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WHITE, Charles Wayne, 1944-
VISUAL MASKING AND THE TEMPORAL COURSE OF
LATERAL INHIBITION IN THE HUMAN VISUAL SYSTEM.

Stanford University, Ph.D., 1970
Psychology, experimental

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VISUAL MASKING AND THE TEMPORAL COURSE OF LATERAL INHIBITION IN THE HUMAN VISUAL SYSTEM

A DISSERTATION

SUBMITTED TO THE DEPARTMENT OF PSYCHOLOGY

AND THE COMMITTEE ON GRADUATE STUDIES

OF STANFORD UNIVERSITY

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

By

Charles Wayne White

August 1970

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PREFACE

The research that is reported here was conducted at the New School for Social Research in New York. Many people there contributed to the making of this dissertation, and I am grateful for all of their contributions. Let me express my appreciation especially to Laura Gleason and Eric Sigman, for their patience and skill as observers, and to Douglas Hyman, for his assistance and for running the experiment whenever I was the observer. Mrs. Regina Wachtel also deserves thanks for typing the final draft.

My deepest gratitude goes to Professor Leon Festinger; during my career as a graduate student, his advice has inevitably been helpful with all kinds of problems. The research was supported by Grant Number MH-16327 from the National Institutes of Health to Dr. Festinger, and by a predoctoral fellowship from the National Institute of Mental Health.

Finally, let me thank my wife Sandy for her encouragement and her endless patience through some difficult years.

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ABSTRACT

Lateral inhibition has been suggested to account for many visual phenomena, but the temporal properties of inhibition have often been ignored in favor of steady-state conditions. Some electrophysiological experiments reveal the importance of excitatory and inhibitory transients. Moreover, visual masking experiments suggest that similar transient responses are active in temporal phenomena of human vision.

To determine the role played by transient inhibition in masking and metacontrast, increment thresholds for 5 msec. foveal test flashes on an adapting field were obtained at various times before and after the onset of a 500 msec. masking annulus. Since the effectiveness of a brief test flash is a measure of the magnitude of the inhibitory transient at various points in its time course, the visual masking functions constructed from the threshold data represented an indirect picture of the temporal course of lateral inhibition.

The results clearly demonstrated that increasing the retinal illuminance of the masking annulus increased the magnitude and decreased the latency of the peaks of the masking functions. As the retinal illuminance of the masking flash was increased by three log units, the peak masking effect for three observers shifted from test flashes presented 50 msec. after the mask onset to flashes presented simultaneously with the mask.

The masking functions were interpreted in terms of a transient inhibition theory, and the results were compared with other visual masking theories.

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Chapter I

LATERAL INHIBITION AND VISUAL MASKING

Lateral inhibition is a neural process by which certain neurons inhibit the activity of other neurons. Since it is a fundamental process in visual systems, it has been proposed to account for many visual phenomena. Weisstein (1968, p. 499) referred to lateral inhibitory explanations for contour formation, flicker fusion, light and dark adaptation, brightness constancy, figural aftereffects, and Mach bands. Simultaneous brightness contrast (Cornsweet & Teller, 1965; Alpern & David, 1959) should be added to the list along with many suggestions that visual masking and metacontrast involve lateral inhibition (Ratliff, Hartline, & Miller, 1963; Robinson, 1966, 1968; Dember & Purcell, 1967; Purcell, Stewart, & Dember, 1968; Schiller, 1968; Weisstein, 1968; Battersby & Sturr, 1970; and Shickman, 1970).

Several results from psychophysical experiments suggest that the time course of lateral inhibition is an important factor in human vision (Sherrington, 1897; Békésy, 1968a, 1968b; Ratliff, 1965). For example, in a series of subjective color experiments, Festinger, Allyn, and White (in preparation) found that observers matched certain spatial-temporal combinations of achromatic stimuli with comparison fields of different hues and saturations. In addition to chromatic shifts, however, they also found that brightness matches of certain pairs of stimuli differed reliably by more than one-half log unit, although the luminances of the stimuli in each pair were the same

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(Festinger, 1969). For example, a small 75 msec. test stimulus with most of its energy in the first 50 msec. was compared with another 75 msec. test stimulus that contained most of its energy in the last 50 msec. If each test stimulus was presented simultaneously with a 75 msec. square pulse in adjacent areas, observers set the matching field to lower luminance levels to match the test stimulus that had most of its energy concentrated in the early part of the pulse.

The concept of a temporal transient of inhibition was useful in explaining these results as follows: A transient burst of inhibition from the adjacent area inhibited the early part of the on-response to the test-stimulus. The later test stimulus excitation was inhibited less than the early on-response, since the inhibitory activity decreased during the 75 msec. period. Thus the subjective color results implicated transient overshoots of inhibition. This led to a search for electrophysiological studies of the time course of inhibition. The main interest, of course, was in the transient inhibitory responses to suddent increments in illumination.

Temporal Properties of Lateral Inhibition

In the early work on lateral inhibition, the temporal properties of the neural responses were often neglected in favor of steady-state firing rates that were attained after the test units had adapted to the stimulus pattern. Since studies of the steady-state responses of lateral inhibition ignore the temporal transients that almost invariably occur, the extensive literature that deals with that problem is not covered here in detail. The mechanisms of lateral

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inhibition have been extensively investigated in the lateral eye of the horseshoe crab Limulus. Ratliff (1965) and Hartline (1969) provided excellent reviews of that work.

The temporal properties of lateral inhibition in Limulus were investigated by Ratliff, Hartline, & Miller (1963). They observed transient undershoots in the firing rate of one ommatidium when surrounding ommatidia were suddenly illuminated. They also simulated a backward masking experiment by stimulating a test ommatidium with a brief low-intensity test flash at various times before and after an adjacent group of ommatidia received a high-intensity flash. The relatively longer latency of excitation in the test unit produced maximum inhibitory effects when the test flash was presented before the adjacent (masking) flash.

Lange (1965) extended the study of temporal properties of lateral inhibition in Limulus. He controlled the temporal properties of the lateral inhibition more effectively by antidromic stimulation than by stimulating with pulses of light (Hartline, 1969). Lange reported several important temporal properties of the Limulus lateral inhibitory system: (a) The latency of inhibition depended on the input amplitude and the previous level of inhibition. (b) There was frequent transient overshooting of inhibitory effects. (c) The steady-state inhibition increased linearly with inhibitory input. (d) The offset of inhibition was rapid and was followed by post-inhibitory rebounds. Lange added new terms to the steady-state equations (Ratliff, 1965) to account for the temporal dynamics of the

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system. Although the extended model accounted satisfactorily for the Limulus data, the applicability of the model to temporal properties of human vision was unclear.

The mechanism that produces inhibitory transients in a vertebrate retina, that of the mudpuppy Necturus, has been elucidated by Werblin and Dowling (1969). Responses of neurons in different retinal layers were recorded intracellularly, and single cells were subsequently stained for histological identification. Receptors and horizontal cells responded to photic stimulation anywhere in their receptive fields with relatively slow hyperpolarizations. Some bipolar cells responded to central stimulation by hyperpolarizing, but others responded by depolarizing. In both cases the central responses were antagonized by peripheral illumination. The central-peripheral antagonism was presumably mediated by horizontal cells, since they had larger receptive fields than the receptors and made synaptic contacts with receptor terminals and bipolar dendrites. The first spike activity was observed in the inner plexiform layer in amacrine cells, which were driven by bipolars and responded transiently to changes in illumination. Most of the retinal ganglion cells followed the amacrine response and responded to temporal transients with on- and off-bursts of impulses. A few ganglion cells, probably driven by bipolars, responded directly to the steady-state level of illumination.

Thus lateral inhibition takes place in at least two levels of the Necturus retina. In the outer plexiform layer, horizontal cells inhibit adjacent bipolars to form networks that detect spatial differ-

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ences in illumination. In the inner plexiform layer, amacrine cells inhibit other amacrines and drive ganglion cells to form networks that respond primarily to temporal transients of illumination. The principle difference to be expected between the Necturus retina and primate retinas is in the relative numbers of transiently-responding and tonically-responding ganglion cells (Dowling & Werblin, 1969); Dowling & Boycott, 1966). The primate retina has relatively fewer amacrine-driven ganglion cells; most of its ganglion cells are driven directly by bipolars.

Some of the most important physiological experiments used stimuli that produce visual masking in human observers. Responses of single cells in the lateral geniculate nucleus of the cat were recorded, and post-stimulus spike frequency histograms were constructed by averaging the temporal responses. Schiller (1968) recorded single-unit responses as he varied the temporal separation between a brief test stimulus and a subsequent masking stimulus. The magnitude of the inhibitory effect increased steadily as the temporal separation of the two stimuli was decreased from 100 to 10 msec. for both overlapping stimuli (concentric discs) and nonoverlapping stimuli (disc and ring). Grusser, Petersen, and Sasowski (1965) obtained similar results with nonoverlapping stimuli.

Poggio, Baker, Lamarre, and Sanseverino (1969) obtained more complete results for eight on-center units in the geniculo-cortical radiation fibers. Nonoverlapping disc and ring stimuli were adjusted for the size of each cell's receptive field so that the disc stimulated mainly the excitatory center and the ring stimulated the

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inhibitory surround. Single-cell responses were recorded for responses to the disc alone, to the ring alone, and to both stimuli separated by various temporal intervals. (Negative delays mean that the ring followed the disc.) As the test stimulus (disc) delay was increased from -25 msec., the magnitude of the disc plus ring responses decreased steadily until they reached minimum values at delays of zero to 20 msec. As the delay of the disc was further increased to 120 msec., the responses increased and eventually reached the same magnitude as the disc-alone responses.

Thus there is ample physiological evidence for the temporal transients of inhibition that were suggested to explain the subjective color brightness matches. The problem that remains is to interpret the visual masking data in terms of transient lateral inhibition.

Visual Masking

"Visual masking" refers to the decreased effectiveness of one stimulus as a function of the presentation of another stimulus at nearly the same instant (Kahneman, 1968). Depending on whether the masking stimulus occurs before or after the masked (test) stimulus, the masking is called forward or backward masking respectively.

In the literature, various terms are used to classify visual masking paradigms. Some make a distinction between situations that involve spatially overlapping stimuli and those in which the test and masking stimuli are presented to different retinal areas. In the latter case, the situation is called metacontrast. Another classification of

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stimulus conditions reserves "metacontrast" for cases of backward masking in which the stimuli do not overlap spatially and uses "paracontrast" for nonoverlapping forward masking (Kahneman, 1968).

Readers of the experimental literature on visual masking are sometimes confused by the ambiguity of several expressions that have been used to refer to the differences in the times of presentation of the two stimuli. For example, different experimenters have used exposure asynchrony (Alpern, 1953), interstimulus interval (Schiller, 1968), conditioning interval (Boynton & Kandel, 1957), Δt (Weisstein, 1968, τ (Sperling, 1965), and stimulus-onset-asynchrony (Kahneman, 1968). Kahneman pointed out that the interval between the onsets of test and masking stimuli is more closely related to masking effects than the interstimulus interval between the offset of the first and the onset of the second stimulus.

Another point of confusion is that some experimenters (Alpern, 1953) used positive values whenever the test stimulus preceded the masking stimulus while others (Boynton & Kandel, 1957) used positive values for situations in which the test stimulus followed the masking stimulus. In the present discussion, "test flash delay" refers to the temporal interval between the onsets of the masking and test stimuli. Positive values refer to the delay of the test stimulus after the onset of the masking stimulus; negative values are used whenever the test stimulus occurs before the masking stimulus.

Masking functions. Experiments that used various visual masking paradigms have been reviewed by Alpern (1952), Raab (1963), and Kahneman (1968). The results of many such experiments are described

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by masking functions -- graphs of some measure of the test stimulus effectiveness plotted against test flash delay. Kahneman described two types of masking functions that are obtained in metacontrast studies: (a) The type A function rises from negative test flash delays to a peak at the point of simultaneous presentation and then decreases as the test flash delay is increased. This type of masking function resembles the function that is usually found with spatially overlapping test and masking stimuli (Crawford, 1947; Sperling, 1965). (b) The other type of masking function, type B, is a frequent result of metacontrast studies. Type B curves have maximum points at some negative delay of the test flash, in the region of backward masking (Alpern, 1953; Weisstein & Haber, 1965). The conditions that determine which type of function should be expected to occur are not agreed upon. For example, Kahneman (1968) asserted that the major determinants of the type of function that will occur are the qualitative criteria that observers adopt in responding to test stimuli under masking conditions. Weisstein (1968), however, used stimulus parameters such as the contrast ratio of the test stimulus to the masking stimulus to predict whether type A or type B masking functions would occur. Since Weisstein was primarily concerned only with backward masking (negative test flash delays), she referred to type A functions as "monotonic." Such masking functions increase steadily as the test flash delay increases from large negative values to zero. The peak of the type A function,

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however, occurs around zero delays, and the value of the function decreases as the test flash delay becomes increasingly positive. The shapes of the two types of functions are actually similar if the entire range of possible test flash delays is considered. The principal difference between type A and type B masking functions is in the test flash delay at which the test stimulus is least effective, the position of the peak of the masking function along the test flash delay axis.

Where the masking function is located along the test flash delay axis and which delay produces maximal masking are functions of the relative latencies of excitation and inhibition. Several visual masking experiments have reported some shifts in the masking function peaks as the intensity of the masking stimulus was varied. For example, Alpern (1953, p. 650), who used metacontrast stimuli, included a figure that showed masking function peaks shifting from a test flash delay of -50 msec. to -150 msec. delay as the luminance of the masking stimulus increased from 3.6 to 3,000 ft-L. Crawford's (1947) results with concentric discs indicated a slight shift toward shorter test flash delays as the masking stimulus illuminance was increased, and that result has been repeated by several other experiments with overlapping stimuli: Sperling (1965, p. 548) reported a peak shift from zero delay to a -5 msec. delay for one of his two observers at the highest intensity of the masking flash. Frumkes and Sturr (1968, p. 1661) noted that their peak test flash thresholds were reached more rapidly at higher luminances.

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Finally, Schiller (1968, p. 681) found that inhibitory responses in cat lateral geniculate cells occurred at more negative delays if the luminance of the masking stimulus was increased.

All of the reported peak shifts are consistent with the notion that the inhibitory effects of the masking stimuli reach their maxima faster with more intense masking stimuli. The suggested inverse relationship between intensity of stimulation and latency of inhibition resembles the reciprocity of latency and intensity for excitatory responses. The latter relationship has been well established by experiments with the Pulfrich effect (Alpern, 1968; Prestrude & Baker, 1968), the apparent simultaneity of asynchronous flashes of different intensities (Alpern, 1954), and reaction-time measures and "eye and ear" comparisons (Roufs, 1963).

Relation to transient inhibition. Visual masking functions are closely related to the temporal course of lateral inhibition, because the effectiveness of a brief test flash at various delays is a measure of the magnitude of the inhibitory transient at various times after its onset. Thus, a visual masking function represents an indirect picture of the temporal course of the lateral inhibition.

The picture of the inhibitory time course that most masking functions present is not entirely clear, however; it is distorted by various complications. The main difficulty in interpreting most visual masking paradigms in terms of transient inhibition is that excitatory responses are inextricably confused with inhibitory responses. In order to investigate the temporal course of lateral inhibition, the

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present experiment was designed to eliminate as much confounding of excitation and inhibition as possible. The experiment follows Hartline's (1969, p. 275) suggestion for obtaining pure inhibitory responses: "If responses are recorded from representative receptors in two interacting groups in a Limulus eye, and one group subjected to a small increment in intensity, the other, steadily illuminated, will be disturbed only by the inhibitory influence exerted by the first." Hartline was prescribing two conditions that must be met if the inhibition is to be separated from excitatory responses: (a) The test and masking stimuli must illuminate nonoverlapping retinal areas, and (b) the retinal area that is stimulated by the test flash must be adapted to some constant level of illumination before each trial. There are three additional conditions that increase the extent to which masking functions depict the inhibitory time course. (c) The masking stimulus must be long enough so that the on- and off-effects in the responses to the masking stimulus are not mixed (Boynton & Ikeda, 1965; Ikeda, 1965). (d) The test and masking stimuli must not be too widely separated spatially. Cornsweet and Teller (1965), for example, varied the illuminance of an annulus with an inner diameter of 8.5 degrees and measured increment thresholds for a concentric 24 min. test spot. The increment threshold was constant over a wide range of annulus illuminances, and the small increases in thresholds that occurred at the highest illuminances were attributed to stray light fom the annulus. (e) Finally, repeated stimulus presentations must be separated by a sufficiently long interval that

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cumulative effects do not occur during series of trials (Sperling, 1965).

Theory and Expected Results

Several conclusions were drawn from the electrophysiological evidence concerning temporal properties of excitation and inhibition: (a) The latency of the peak of an excitatory response is inversely related to the intensity of stimulation. (b) Within limits, the peak magnitude of the excitatory response is directly related to the illuminance change above the background level. (c) Lateral inhibitory responses to an increase in stimulation follow a time course that closely resembles the excitatory responses to the same stimulus. (d) Excitatory responses are maximally inhibited when the peaks of the excitatory and inhibitory responses coincide.

Visual masking is attributed to the interaction of excitation and inhibition as follows: Test stimuli produce excitatory responses that are inhibited by the response of adjacent areas to the masking stimulus. The degree to which a test flash response is inhibited depends on when the excitatory peak occurs during the time course of the inhibition. For example, if the peak excitation coincides with the peak inhibition for simultaneous onsets of the test and masking stimuli, then the peak of the masking function occurs at zero delay. However, if the inhibition reaches its peak 30 msec. more slowly than does the excitation, then the peak of the masking function occurs when

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the excitation and inhibition peaks are simultaneous at the point of interaction, i.e., when the test flash is delayed by 30 msec. The instantaneous value of the inhibitory process is indicated, therefore, by masking functions -- graphs of test flash thresholds plotted against the test flash delay.

Expected results. Several experimental conditions were designed to investigate the extent to which the implications of the physiological data were confirmed by psychophysical results of visual masking. In order to test the lateral inhibitory interpretation of visual masking, several specific hypotheses were proposed:

(1) Increasing the illuminance of a masking annulus was expected to increase the magnitude of the masking functions (increase the test flash thresholds), since the peak magnitude of inhibition increases with increasing illuminance of the masking stimulus.

(2) Increasing the illuminance of a masking flash was expected to shift the peak of the masking function toward shorter test flash delays. The latency of the peak inhibition produced by the masking stimulus decreases as masking illuminance increases. As a consequence, in order to make the excitatory and inhibitory peaks coincide as the illuminance of the masking stimulus is increased, the test stimulus must be presented earlier in relation to the masking stimulus.

(3) Separating the disc and annulus contours by occluding the inner margin of the annulus was also expected to decrease the magnitude of the masking function, since the area illuminated by the

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annulus was reduced (by approximately 11 percent in the actual experiment). The masking was also expected to decrease because the areas that were illuminated by the inner margin of the contiguous annulus exerted relatively more inhibition on the disc than the more distant regions. To the extent that the lateral inhibition took longer to cross the widened contour region, the peak threshold was expected to shift to longer test flash delays.

(4) Lowering the level of adaptation in the disc was expected to increase the latency of excitation in the disc such that the test stimulus would have to be presented at shorter test flash (or more negative) delays in order to coincide with the peak of the inhibitory response. The expected result was a peak shift toward shorter test flash delays. The absolute magnitude of the masking function was expected to be less on the lower adapting background, of course, in agreement with Weber's law.

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Chapter II

EXPERIMENTAL METHOD

Apparatus

The Maxwellian view system that was used in the present experiment is presented schematically in Figure 2-1. The optics may be described simply. Two glow modulator tube light sources (GM_1 and GM_2) were collimated by achromatic lenses (L_1 and L_2). High-contrast photographic transparencies formed a disc (T_1) in one channel and an annulus (T_2) in the other. The two beams were combined by a beam-splitter cube (BS_2), and another achromatic lens focused the images of the glow modulator tube craters in the plane of the pupil of the observer's right eye, approximately 3 mm. behind an artificial pupil (P).

After dark-adapting for 5 min. before each session, the observer adjusted the voltage across the fixation lamp (FL) so that the image of its filament, as reflected by a thin cover glass beam-splitter (BS_1), was barely visible in the center of the dark field. The fixation point subtended approximately one min. of arc and was replaced by a congruent dark spot in the same location when the disc was turned on.

The inset in Figure 2-1 depicts what the observer would see if both the test field (disc) and the masking field (annulus) were continuously illuminated. The disc subtended 39 min. of visual angle (0.65 degrees) and the outer diameter of the annulus subtended

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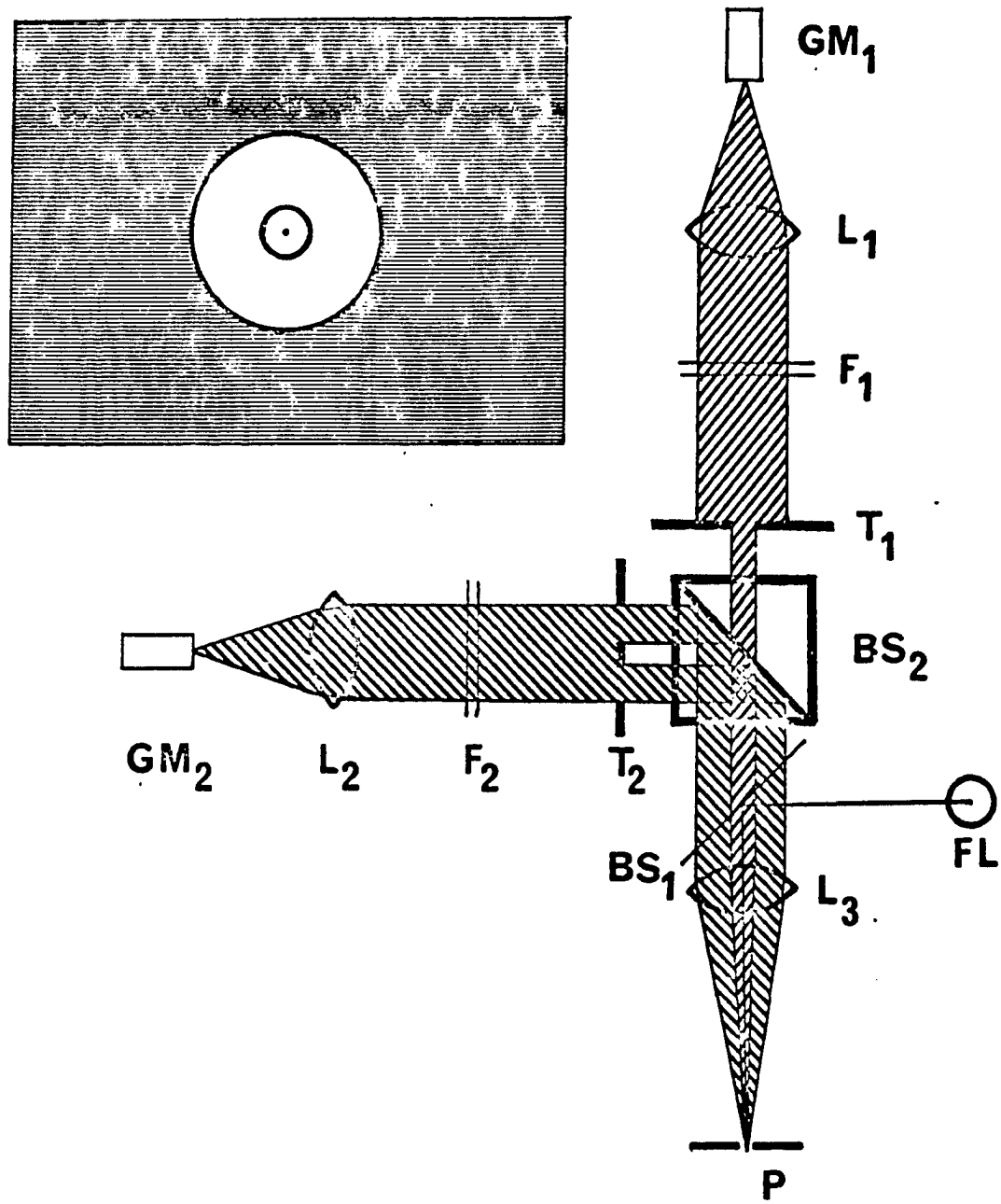

Fig. 2-1. Apparatus diagram. (Inset shows appearance of the stimuli to the observer.) BS, beam splitter; F, neutral density filters; FL, fixation lamp; GM, glow modulator tube; P, artificial pupil; and T, photographic transparency apertures.

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134 min. (2.23 degrees). Observers viewed the stimuli through an artificial pupil of 2 mm. diameter; their head position was maintained by a bite plate with a dental impression and a forehead rest. The light sources for each channel were Sylvania R1131C glow modulator tubes operated at only 15 mA. peak current, to avoid the relatively slow increase in luminance that occurs with higher currents as the glow tubes warm up (Matin, 1964, and Buchman-Olsen & Rosenfalck, 1957). The durations of the light flashes, the intertrial intervals, and the warning tone were controlled by circuits constructed from Digital Equipment Corporation logic modules. Two output voltages from the logic circuits that were set by calibrated ten-turn potentiometers controlled the glow modulator driver circuits and regulated the amount of time that each tube was turned on during each one msec. period. Thus the luminances of the pulses of light were continuously variable by modulating the 1000 Hz duty cycle at which the glow modulator tubes were operated. Larger luminance changes were made by inserting calibrated neutral density filters (Wratten No. 96) at F_1 and F_2 in Figure 2-1.

The luminances of the glow tubes were calibrated by a matching technique. A mirror was inserted between the eye lens and the beam-splitter cube to create a split field. The matching field was illuminated by the diffuse opal-glass surface of a three-filter colorimeter (Burnham, 1952). The chromaticity and luminance of the matching field was adjusted to match each of the other two fields over a wide range of duty cycle settings. After each match, the

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luminance of the colorimeter was measured with a Gamma Scientific log-linear photometer and fiber optics probe. Finally, graphs of luminance versus potentiometer readings were drawn for each of the glow tubes.

Subjects

All three observers were between 23 and 26 years of age. They were tested with the Keystone Telebinocular acuity test cards and with the American Optical H-R-R pseudoisochromatic color vision plates. Each observer had at least 20/30 acuity in each eye and normal color vision. Before the experiment began, Observers LG and ES were given at least six hours practice at determining test stimulus thresholds under conditions of visual masking. Observer CW, the experimenter, had considerably more practice in previous experiments.

Procedure

The sequence of presentation of the stimuli is diagrammed in Figure 2-2. The following cycle of events was repeated every 10 sec.: (a) The disc (adapting field) was illuminated. (b) After 2.5 sec., a one-half sec. warning tone sounded. (c) One-half sec. after the tone ended, the annulus was turned on for one-half sec. (masking stimulus, MS). (d) One sec. after the end of MS, the disc was turned off. (e) The fixation point was barely visible for 5 sec. before the next disc onset. At various times before and after the onset of the annulus during each cycle, the luminance of the disc was increased for a 5 msec. period (test stimulus, TS).

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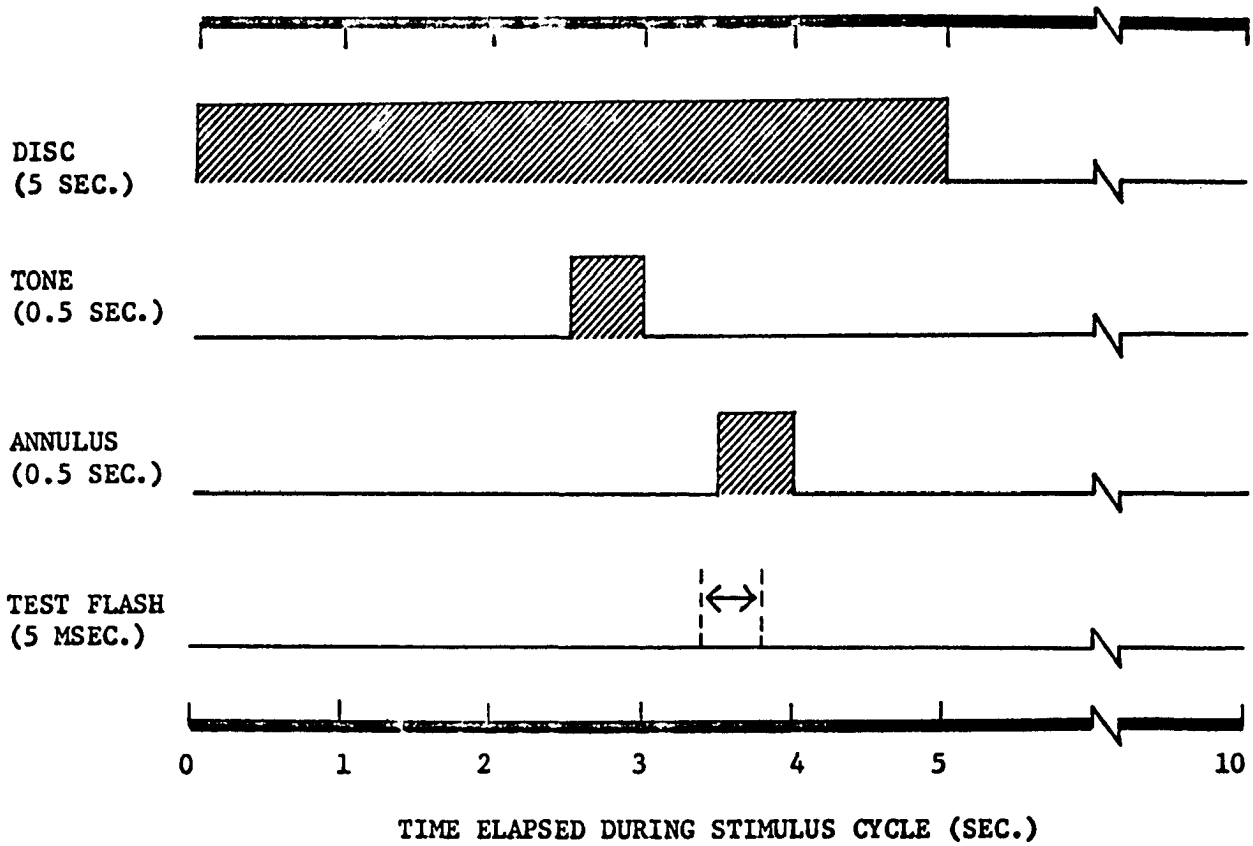

Fig. 2-2. Sequence of stimuli. The ten-second cycle was repeated continuously during each experimental session.

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Observers were dark-adapted for five minutes before beginning an experimental session. The sequence described above was repeated throughout the session while test flashes were presented at various times in relation to the onset of the annulus. Thresholds for the test flash at various delays were determined by a method of adjustment. Observers turned a calibrated ten-turn potentiometer to adjust the retinal illuminance of TS after each trial so that it was just visible on the next trial. No more than ten trials were required to determine each threshold. By bracketing the settings, the observer was able to use the adjustment method as an efficient method of limits (Sperling, 1965). The observer took only as many trials as he required to be satisfied that his setting of the TS illuminance met his just visible criterion.

Each observer made nineteen threshold settings in each experimental run. The 16 test flash delays that were presented in each run were -100, -50, -40, -30, -20, -10, 0, 10, 20, 30, 40, 50, 100, 150, 200, and 300 msec. Negative delays mean that TS preceded MS (backward masking). Zero delay indicates that the onsets of TS and MS were simultaneous. A positive delay refers to a TS that occurred after the onset of MS (forward masking). In addition, three other thresholds were determined in each run: one with no MS, one with the annulus constantly illuminated, and one catch trial during which no TS was presented. The order in which the different thresholds were determined in each run was arranged by random permutations of the stimulus conditions. Two or three runs made up an experimental session that lasted approximately 90 minutes.

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Description of Experimental Conditions

Each observer completed nine runs in each of six experimental conditions. In the main experiment (Conditions 1 through 4), the retinal illuminance of the disc (adapting field) was always 2.66 log trolands, and the retinal illuminance of the annulus in log trolands was 0.82 in Condition 1, 1.82 in Condition 2, 2.82 in Condition 3, and 3.82 in Condition 4. Thus, in the main experiment the retinal illuminance of the masking stimulus was varied over a range of four log units.

Two additional conditions, Conditions 5 and 6, were run simultaneously with the main experiment. In both conditions, the illuminance of MS was 2.82 log trolands, the same as in Condition 3. When compared with the Condition 3 data from the main experiment, Conditions 5 and 6 were treated as two separate experiments: (a) In the contour separation experiment (Condition 5), the disc and the inner contour of the annulus were separated by a dark ring, 10 minutes of arc in width, that was never illuminated. The outer contour of the annulus was the same as in Condition 3. (b) In the adaptation level experiment (Condition 6), the retinal illuminance of the adapting field in the disc was decreased to 1.66 log trolands. In all of the other conditions, the adaptation field remained at 2.66 log trolands.

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Chapter III

RESULTS AND STATISTICS

Typical Masking Functions

Masking functions were constructed for each observer in each experimental condition by the following procedure: Each of the threshold settings was converted from a reading of the observer's potentiometer dial to the common logarithm of the retinal illuminance value in trolands. (The troland values refer to the retinal illuminance that the 5-msec. test flash would produce if it were illuminated continuously.) Next, the means of the nine threshold settings at each of the 16 test flash delays were computed. Finally, the mean thresholds were plotted and connected by line segments to form the masking functions.

The thresholds obtained from Observer LG in Condition 3 are presented in Figure 3-1. All nine thresholds for each delay were plotted in order to indicate how the threshold determinations varied among different experimental sessions. An important point to observe in Figure 3-1 is that the ranges of the log threshold settings at various delays are approximately the same size. If the data had been plotted as linear units of illuminance, of course, the variability would have increased in proportion to the mean threshold for each delay, in accordance with Weber's law. Thus the logarithmic transformation helps to assure homogeneity of the variances at different delays.

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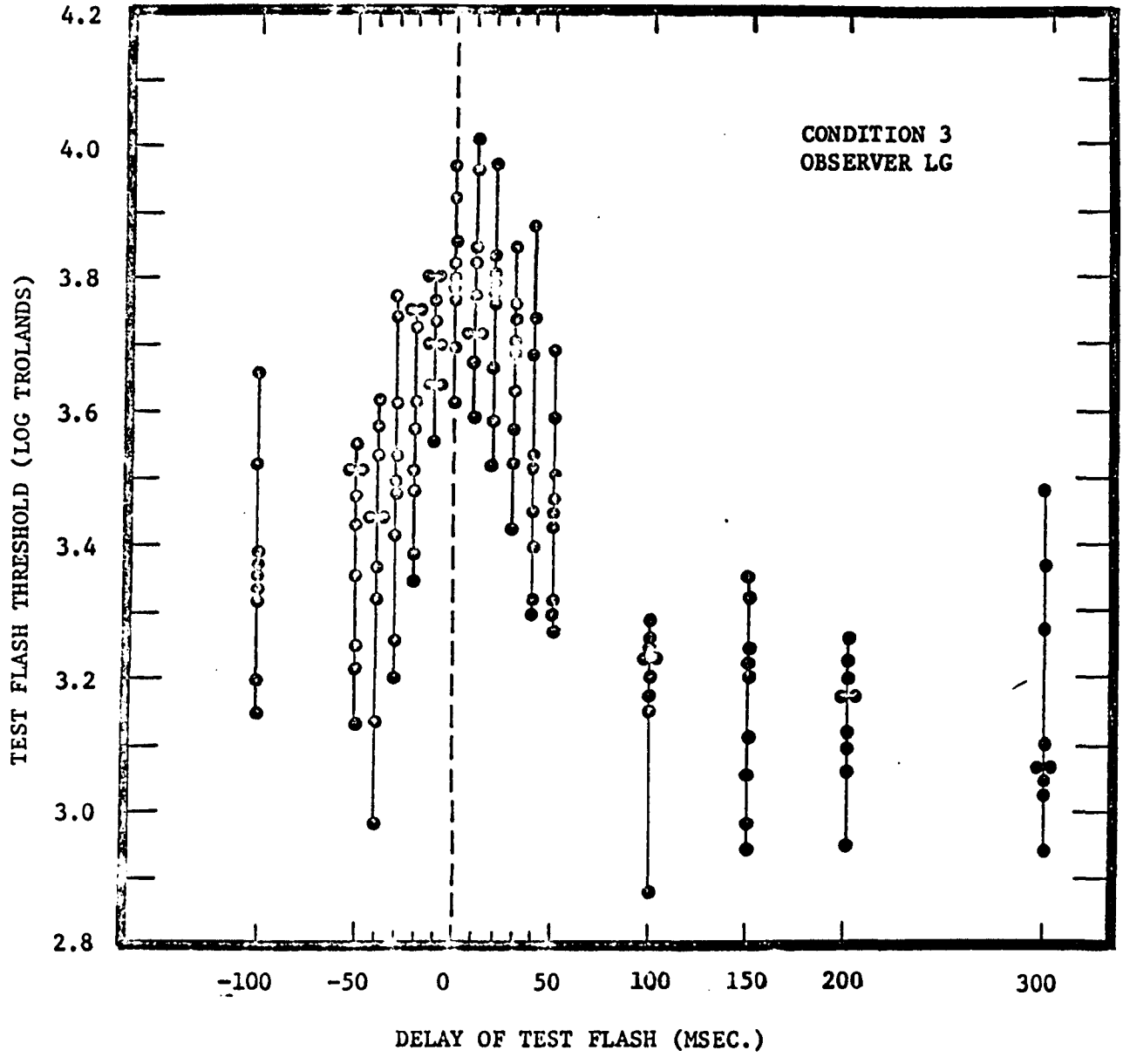

Fig. 3-1. Complete results for Observer LG in Condition 3. Each data point represents one setting of the illuminance of the test flash to the just visible criterion. Vertical bars indicate the range of thresholds for each test flash delay.

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The mean thresholds for the data in Figure 3-1 are replotted in Figure 3-2 with vertical bars drawn through each mean to indicate the extent of the 95 percent confidence intervals for the mean. (The calculation of the confidence intervals is described in the next section.) The masking function in Figure 3-2 is similar to most of the masking functions that were obtained. Since the masking functions resembled each other in many features, the general shapes of the masking functions may be simply described: The log threshold rises from a test flash delay of -100 msec. to a peak that falls between zero delay and a delay of 50 msec. Then the log threshold curve decreases and reaches a relatively stable low value for delays between 100 and 300 msec. The maximum value that the masking function attains and the test flash delay at which the peak occurs depend on the retinal illuminance of the masking flash.

All the observers appeared to maintain a high criterion for setting test flash thresholds throughout the experiment. Of course, there is no way to ascertain directly the observer's criterion level by the psychophysical method of adjustment, but evidence from the catch trials suggests that the criteria were quite high. Each observer was presented one catch trial in each run, during which TS was switched off. Only once out of 162 catch trials did an observer fail to recognize that the test flash was not present.

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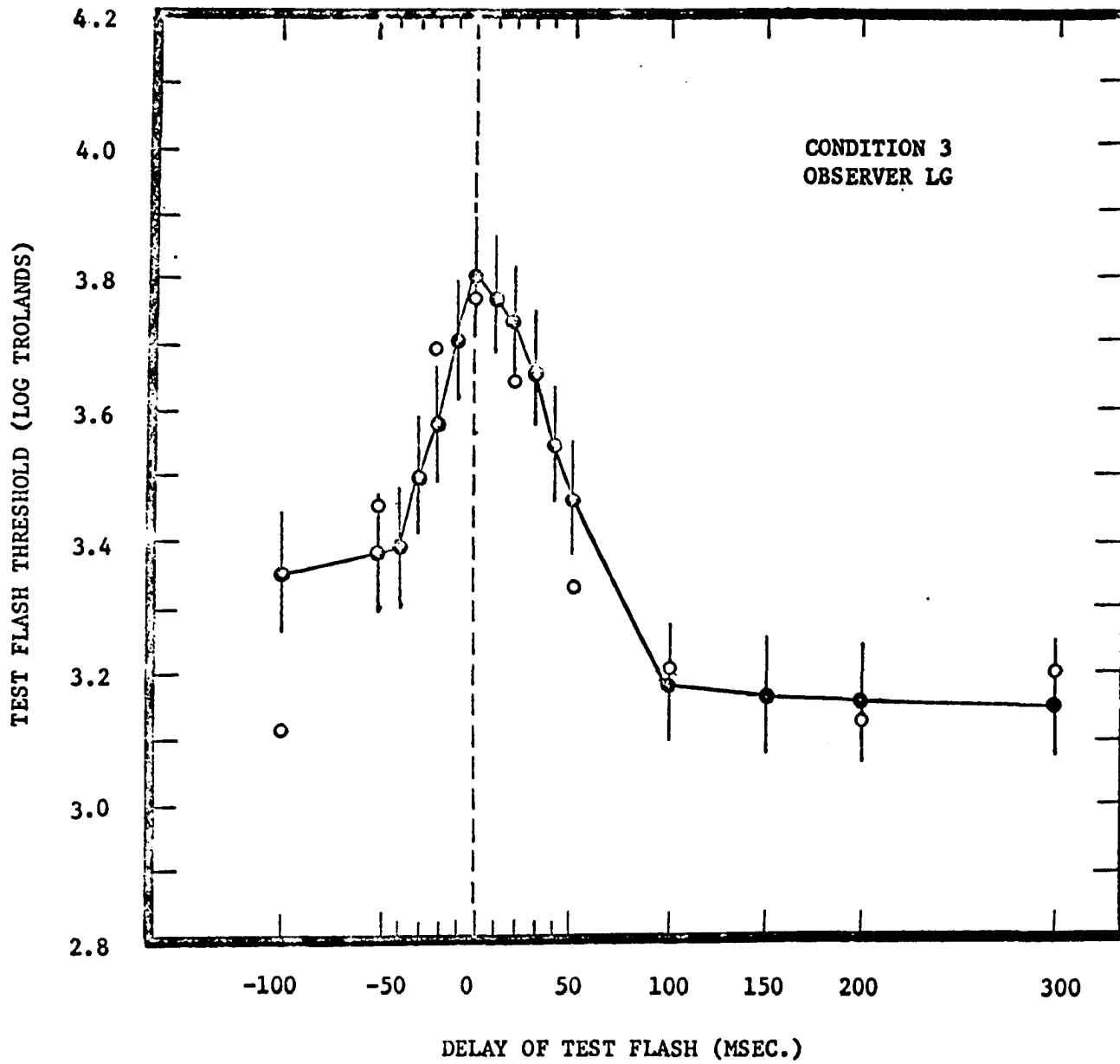

Fig. 3-2. Typical masking function. Filled circles are mean test flash thresholds plotted against the test flash delay for Observer LG in Condition 3. The vertical bars are 95 percent confidence intervals for each mean. The open circles are thresholds obtained by a forced-choice constant stimulus method. (See text for details.)

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For Observer LG, some pilot data were available that were obtained with a constant stimulus method. Test flashes were presented at different delays and at different retinal illuminances, and LG responded by indicating whether or not she saw a test flash. The probability of seeing the flashes was plotted on normal probability paper and cumulative normal probability distributions were fitted by eye for each test flash delay. Masking functions were calculated from those distributions by plotting the retinal illuminance values of the test flash at which the cumulative probability curves reached different probability levels. The shapes of all the functions were similar to the shape of the curve that was obtained by the adjustment method (filled circles in Figure 3-2). Increasing the probability level raised the masking function at all points and sharpened the peak of the function somewhat. The open circles in Figure 3-2 are thresholds that were determined by the constant stimulus technique with a high probability level of 99.99 percent. The similarity of the masking functions determined by the two psychophysical methods suggests that the forms of the masking curves cannot be attributed to the method of adjustment that was adopted.

Statistical Analysis

A three-way analysis of variance was computed for the main experiment data (Conditions 1 through 4). The three factors in the analysis were Observers, Conditions, and Delays. The design included repeated measures, since thresholds were determined for each observer for all delays and in all conditions (Winer, 1962). Consequently, the appropriate error term that was used to test the significance of the

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Conditions and Delays main effects was the interaction of each factor with the Observers factor (McNemar, 1962). Similarly, two-way interactions were tested against the three-way interaction. Values of F that exceeded the 95th percentile of the appropriate F distribution were significant.

The other two conditions, 5 and 6, were each compared with Condition 3 in the main experiment, since the illuminance of MS (2.8 log td.) was the same for Conditions 3, 5, and 6. Separate analyses of variance were computed for the combined data from Conditions 5 and 3 and for the data for Conditions 6 and 3 grouped together. The same type of analysis was used for these comparisons that was used for the main experiment; the only difference was that the number of conditions for each analysis was two instead of four. Summary tables for all of the analyses of variance are in the Appendix.

Post hoc comparisons of differences between means were made by calculating 95 percent confidence intervals for each mean threshold, using the within-cell error from the appropriate analysis of variance. The standard error of each mean was one-third of the square root of the within-cell mean square, and the 95 percent confidence intervals were the means plus and minus 1.96 times the standard error.

Main Experiment

The purpose of the main experiment was to vary the retinal illuminance of the masking stimulus and examine the effects on the masking functions. The results of the main experiment are presented as separate masking functions for each observer. The curves that were obtained in Conditions 1 and 2 are presented in Figure 3-3, and the

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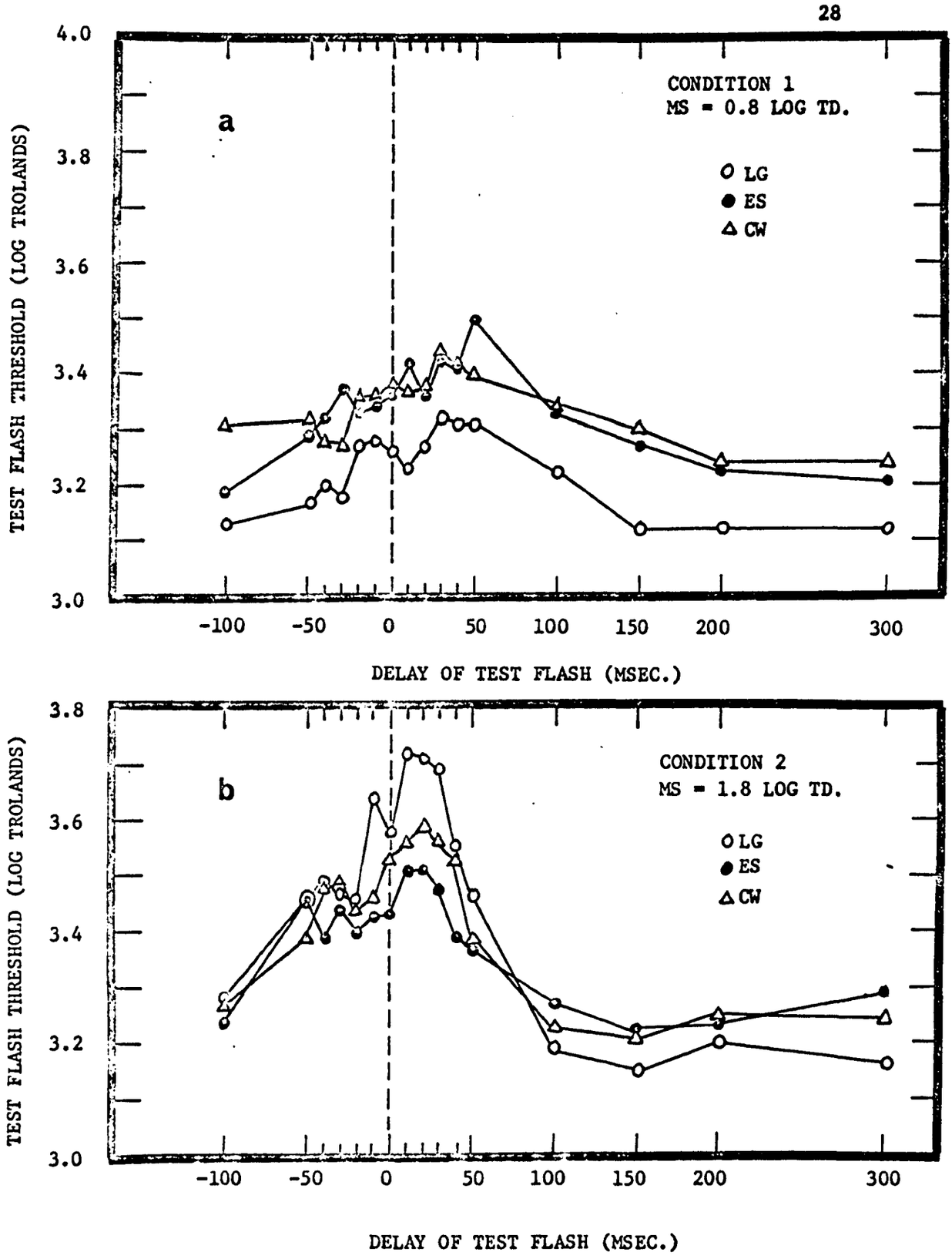

Fig. 3-3. Results of the main experiment. (a) Condition 1 (disc = 2.7 log td.; annulus = 0.8 log td.). (b) Condition 2 (disc = 2.7 log td.; annulus = 1.8 log td.). Mean test flash thresholds are plotted against test flash delay for three observers: LG, open circles; ES, filled circles; and CW, triangles.

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individual masking functions for Conditions 3 and 4 are shown in Figure 3-4. The most critical features in Figures 3-3 and 3-4 are the changes in the magnitude of the maximum test flash threshold and the changes in the test flash delay at which the peak threshold occurs.

Analysis of variance. The analysis of variance for the main experiment (Table 2 in Appendix) yielded significant main effects for Conditions and Delays, and all of the interactions were significant. The effect of Delays is obvious; it merely indicates that the masking functions are not flat. The Conditions effect reflects the overall increase in test flash thresholds that occurs as the illuminance of MS increases. The Observers effect was not significant.

The two interactions with the Observers factor may be understood as well: The significant Observers X Conditions interaction means that thresholds did not increase across conditions by the same amounts for different observers. For example, in Figure 3-3, the Condition 1 curve for LG was consistently lower than the curves of the other two observers, but LG's masking function for Condition 2 had the highest peak threshold of the three observers. The Observers X Delays interaction indicated that there were differences among the observers in the shapes of the masking functions. In Figure 3-4, for example, LG and ES both produced relatively smooth, single-peaked functions, but CW's masking functions were less peaked and contained suggestions of secondary maxima. The most important interaction for the expectations of the main experiment, of course, was the Delays X Conditions interaction. The significance of that interaction effect indicated that varying the illuminance of the masking stimulus did produce changes in the shapes

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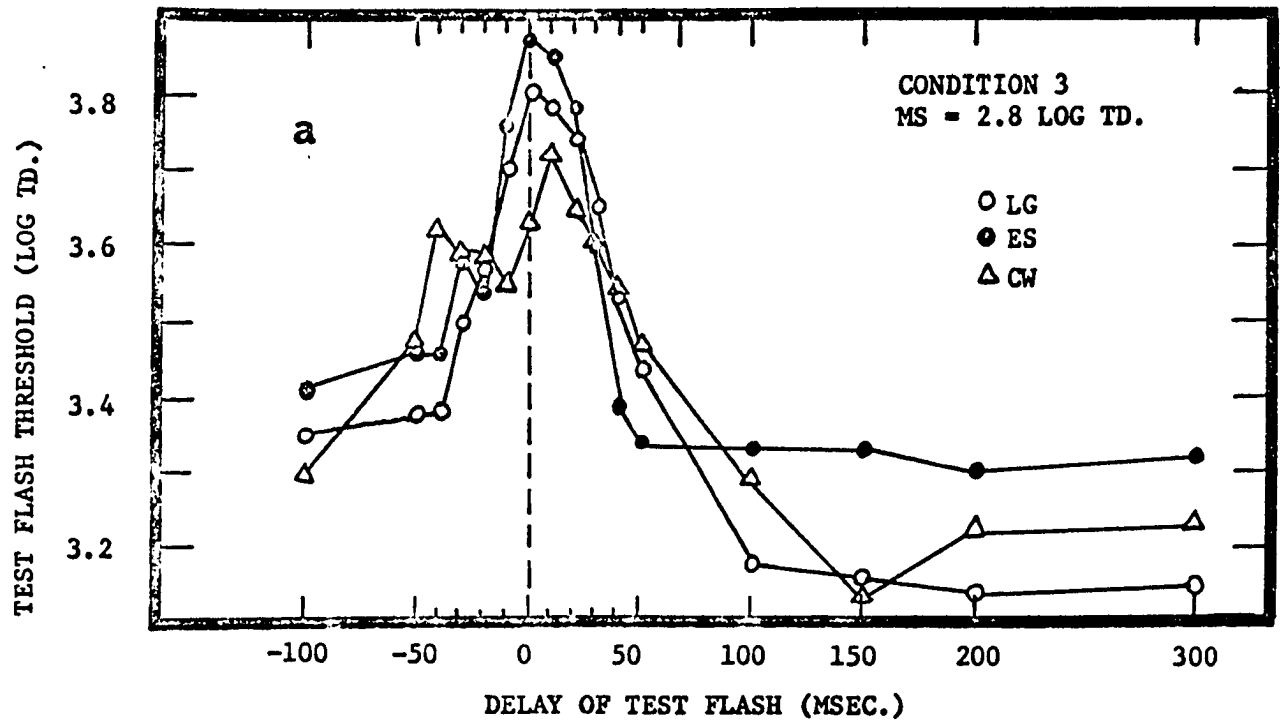

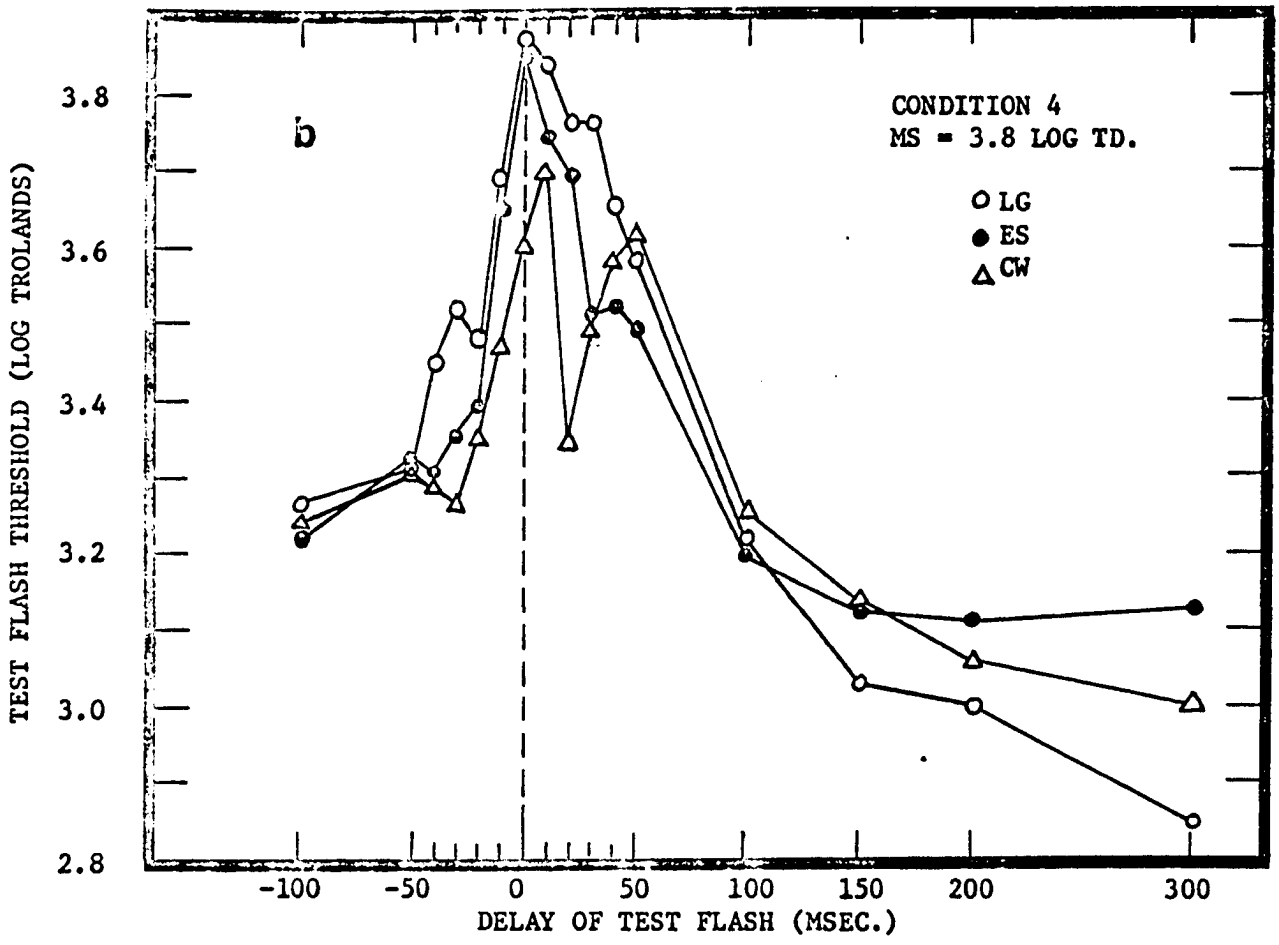

Fig. 3-4. Results of the main experiment. (a) Condition 3 (disc = 2.7 log td.; annulus = 2.8 log td.). (b) Condition 4 (disc = 2.7 log td.; annulus = 3.8 log td.). Mean test flash thresholds are plotted against test flash delay for three observers: LG, open circles; ES, filled circles; and CW, triangles.

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of the masking functions. Two types of changes are described next: magnitude effects (changes in the height of the peaks of the masking functions) and peak shifts (changes in the test flash delays that produced the greatest masking effects).

Magnitude effects. The changes in the height of the masking function peaks are apparent in Figure 3-5. For observers LG and CW, the test flash thresholds at the peaks of the masking functions increased smoothly as the illuminance of MS increased. The peak thresholds increased somewhat less regularly in the case of ES, and they exhibited a slight reversal of the trend at the highest illuminance level of MS. Post hoc comparisons of the changes for each observer revealed that none of the changes between the two highest MS levels was significant. All of the other differences in peak thresholds between MS illuminance levels were significant, with the exception of the two lowest MS levels for ES and the two middle levels for CW.

Peak shifts. As the illuminance of MS was increased by three log units in one log unit increments, the peak of the average masking functions shifted from a test flash delay of 50 msec. to a 20 msec. delay, then to a delay of 10 msec. and finally to zero delay. The arrows in Figure 3-6 clearly show the peaks shifting to shorter delays as the illuminance of MS was increased. There were individual differences, of course, in the way the peaks shifted for each of the observers. The individual results are presented in Table 1. The peaks for each observer shifted by 10 to 30 msec. each time the illuminance of MS was increased by a log unit, except in the case of the 3.8 log td. MS; it produced no additional shift in the masking peaks.

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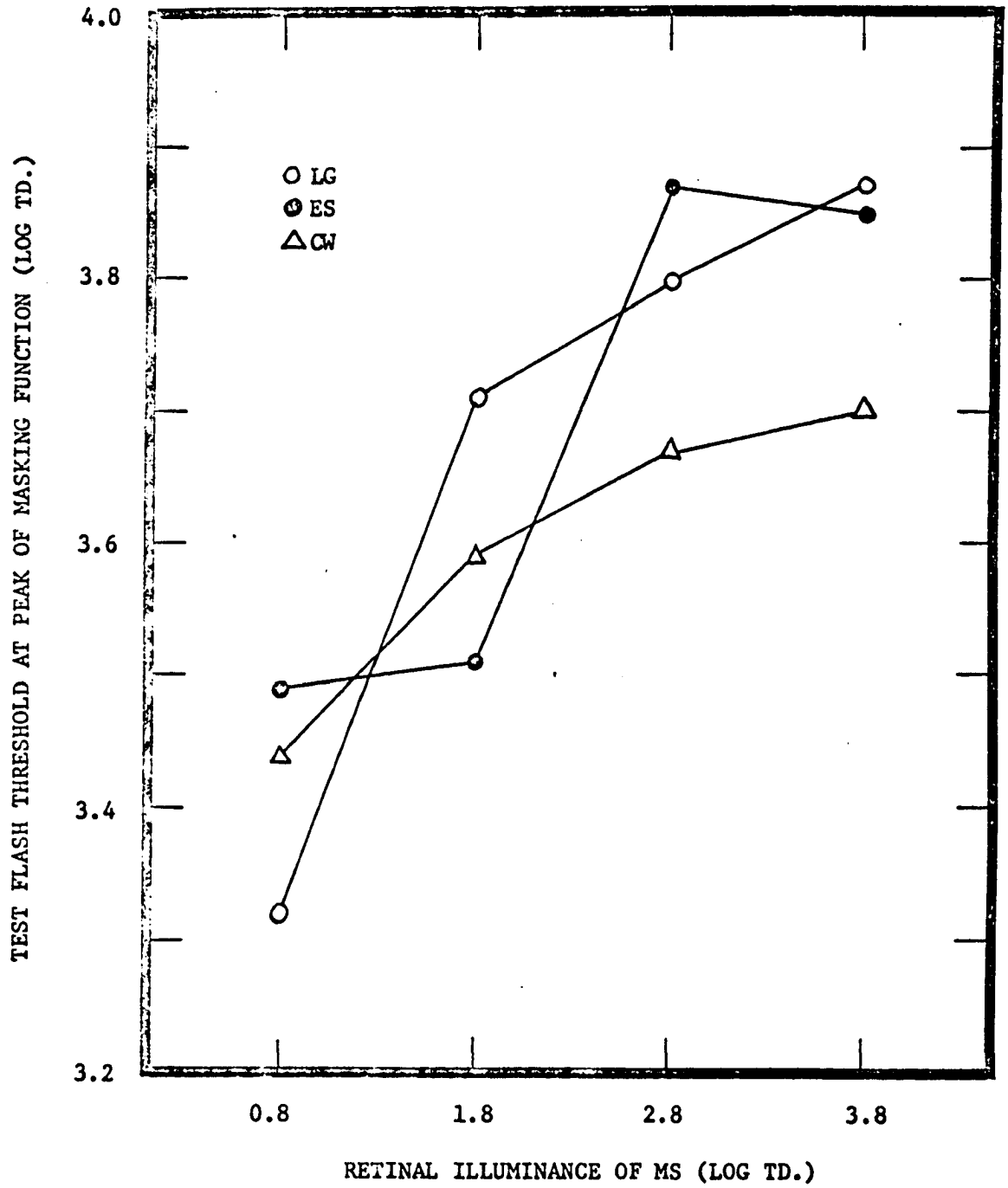

Fig. 3-5. Magnitude results of the main experiment. Mean test flash thresholds at the peaks of the masking functions as a function of the retinal illuminance of the masking flash for three observers: LG, open circles; ES, filled circles; and CW, triangles.

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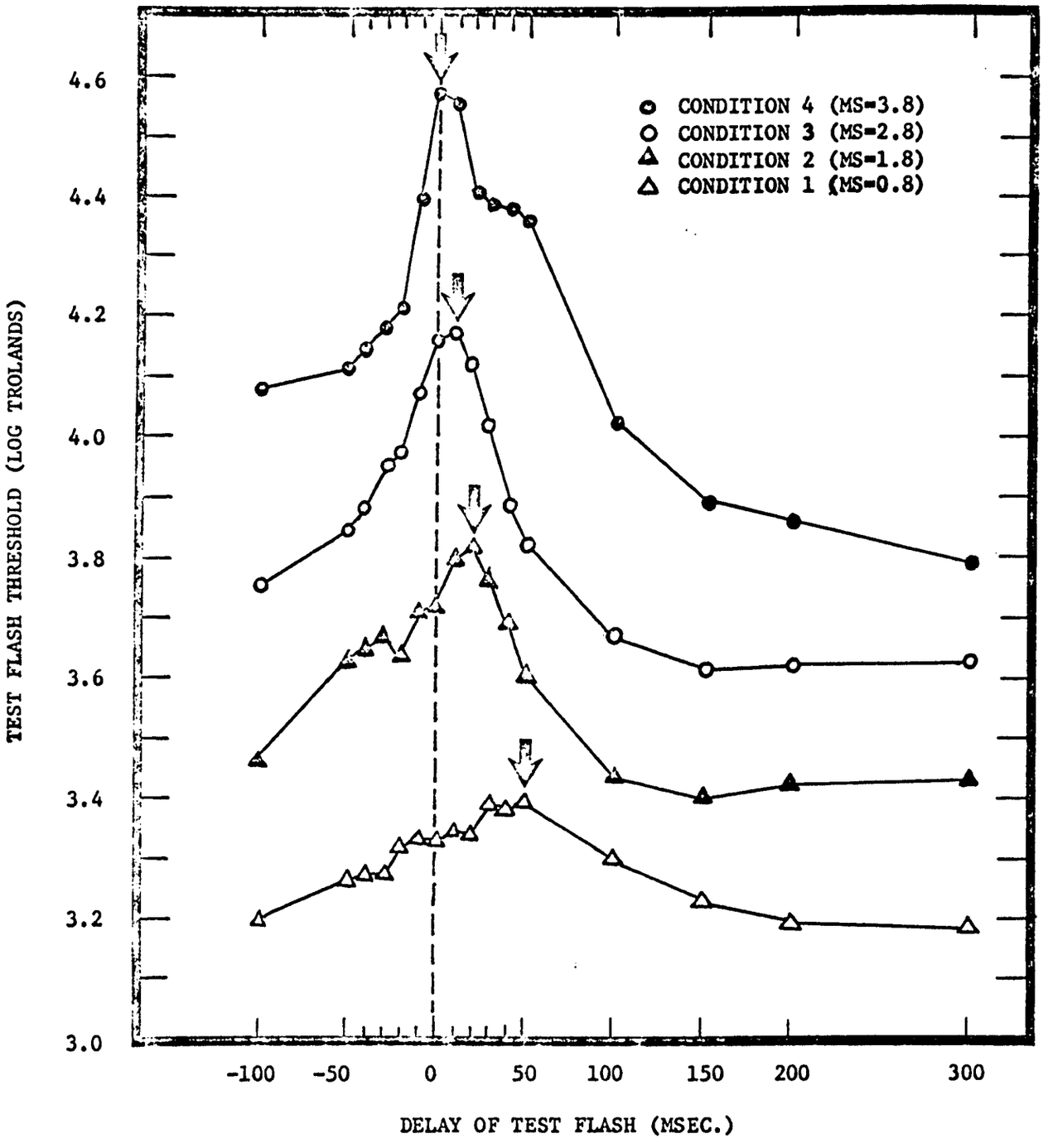

Fig. 3-6. Peak-shift results of the main experiment. Mean visual masking curves for all three observers as a function of the retinal illuminance of the masking stimulus. The curves for Conditions 2, 3, and 4 have been displaced upward by 0.2, 0.4, and 0.8 log trolands respectively. Arrows indicate the maximum threshold for each condition.

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TABLE 1

TEST FLASH DELAYS (MSEC.) AT PEAKS OF MASKING FUNCTIONS

Experimental Condition	Observers			
	LG	ES	CW	Mean curves for all observers
Main Experiment: Effects of MS illuminance				
1 Disc=2.7 MS=0.8	30	50	30	50
2 Disc=2.7 MS=1.8	10	20	20	20
3 Disc=2.7 MS=2.8	0	0	10	10
4 Disc=2.7 MS=3.8	0	0	10	0
Contour Separation Experiment				
5 Disc=2.7 MS=2.8	30	10	10	10
Adaptation Level Experiment				
6 Disc=1.7 MS=2.8	0	10	40	10

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Since the variability of the peak delays for each observer was unknown, the peak shift results were tested by the Friedman analysis of variance by ranks (Siegel, 1956). The two-way (Observers X Conditions) analysis of the delays of the masking function peaks yielded a significant effect of the masking stimulus illuminance. ($p < .033$).

Contour Separation Experiment

The results of the analysis of variance for the second experiment (Table 3 in Appendix) included significance for the main effects of Observers and Delays, but not for Conditions. The Delays effect, as always, indicated that significant masking occurred in the experiment. The Observers effect suggested that there were differences among observers in the absolute levels of the masking functions across the two experimental conditions. The interactions of Observers with Delays and Conditions were both significant; they suggested individual differences in the shapes of the masking functions and in the effects of the contour separation among observers. For example, the two masking functions of Observer ES for Conditions 3 and 5 were nearly identical. However, the corresponding curves for LG and CW resembled ES's masking function for Condition 3, but not for Condition 5 (Figure 3-7a).

The magnitude of the masking function was expected to be less in Condition 5 than in Condition 3. The peak thresholds in Condition 5 in Figure 3-7a were lower by 0.26 log td. for LG and by 0.07 log td. for CW, but the peak of ES's masking function was 0.03 log td. greater in Condition 5 than in Condition 3. In the absence of a

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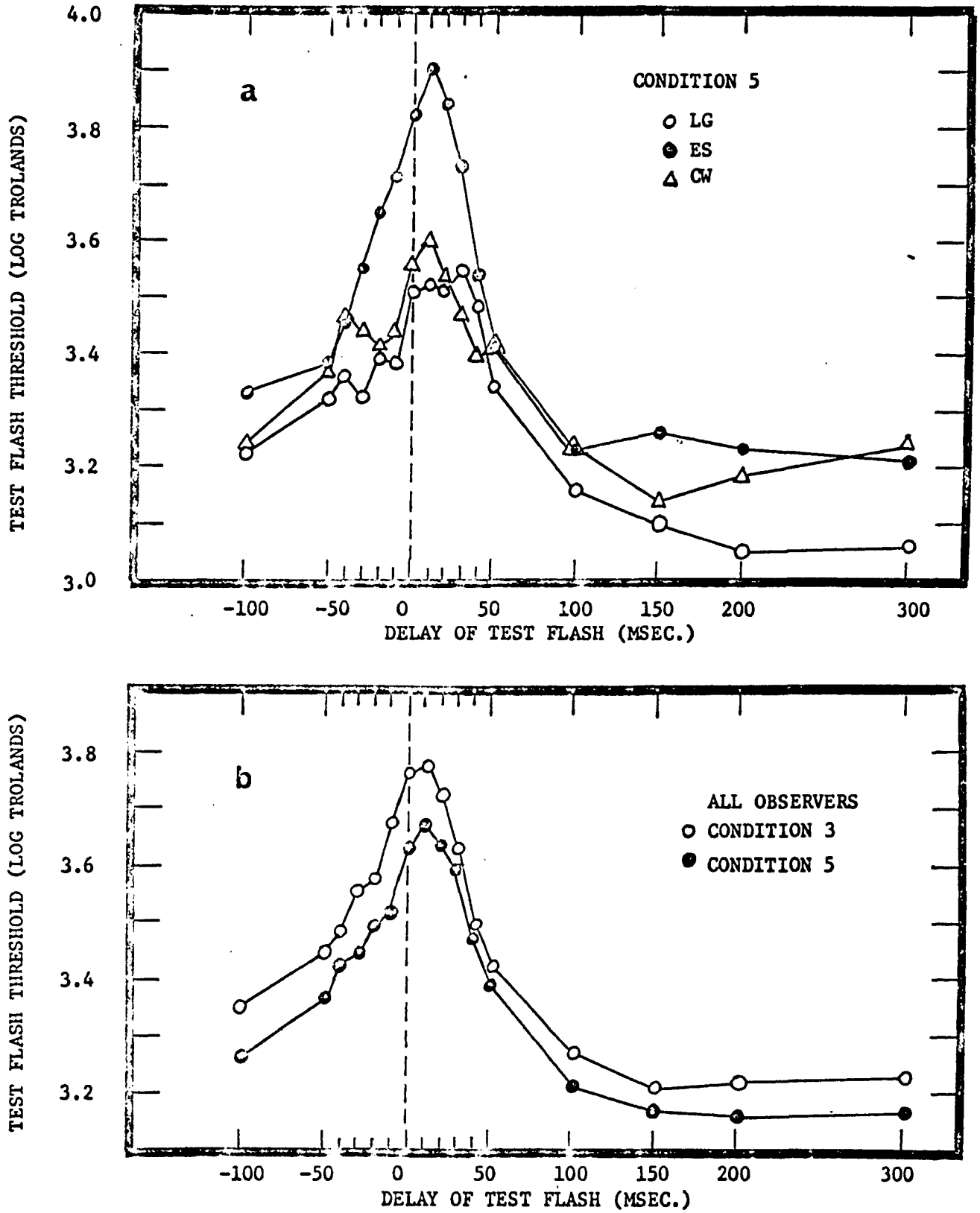

Fig. 3-7. Results of contour separation experiment. Annulus and disc separated by 10 min. of arc (disc = 2.7 log td.; annulus = 2.8 log td.). (a) Individual masking functions in Condition 5. (b) Average masking functions for all observers in Conditions 3 and 5.

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significant Conditions main effect, the changes in individual peak magnitudes were not significant. However, the mean threshold curve for all of the observers combined in Figure 3-7b was lower at every point in the separated contour condition.

The inhibitory effects from the portion of the annulus that remained in Condition 5 were expected to take longer to develop than the inhibition from the contiguous annulus in Condition 3. Consequently, the peak of the masking function was expected to correspond to a longer test flash delay in Condition 5. The expected peak shifts did occur for LG and ES (Table 1); their maximum test flash thresholds shifted from zero delay in Condition 3 to delays of 30 and 10 msec. respectively in Condition 5. However, the peak of CW's masking function remained at a delay of 10 msec. in both Conditions 3 and 5. Since the Conditions X Delays interaction was not significant, the individual peak shifts were not attributed to the effects of contour separation. The combined-observer curves in Figure 3-7b agreed with that conclusion in not exhibiting a peak shift between the two conditions.

The outcome of the contour separation experiment was that separating the inner contour of the masking annulus and the edge of the disc by 10 minutes of arc did not significantly change the magnitude or the shape of the masking function.

Adaptation Level Experiment

The analysis of variance for the adaptation level experiment produced significant main effects for Observers, Conditions, and Delays (Table 4 in Appendix). The Observers effect reflected the tendency of

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CW to set lower thresholds than the other observers. The Conditions effect was a consequence of large differences in thresholds between the two conditions for each observer. The Delays effect indicated that the overall masking effects were significant. Neither the Observers X Conditions nor the Conditions X Delays interactions were significant. The conclusions were drawn that the two adaptation levels did not affect different observers in different ways and that the shapes of the masking functions did not vary significantly with the level of adaptation. The significant Observers X Delays effect suggested individual differences in the shapes of the masking functions, as in the two other experiments.

Decreasing the retinal illuminance of the adapting disc by one log unit was expected to reduce the absolute value of the increment threshold by about one log unit also, in accordance with Weber's law. The individual masking functions that were obtained in Condition 6 were plotted in Figure 3-8a. The peak thresholds in Condition 6 were significantly lower than the corresponding peaks in Condition 3 by 0.93 log td. for LG and ES and by 0.98 log td. for CW. In Figure 3-8b, all of the thresholds in Condition 6 fell almost one log unit below the corresponding values that were obtained in Condition 3 with a masking stimulus of equal troland value. Note that the masking function for Condition 3 has been arbitrarily lowered by one log unit to make it easier to compare the shapes of the two curves.

The peaks of the masking functions were expected to shift to shorter test flash delays as the level of adaptation was lowered.

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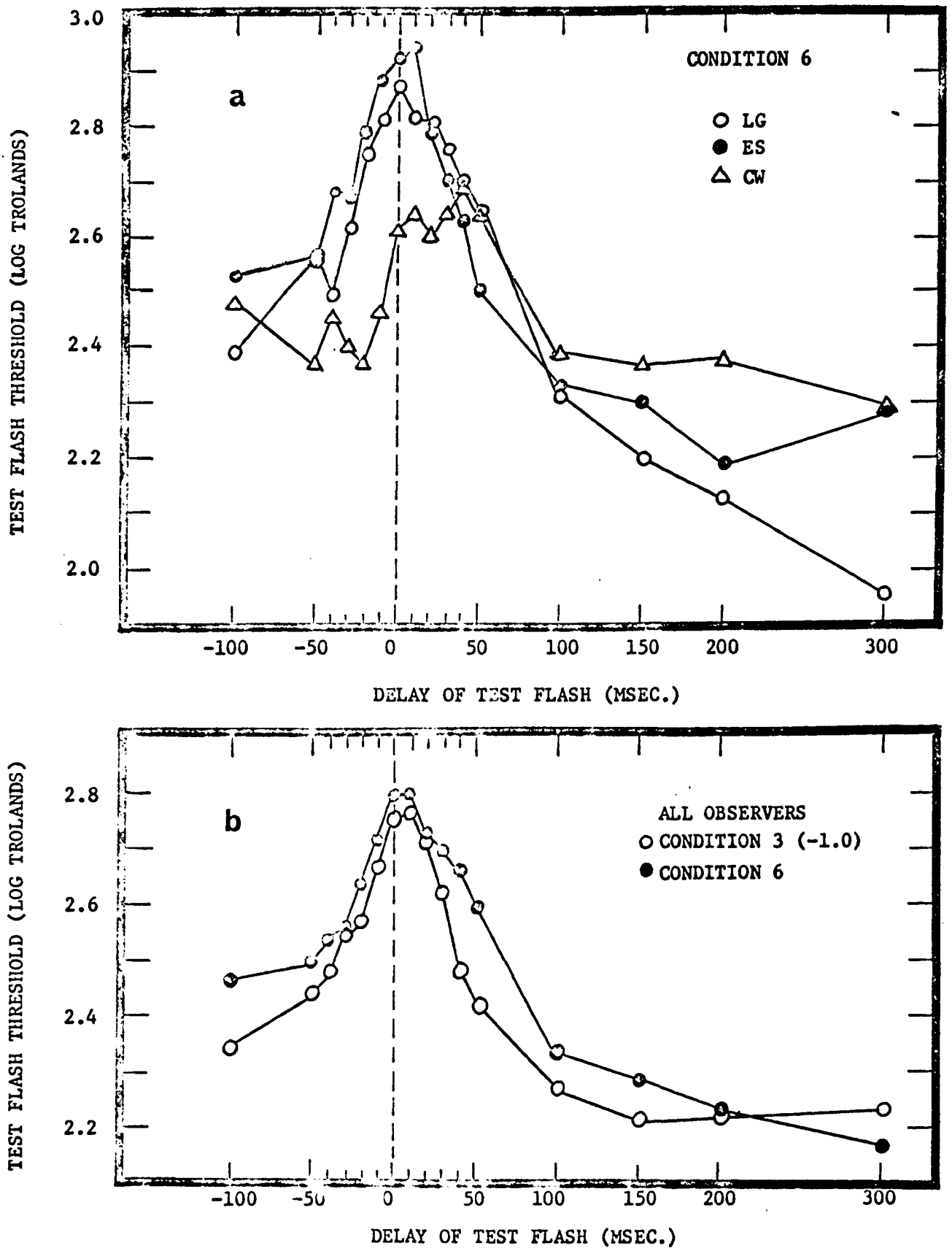

Fig. 3-8. Results of adaptation level experiment (disc = 1.7 log td.; annulus = 2.8 log td.). (a) Individual masking functions obtained in Condition 6. (b) Average masking functions for all observers in Conditions 3 and 6. The Condition 3 curve has been lowered by one log unit to facilitate comparison of the curves.

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Contrary to the expectation, the masking peaks shifted toward longer test flash delays by 10 msec. for ES and by 30 msec. for CW (Table 1). The peaks of LG's masking functions were at the same delay at both adaptation levels. Since the Conditions X Delays interaction was not significant, the peak shifts between Conditions 3 and 6 were attributed to random changes. The peaks of the average masking functions for all observers combined in Figure 3-8b occurred when the test flash was delayed by 10 msec. in both conditions.

In conclusion, lowering the adaptation level in the disc from 2.7 to 1.7 log trolands without changing the illuminance of the masking annulus merely lowered the masking functions by approximately one log unit and did not significantly change the form of the functions.

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Chapter IV

DISCUSSION AND CONCLUSION

The results of the main experiment -- increased magnitude and decreased latency of the masking peaks with increased masking intensity -- were predicted by the transient inhibition theory of visual masking. There are many other theories of visual masking, of course. Those that are especially pertinent to the present experiment were formulated by Boynton and Kandel (1957), Weisstein (1968), Dember and Purcell (1967), and Kahneman (1967).

Boynton and Kandel (1957) argued that masking of the test stimulus response was due to the overloading of the system by massive on-responses to the masking stimulus. Schiller's (1968) single-unit recording in the cat lateral geniculate showed that effect clearly with overlapping stimuli. Boynton and Kandel applied the theory only to conditions in which both test and masking stimuli stimulated the same retinal areas. However, the on-response theory could be applied to the nonoverlapping, but adjacent, stimuli in the present experiment. The overloading would be assumed to occur in neural channels near the disc-annulus junction that transmit information about both stimuli. If the on-responses to masking stimuli of different intensities resemble the excitatory responses that were recorded in the cat lateral geniculate by Baker, Sanseverino, Lamarre, and Poggio (1969), then the theory of Boynton and Kandel could predict the magnitude changes and the peak shifts of the main experiment. However, the theory is not compatible with electrophysiological evidence

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for nonoverlapping stimuli. For example, Poggio et al. (1969) demonstrated conclusively that test stimulus responses of lateral geniculate cells were inhibited by the response to a masking annulus, not merely obscured by a larger on-response.

Weisstein (1968) proposed a model for metacontrast in terms of a network of five two-factor (excitatory and inhibitory) neurons. The temporal responses of the model were determined by selecting time constants and weighting parameters for each neuron to fit the metacontrast data of Weisstein and Haber (1965). At least two difficulties arose when Weisstein's model was compared with the main experiment results. The first difficulty was that all of the masking functions in the present experiment had maxima at zero or positive test flash delays. Since inhibition develops faster than excitation in Weisstein's model, only peaks at negative delays were expected. Weisstein suggested that, with the addition of other inhibitory neurons with slower time-constants, the model could handle forward masking peaks. It is difficult to understand, however, why the original fast inhibitory responses should be suppressed in the forward masking case. Nevertheless, there is a still more serious discrepancy; the peak-shift prediction implied by the model is in the wrong direction. Weisstein asserted, "U-shaped backward masking functions will be obtained, if equal energy stimuli are used. If monotonic functions are to be obtained, the mask energy must be increased. This will adjust latencies of maximum excitation and inhibition so that they coincide." (1968, p. 508). In other words, Weisstein would expect that increasing the mask energy, holding durations constant, would shift the masking function's peak from some

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negative value toward zero delay. Physiological evidence and the results of the main experiment, however, refute this position. Increasing the mask intensity should decrease the latency of the inhibition (Lange, 1965); consequently, the masking peak should shift to even more negative delays. That was precisely the result of Alpern's (1953) metacontrast experiment. In a subsequent paper (Weisstein & Growney, 1969), Weisstein indicated that predicting metacontrast functions for changes in test and masking energy appeared to be a more complicated matter than it had appeared initially. Her revised prediction was "simply, very generally, that metacontrast functions would vary a great deal with changes in energy" (1969, p. 322).

Dember and Purcell have developed a lateral inhibitory explanation for masking of dark targets (Dember & Purcell, 1967; Purcell & Dember, 1968). The theory is based upon the assumption that the decay of inhibition is a monotonic function of time since termination of stimulation (Purcell, Stewart, & Dember, 1968). Not much has been said about off-transients in the present paper, since the main concern was inhibitory responses to illumination increments. However, the physiological evidence is quite clear that the time course of the inhibitory decay is not monotonic; in nearly every case the inhibitory off-transient is a near mirror-image of the on-transient and exhibits similar overshooting. As a consequence, neurons usually exhibit post-inhibitory rebounds in firing rates (Ratliff, Hartline, & Miller, 1963; Ratliff, 1965; Lange, 1965). Dember and Purcell's theory is not readily applied to light targets and what their explanation of the main experiment results would be is unclear. The transient inhibition theory described

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previously, however, can explain the masking of dark targets in terms of inhibitory transients of off-center cells that presumably respond to decrements in illumination. Poggio et al. (1969), for example, recorded single-cell responses of off-center cat geniculate cells for various delays between "dark flashes" of discs and annuli. The response of the off-center cell to the presentation of a dark disc was maximally inhibited by presenting a dark annulus about 10 msec. before the disc. A masking function constructed from the off-center data would be very similar to those obtained for on-center cells in the experiments described previously. The transient inhibition approach, therefore, is able to account for masking of both light and dark targets with the same basic principles.

According to Kahneman's (1967, 1968) explanation of metacontrast in terms of "impossible" apparent motion, observers tend to suppress targets that apparently move in unlikely patterns, for example, a square that moves in two directions at once. The stimuli that were used in the present experiment, however, did not elicit reports of apparent movement from the observers. This was probably due to the unequal durations and troland values of the stimuli and to the disc and annulus configuration. Weisstein and Growney (1969) criticized Kahneman's theory on logical grounds and presented results showing differences between apparent movement and metacontrast as various stimulus parameters were varied. Weisstein made the important point that metacontrast and apparent motion both might be related by lateral inhibitory processes. Relatively simple inhibitory networks have

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already been suggested as movement analyzers. For example, Barlow and Levick (1965) proposed a lateral inhibitory model for detection of movement in the rabbit retina. Similar mechanisms, that mediate both apparent motion and metacontrast, could be understood in terms of temporal inhibitory transients.

Thus the visual masking effects in the present experiment are best understood in terms of transient lateral inhibition. How can the theory be applied to other visual masking results?

The basic problem is that many metacontrast studies report maximum masking at negative delays of the test stimulus (Alpern, 1953; Schiller & Smith, 1966). According to the theory, maximum masking occurs whenever the excitatory and inhibitory response peaks are simultaneous at the locus of interaction. Masking peaks fall at negative test flash delays, therefore, when the inhibition rises to its peak more rapidly than the excitation at the point where the two processes interact. There are two main possibilities for attacking the problem of why some masking paradigms yield peaks at negative delays. The first possibility is that different paradigms use different values for stimulus parameters such as test and masking luminance, duration, area, and adaptation level. These parameters determine the latencies of the peak excitation and inhibition throughout the visual system. For example, Alpern (1953) reported masking functions that resembled the present experiment's results, despite the fact that he used a 5 msec. masking stimulus and a brightness matching method, and presented rectangular stimuli to a dark-adapted

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region of the peripheral retina. The similarity of the peak-shift results is surprising, considering the many differences in technique. The only important discrepancy was that Alpern's curves peaked at delays around -100 msec. instead of around zero delays. Schiller and Smith (1966) obtained a similar masking function that peaked at -60 msec. under comparable conditions. More research is needed in order to identify the critical differences between the two paradigms, Alpern's and the present experiment's. It might be that foveal-peripheral differences are important. Alpern (1953) found no metacontrast effects with foveal stimuli. But he reported results for only the -100 msec. test flash delay that produced maximum peripheral metacontrast. Perhaps he would have found foveal effects if the test and masking stimulus had been presented simultaneously. Another important difference between the present paradigm and other conditions that produced maximum masking at negative delays was the preliminary adaptation of the test stimulus retinal area by the disc. The pre-adaptation decreased the latency of the excitatory response to the test stimulus (Alpern, 1968). Speeding up the excitation, of course, shifts the masking function in the same direction as slowing down the inhibition, that is, to later test flash delays. Thus another factor contributing to negative delay peaks could be the slower responses to test stimuli at lower adaptation levels.

The second possible reason for backward masking peaks is that the observer's responses for different tasks may be determined at different neural levels. Identification of letters (Weisstein & Haber,

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1965), for example, probably occurs only "higher up" in the visual system than, say, detection of a brief flash. Since inhibition and excitation probably develop at different rates at different neural sites, the latency of the peak of the masking function probably varies with the neural level at which the response is determined. The question of where the excitatory-inhibitory interaction occurs cannot be answered for every response task. But there are several ways of getting partial answers to that question. Single-unit recording with visual masking stimuli is one way. Poggio et al. (1969) and Schiller (1968) found that metacontrast effects were well developed in single neurons in the cat lateral geniculate body. From the masking functions for single cells that Poggio, Baker, Lamarre, and Sanseverino (1969) presented, it appeared that similar neurons could have been responsible for detecting the test flashes in the present experiment. Another way to get information about where the excitatory response is inhibited is to present the test and masking stimuli to opposite eyes. Kahneman (1968) reviewed several dichoptic masking experiments that indicated that masking can also occur in the visual cortex, where the inputs from the two eyes first interact.

Some additional evidence for the importance of lateral inhibitory transients was provided by several experiments that demonstrated disinhibition of a previously masked test stimulus by masking the masking flash with a third flash (Robinson, 1966, 1968; Dember & Purcell, 1967; Purcell & Dember, 1968). Robinson (1968), for example, found appreciable dichoptic masking of the test stimulus by the

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masking stimulus, but found no disinhibition effects interocularly.

In order to understand more precisely how the temporal course of lateral inhibition is involved in various masking paradigms, several shortcomings of the present experiment should be overcome by further research. First, the contour separation condition (Condition 5) failed to significantly delay or diminish the masking effect. This would almost certainly not be the case for greater separations of test and masking stimuli, since Alpern (1953) found that increasing the separation of rectangular stimuli to about 2.5 degrees shifted the maximum masking for one observer from about -100 msec. to approximately -40 msec. delay. Similarly, the adaptation level experiment (Condition 6) may not have lowered the adaptation level enough to produce a significant effect. For example, a one log unit change in luminance at a relatively high luminance level changes the excitatory latency much less than the same luminance change at low intensities (Alpern, 1968; Prestrude & Baker, 1968). Finally, the masking stimulus with the highest troland value in the main experiment failed to shift the masking peak to a negative test flash delay. The upper level of illuminance for the masking stimulus was limited by the apparatus. If the troland value of the masking stimulus had been two or three log units above that of the disc, then perhaps the masking function's peak would have shifted into the backward masking region.

In conclusion, the significance of understanding the temporal properties of the neural processes involved in vision can hardly be underestimated. The idea that excitatory and inhibitory

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components interact is not new; many experimenters have postulated temporal interaction of excitation and inhibition to explain both psychophysical data (Baumgardt & Segal, 1942-43; Ikeda, 1965; Sperling & Sondhi, 1968) and physiological results (Pickering & Varjú, 1969; Licker, 1969; Fuortes & Hodgkin, 1964; Rodieck & Stone, 1965). However, recent advances in neurophysiology continue to elucidate the transient responses of visual systems. As a consequence, theories that incorporate the temporal properties of lateral inhibition may eventually account for the many temporal phenomena of human vision.

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APPENDIX:

ANALYSES OF VARIANCE SUMMARY TABLES

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TABLE 2

ANALYSIS OF VARIANCE FOR THE MAIN EXPERIMENT

Source	df	MS	F
Observers (A)	2	0.04963	2.64
Conditions (B)	3	2.66211	6.46 *
Delays (C)	15	2.57533	30.98 **
A X B	6	0.41186	12.74 **
B X C	45	0.23499	7.27 **
C X A	30	0.08314	2.57 **
A X B X C	90	0.03233	1.72 **
Within	1536	0.01878	

* $p < .05$

** $p < .01$

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TABLE 3

ANALYSIS OF VARIANCE FOR CONTOUR SEPARATION EXPERIMENT

(CONDITIONS 3 AND 5)

Source	df	MS	F
Observers (A)	2	1.13763	54.20 **
Conditions (B)	1	1.22649	3.86
Delays (C)	15	1.82661	26.56 **
A X B	2	0.31755	9.47 **
B X C	15	0.02006	1.67
C X A	30	0.06878	2.05 *
A X B X C	30	0.03354	1.60 *
Within	768	0.02099	

* $p < .05$

** $p < .01$

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TABLE 4

ANALYSIS OF VARIANCE FOR ADAPTATION LEVEL EXPERIMENT

(CONDITIONS 3 AND 6)

Source	df	MS	F
Observers (A)	2	0.53736	19.97 **
Conditions (B)	1	190.29900	1524.34 **
Delays (C)	15	2.03500	15.20 **
A X B	2	0.12484	1.94
B X C	15	0.05343	1.20
C X A	30	0.13384	2.08 *
A X B X C	30	0.06424	2.39 **
Within	768	0.02691	

* $p < .05$

** $p < .01$

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