peripheral retina. Journal of the Optical Society of America, 1951, 41, 743-747.

Matin, L. Binocular summation at the absolute threshold of peripheral vision. Journal of the Optical Society of America, 1962, 52, 1276-1286.

Matin, L. Critical duration, the differential luminance threshold, critical flicker frequency, and visual adaptation: A theoretical treatment. Journal of the Optical Society of America, 1968, 58, 404-415.

Normann, R. A., & Werblin, F. S. Control of retinal sensitivity: I. Light and dark adaptation of vertebrate rods and cones. Journal of General Physiology, 1974, 63, 37-61.

Pierōn, H. The sensations: Their functions, processes, and mechanisms. Paris: Editions Gallimard, 1945. Translated by M. H. Pierenne & B. C. Abbott, New Haven: Yale University Press, 1952.

Pirenne, M. H. Dark-adaptation and night vision. In H. Davson (Ed.), The eye. New York and London: Academic Press, 1962.

Poggio, G. F., Baker, F. H., Lamarre, Y., & Sanseverino, E. Afferent inhibition at input to visual cortex of the cat. Journal of Neurophysiology, 1969, 32, 892-915.

Riggs, L. A. Vision. In J. W. Kling & L. A. Riggs (Eds.), Woodworth and Schlosberg's experimental psychology (3rd ed.). New York: Holt, Rinehart and Winston, Inc., 1971.

Rodieck, R. W., & Stone, J. Analysis of receptive fields of cat retinal ganglion cells. Journal of Neurophysiology, 1965, 28, 833-849.

Roufs, J. A. J. Dynamic properties of vision - I. Experimental relationships between flicker and flash thresholds. Vision Research, 1972, 12, 261-278.

Roufs, J. A. J. Dynamic properties of vision - III. Twin flashes, single flashes and flicker fusion. Vision Research, 1973, 13, 309-323.

Rushton, W. A. H. Rhodopsin measurement and dark-adaptation in a subject deficient in cone vision. Journal of Physiology, 1961, 156, 193-205.

Rushton, W. A. H. Cone pigment kinetics in the protanope. Journal of Physiology, 1963b, 168, 374-388.

Rushton, W. A. H., & Cohen, R. D. Visual purple level and the course of dark adaptation. Nature (London), 1954, 173, 301-304.

Rushton, W. A. H., & Henry, G. H. Bleaching and regeneration of cone pigments in man. Vision Research, 1968, 8, 617-631.

Rushton, W. A. H., Campbell, F. W., Hagins, W. A., & Brindley, G. S. The bleaching and regeneration of rhodopsin in the living eye of the albino rabbit and of man. Optica Acta, 1955, 1, 183-190.

Shickman, G. M. Brief illumination and visual temporal resolving power. Unpublished doctoral dissertation, Harvard University, 1960.

Sillman, A. J., Owen, W. G., & Fernandez, H. R. Rapid dark adaptation in the frog rod. Vision Research, 1973, 13, 393-402.

Sperling, H. G., & Jolliffe, C. L. Intensity-time relationship at threshold for spectral stimuli in human vision. Journal of the Optical Society of America, 1965, 55, 191-199.

Sperling, H. G., & Sondhi, M. M. Model for visual luminance discrimination and flicker detection. Journal of the Optical Society of America, 1968, 58, 1133-1145.

Stewart, B. R. Temporal summation during dark adaptation. Journal of the Optical Society of America, 1972, 62, 449-457.

Uetsuki, T., & Ikeda, M. Study of temporal visual response by the summation index. Journal of the Optical Society of America, 1970, 60, 377-381.

van den Brink, G., & Bouman, M. A. Variation of integrative actions in the retinal system: An adaptational phenomenon. Journal of the Optical Society of America, 1954, 44, 616-620.

Wagman, I. H., & Battersby, W. S. Neural limitations of visual excitability: II. Retrochiasmal interaction. American Journal of Physiology, 1959, 197, 1237-1241.

Werblin, F. S. Control of retinal sensitivity: II. Lateral interactions at the outer plexiform layer. Journal of General Physiology, 1974, 63, 62-87.

Werblin, F. S., & Copenhagen, D. R. Control of retinal sensitivity: III. Lateral interactions at the inner plexiform layer. Journal of General Physiology, 1974, 63, 88-110.

Whitten, D. N., & Brown, K. T. The time courses of late receptor potentials from monkey cones and rods. Vision Research, 1973, 13, 107-135.

Whitten, D. N., & Brown, K. T. Slowed decay of the monkey's cone receptor potential by intense stimuli, and protection from this effect by light adaptation. Vision Research, 1973, 13, 1659-1667.

Zwislocki, J. J. Theory of temporal auditory summation. Journal of the Acoustical Society of America, 1960, 32, 1046-1060.

Zwislocki, J. J. Temporal summation of loudness: An analysis. Journal of the Acoustical Society of America, 1969, 46, 431-441.