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A PSYCHOPHYSICAL INVESTIGATION OF TRANSIENT AND SUSTAINED MECHANISMS IN HUMAN VISUAL MASKING

by

Joyce B. Schenkein

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

1982

Schenkein

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.

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Abstract

A PSYCHOPHYSICAL INVESTIGATION OF TRANSIENT AND SUSTAINED MECHANISMS IN HUMAN VISUAL MASKING

by

Joyce B. Schenkein

Adviser: Ivan Bodis-Wollner, M.D.

The threshold of an 8.3 msec sinusoidal test grating was measured as a function of its onset asynchrony (SOA) with respect to a 725 msec mask of 2.6% contrast and the same spatial frequency (5, 4 or 6 c/d). The test grating was either in the same spatial phase as the mask, or laterally displaced by 180°.

Large "primary" peaks occurred with mirror-like symmetry in time at small (25 msec) asynchronies from mask onset and offset. The timings (but not the magnitudes) of these peaks were phase-dependent suggesting that spatial phase is processed in a temporal way.

The same SOAs associated with a primary peak to gratings in one spatial phase, were associated with troughs, or facilitation for gratings of the opposite spatial phase. Peaks and especially troughs decreased in magnitude as spatial frequency increased. The fact that the primary peaks occurred at short latency and that their amplitudes decreased

with spatial frequency suggest that they represent transient neural responses.

At longer (40-100 msec) delays and on opposite "sides of the temporal edge from the primary peaks, were smaller "secondary" peaks. The magnitudes and delays of these peaks increased with spatial freqency suggesting the importance of sustained neural mechanisms.

To test this theory, monocular masking thresholds of 5 and 4 c/d test gratings were measured following 3 min adaptation to low contrast (1-4%) counterphase (TA; transient adapting) or stationary (SA; sustained adpating) gratings of the same spatial frequency (5 or 4 c/d) Adaptation was either in the same or contralateral eye.

TA altered detection at both spatial frequencies whereas SA affected only 4 c/d. SA DECREASED whereas TA INCREASED all masking peaks, suggesting that the sustained system ordinarily masks, whereas the transient system ordinarily enhances test detection. SA reduced the primary and secondary peaks by the same magnitude indicating that sustained influences at these different SOAs are equal. However, TA, raised secondary peaks more than primaries, indicating unequal transient influence at these SOAs. Ipsilateral and contralateral effects were identical after SA ONLY, suggesting that the sustained system is binocular whereas the transient system is predominantly monocular.

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A PSYCHOPHYSICAL INVESTIGATION OF TRANSIENT AND SUSTAINED MECHANISMS IN HUMAN VISUAL MASKING

Joyce B. Schenkein

CHAPTER 1

I. Introduction

When two visual stimuli are presented in close temporal succession, the perception of the first (refered to as the test) may be enhanced or diminished by the presentation of the second (refered to as the mask) (Kahneman, 1968). This phenomenon, called masking, is currently attributed to neural interactions between two visual subsystems which detect the stimuli; one, a short latency (transient) system carrying information about change, and the other, a slower (sustained) system which carries pattern information (Breitmeyer & Ganz, 1976).

The present study explores these test-mask interactions more closely. In Experiment I, the baseline condition, the contrast threshold of a brief (8 msec) test grating was measured at varying temporal asynchronies before, during and after the presentation of a long duration (725 msec) mask. As will be seen, there were several temporal asynchronies at which the threshold of the test presented with the mask was substantially greater or lower than that of the test presented alone. To investigate the contributions of the transient and sustained systems to these changes, a second study was conducted, using adaptation to partial out the influences of these two systems. As will be seen, this approach offered considerable insight into the underlying process.

A review of the relevant issues in masking and of the adaptation procedure is presented below. Following this, baseline and adapted conditions will be reported and discussed separately. Finally, a model to explain the data appears at the end. A glossary of terms frequently used in this paper is listed in the Appendix.

II. Related experimental paradigms

Changes in visual sensitivity due to the interaction of temporally discrete stimuli has been explored in a variety of paradigms under the names of rapid light adaptation, temporal resolution, metacontrast and masking. One stimulus, often the briefer, smaller or dimmer is designated as the TEST and the other as the MASK. The subject's task is to detect the test.

III. Experimental variables

A. The INDEPENDENT Variable

- is always the temporal relationship between the test and the mask stimuli. Many investigators have measured this delay from the offset of the first stimulus to the onset of the second; that is, the interstimulus interval (ISI). However, later analyses showed greater consistency across studies when the delay is measured from the ONSET of the first stimulus to that of the second (Boynton, 1972; Kahneman, 1967). Referred to as the stimulus onset asynchrony (SOA), this is the most frequently used measure of temporal delay.

The SOA of zero (that is, the simultaneous onset of the test and mask) is commonly explored in two-pulse studies. However, test thresholds at non-zero delays DURING mask presentation are not always sampled although, as will be seen, sensitivity fluctuates greatly during this time (Crawford, 1947).

B. The DEPENDENT VARIABLE differs among investigators from percent detection of a test stimulus of fixed luminance or contrast (Kietzman, Boyle & Lindsely, 1971) to magnitude estimation (Weisstein, 1971) to measurement of the actual luminance or contrast increment necessary to detect the test stimulus (Battersby & Wagman, 1959, Tolhurst, 1975b). Masked thresholds are always compared to those of the test presented alone.

IV. Typical Stimuli and Findings

The terms masking and metacontrast have been used to describe temporal interactions between stimuli. The term masking, which tends to include metacontrast, is more strictly defined as the condition in which the test and mask are spatially overlapping (Kahneman, 1968). Concentric circles of light are typical stimuli, although letters, lines and random noise have also been used (Kahneman, 1968).

In metacontrast, the test and mask are spatially contiguous rather than overlapping; for example, a circular test disc and an annular mask.

In the present discussion, the term masking will be used to include threshold changes associated with the metacontrast paradigm as well as that of masking since, as will be discussed, the present data suggest that the two phenomena are similar.

A broad range of stimulus configurations have been used in masking studies, ranging from letters of the alphabet, geometric shapes, lines and flashes of light. Stimulus sizes, contrasts and durations also vary greatly. However, regardless of stimulus characteristics, the general finding in these studies is that the detectability of the test stimulus is greatly reduced if mask is presented shortly before or after it.

V. Types of Masking Functions.

When test threshold is plotted as a function of SOA, two basic types of functions have been described.

A. Type A masking: This function is U-shaped, rises some 50-200 msec before the onset of the mask (backwards masking) reaches a maximum when the test and mask are simultaneous (SOA = 0) and falls in an assymetrical way showing slightly more forward than backward masking as SOA is increased (Kahneman, 1968). Type A masking tends to occur when the mask is approximately 1 log unit or greater in intensity than the test (Weisstein, 1972).

B. *TYPE B MASKING*: is predominantly backwards, that is, thresholds peak when the test precedes the mask by 50-100 msec (Alpern, 1953, Schiller & Smith, 1966; Weisstein, 1968; Kahneman, 1968) and are usually back to baseline by the SOA of 0. Forward masking, if it occurs, is very slight in comparison to the backward effect (Alpern, 1953) and in recent studies, threshold sampling of forward SOAs is often neglected. (e.g., Growney, 1978, Kahneman, 1967; Petry, 1978). Type B functions generally result when the test and mask are approximately equal in intensity and occur primarily when verbal report (as opposed to reaction time) is used as a detection measure (Kahneman, 1968).

Because Type B masking is maximal at the same SOAs associated with apparent motion, whereas this is not true of type A masking, Kahneman (1967) believes that different neural phenomena underly the two functions. Weisstein (1971) however, suggests that the same mechanisms are involved in both functions and that all differences can be attributed to variations in the stimulus parameters. Weisstein's theory will be discussed more fully in a later section in reference to my findings and a new view of Type A and Type B masking will be suggested.

C. *Crawford functions*. In opposition to Types A and B classifications (which apply primarily to interactions of brief test and mask stimuli), Crawford (1947) and others have reported a differently shaped function when the duration of the mask is prolonged and test thresholds are sampled concurrently with as well as before and after mask presentation (Crawford, 1947, Baker, 1953, Battersby & Wagman, 1962, Wagman & Battersby, 1959). Under these circumstances, thresholds rise prior to the onset of the masking stimulus, and then fall to a steady but elevated level whose magnitude depends upon mask intensity (Wagman & Battersby, 1959) and duration (Battersby & Schuckman, 1970). When the test and mask are similar in diameter (Battersby & Wagman, 1962; Battersby, Osterreich & Sturr, 1964) and are presented to the same eye, thresholds also rise at offset. "Off" effects are smaller in magnitude than the "on" effect (Baker, 1953, Battersby & Wagman, 1962; Crawford, 1947) and vary with mask luminance (Baker, 1953).

VI. Parameters associated with masking and metacontrast

The findings of interactions between geometric shapes and light flashes will be presented first, followed by masking studies which used sinusoidal gratings as stimuli. Results from both types of studies are presented since it will later be suggested that a common mechanism underlies them.

A. Target size and shape.

1. Masking effects measured psychophysically (Battersby & Wagman, 1962, Markoff & Sturr, 1971; Growney, Weisstein & Cox, 1977; Kandel, 1958) or electrophysiologically using the

Visual Evoked Response (VER: Harter, 1977) are more pronounced when the test and mask are the same size. This is particularly interesting because larger masks have greater luminious energy and would intuitively seem more effective. However, even when the test and mask are circular flashes of the same sizes, inhibitory interactions do not occur unless both stimuli exceed a certain critical diameter (Meijer, Van Der Wildt, & Van den Brink, 1978) or width (Green, 1981). The critical diameter increases with both retinal eccentricity and luminance level, going, for example, from 5.5' to 11' to 22' of arc as retinal eccentricity is increased from 0 to 3.5 to 7 degrees (Meijer etal., 1978).

2. Optimal metacontrast usually occurs when the test and mask borders have the same shape (Alpern, 1953, Battersby, Osterreich &Sturr, 1964, Bobak, 1980, Uttal, 1970) and when the borders are spatially contiguous. Changing the outer border of the annular mask (Westheimer, 1967; Growney & Weisstein, 1972; Polous & Makous, 1980) adding a second larger annular mask (Breitmeyer, 1978a; Sturr & Teller, 1973) or filling in the center of an annular mask (Weisstein, 1971) will all alter the time course and magnitude of masking.

__B. Test Duration.__ is typically brief, ranging from 1.2 to 20 msec (Battersby & Wagman, 1962; Ikeda & Boynton, 1965; Kahneman, 1968; Weisstein, 1971) For test stimuli less than 100 msec in duration, the SOA of maximal masking is inde-

pendent of test duration. This is referred to as the onset-onset law of masking (Kahnamen, 1967).

C. Mask duration. As already mentioned, detection of a relatively brief test flash is impaired at both onset and offset of a long duration mask. However, for briefer masks (about 20 msec), only offset masking occurs (Battersby & Schuckman, 1970); that is, test thresholds increase only when the stimulus is presented at mask offset. A study by Ikeda & Boynton, (1965) has clarified what must underly the condensation of the masking function from a double to single peaked function. Apparently, when a test stimulus is presented in conjunction with a luminance INCREASE, the maximal masking effect occurs at small SOAs FOLLOWING the temporal edge. On the other hand, if the test is presented in conjunction with a luminance DECREASE, maximal masking PRECEDES the luminance change. Obviously then, when the mask is a positive pulse, (a luminance increase followed by a decrease), its associated peaks appear AFTER its onset and BEFORE its offset. Therefore, as the duration betwen these temporal edges shortened, the two peaks appear to merge. However.if the mask is a negative pulse, that is, if it begins with a luminance DECREMENT and ENDS with an INCREMENT, then the time course of masking is reversed. In this case, the initial threshold change associated with onset is maximal BEFORE the mask is presented and the rise associated with offset occurs AFTER the stimulus terminates. Thus, no matter how brief a NEGATIVE mask is, there will always be two tenporally discrete peaks associated with its presentation. The important point here is that regardless of mask brevity, onset and offset masking will occur although double-peaked functions will not be observed for positive pulses. This point will be raised again in a later section.

D. Mask Luminance. Increases in mask luminance both increases the magnitude of the masking effect (Alpern, 1953, Wagman & Battersby, 1959) and shortens the SOA at which these peak effects occur (Ikeda, 1965, Kandel, 1958, Weisstein, 1972) so that, type B functions become Type A.

E. Mask and test stimulus distance. The greater the spatial separation between the test and mask, the less pronounced the masking effect (Alpern, 1953; Growney, 1978, Growney, Weisstein & Cox, 1977; Weisstein & Growney, 1969).

F. Retinal locus. Alpern (1953) reported that metacontrast is pronounced in the peripheral retina but is nearly absent in the fovea. More recently, however, Lyon, Mattison & Marx (1981) have shown that for small test and mask stimuli, foveal metacontrast not only occurs, but may be as pronounced as peripheral metacontrast.

It was previously mentioned that there is a critical test probe size required for masking. This size increases with retinal eccentricity (Meijer, Wildt, Van der Brink, 1974). Although retinal factors are certainly involved in masking, they are not solely responsible for this effect since it can be obtained dichoptically (Schiller & Smith, 1968; Weisstein, 1971; Battersby, Osterreich & Sturr, 1964). Additionally, it must be remembered that in the monocular condition, metacontrast stimuli fall on adjacent although non-homotopic retinal areas, whereas in the dichoptic situation, stimulation is neither retinally adjacent nor homotopic.

G. Luminance Polarity. It has already been suggested that the test and mask stimuli can be either positive or negative going signals, for example, light increments or decrements (Ikeda & Boynton, 1965; Ikeda, 1965) black discs on white backrounds (Weisstein, 1971) or light discs on dark backrounds (Keitzman, Boyle & Lindsely, 1971). The time course of masking depends, not upon the absolute polarities of the test and mask stimuli, but rather upon the relationship between the two (Ikeda, 1965). For example, two stimuli of like-polarity summate maximally at brief SOAs and inhibit each other at asynchronies of approximately 30 to 50 msec regardless of whether they are both positive or negative-going signals (Ikeda, 1965). Opposite polarities however, show the reverse time course of interaction, summating maximally at asynchronies of 30 to 50 msec and masking each other when simultaneously presented. (The time course of these interactions has since been expressed quantitatively by Rashbass, 1970).

Masking and metacontrast stimuli share certain obvious features with like-polarity and unlike-polarity situations, respectively. In the former situation, the test and mask stimulate overlapping retinal areas, whereas in the latter case, the configuration of the mask is opposite in polarity to that of the test. Although it is tempting to attribute the differences in timing between masking and metacontrast functions to luminance polarity, it must be remembered that the stimuli used in metacontrast studies are structurally more complicated than light flashes. Their outer borders have repeatedly been shown to influence the magnitude of masking (Sturr & Teller, 1973, Weisstein & Growny, 1979; Westheimer, 1967).

H. Detection Criteria. The time course of masking is influenced, not only by the stimulus parameters, but also by whether the judgments are based upon brightness, form, or apparent duration (Blanc-Garin, 1968; Petry, 1978). Reaction time measures indicate that test detection can occur when the stimulus is still below psychophysical threshold (Fehrer & Raab, 1962).

VII. Monocular and dichoptic masking with circular test probes or light flashes.

The test and mask can both be presented to the same eye (monocularly) or separately to each eye (dichoptically). Comparisons of the two conditions show that the dichoptic effect tends to be:

1. Smaller in magnitude (Battersby & Defenbaugh, 1969;

Battersby & Wagman, 1962), relatively independent of mask intensity (Kandel, 1958; Wagman & Battersby. 1959; Weisstein, 1971) and relatively long lasting (Wagman & Battersby, 1959).

2. Earlier in temporal delays (Schiller & Smith, 1968; Weisstein, 1971)

3. And is frequently limited to backward masking only (whereas forward and backward masking occur in the monocular condition; Kietzman, Boyle & Lindsley, 1971; Weisstein, 1971). The failure to demonstrate forward masking in dichoptic presentation however, may be a consequence of the stimulus characteristics since cells in the visual cortex respond poorly to diffuse illumination (Hubel & Wisel, 1962;). Forward and backward dichoptic effects have been reported when the test and mask were small discs or similar in size (Schiller, 1965; Wagman & Battersby, 1959).

4. Finally, as in the case with monocular masking, dichoptic interactions are greatest when the test and mask are the same size (Battersby & Wagman, 1962).

VII. Sinusoidal Gratings

In recent years, sinusoidal gratings have been used as stimuli to study the visual system. These gratings look like a series of black and white stripes or bands whose edges are blurred (Campbell, 1974). Both the width of these bands and their contrasts can be varied. The term spatial frequency is used to indicate band width and is expressed as the number of cycles per degree of visual angle. Contrast, which will be defined more precisely in another section, expresses the luminance relationship between the bright and dark bars, taking the average luminance into account.

Electrophysiologically, single units in the cat and monkey visual systems have been shown to be most effectively stimulated by multiply striped patterns (Glezer, Ivanoff & Tscherbach, 1973) which are sinusoidal in nature (Schiller et al., 1976).

Using long duration stimuli, the normal human observer can detect gratings from 0 -48 c/d (Bodis-Wollner & Bender, 1972: Campbell, 1975) and shows the greatest sensitivity to middle-range spatial frequencies of about 3-6 c/d (Robson, 1966: Nachmias, 1967; Schober & Hilz, 1965), having a shallow fall off in the low frequency region and a sharp drop in sensitivity as spatial frequency is increased beyond 10 c/d.

VIII. Temporal-Spatial Interactions

An interaction between temporal and spatial parameters is reported repeatedly in the literature (Breitmeyer, 1975: Breitmeyer & Julesz, 1975; Graham, 1972; Keesey, 1971; Kelly, 1972; Kulikowski, 1975; Kulikowski & Tolhurst, 1973: Legge, 1978 Nachmiasm 1967; Pantle, 1973; Robson, 1966; Tolhurst, 1973 1975a, 1975b, Tolhurst, Sharpe and-Hart, 1973; Tynan & Sekuler, 1974; Watson & Nachmias, 1977.) Temporal characteristics which affect grating detection are listed below.

A. Exposure duration. As exposure duration increases up until at least 100 msec (Arend, 1976b; Tulunay-Keesey & Jones, 1976) the detectability of all spatial frequencies improves. However, beyond this duration, only high spatial frequency detection detection is enhanced. (Breitmeyer & Ganz, 1977; Nachmias, 1967; Spitzberg & Richards, 1975; Legge, 1978).

Brief presentation (less than 500 msec) improves sensitivity to low spatial frequencies but impairs high spatial frequency detection (Breitmeyer & Ganz, 1977; Kulikowski & Tolhurst, 1973). Thus, the contrast sensitity function for brief stimuli has a maximum between 0-2 c/d (Kulikowski & Tolhurst, 1973) whereas, superiority for long duration gratings is at 3-5 c/d.

B. Rise and fall time (temporal edges). A sharp temporal edge, that is, an abrupt (as opposed to gradual) rise and fall time, enhances sensitivity to LOW but not high spatial frequencies (Breitmeyer & Julesz, 1975). In addition, reaction time (RT) response histograms suggest that abruptly presented low spatial frequency stimuli may be detected either at onset or offset (Tolhurst, 1975a) whereas, at high spatial frequencies (above 3-8 c/d) the advantage of abrupt onset is lost and the test stimulus is detected as soon as a "critical" proportion of the energy is delivered (Tolhurst, 1975a).

C. *Flicker or movement.* Flickering or moving stimuli are more detectable when they are of low spatial frequency (Arend, 1976; Tolhurst, Sharpe & Hart, 1973) Several investigators have found two thresholds for low spatial frequency gratings; one at which flicker is seen and a higher contrast at which pattern is recognizable (Keesey, 1971: Kulikwski & Tolhurst, 1973). High spatial frequencies, on the other hand, seem to have only one threshold; that for pattern. (Keesey, 1971) Even when flickering, gratings at high spatial frequencies appear to be steady (Tolhurst, Sharpe & Hart, 1973) The optimal flicker rate for the detection of low spatial frequency patterns is 5-10 Hz (Kulikowski & Tolhurst, 1973, Koenderick & Van Doorn, 1979).

D. *Stationary versus moving gratings.* Optimal sensitivity to stationary gratings occurs at 3-5 c/d. (Robson, 1966). However, when the same patterns drift at 6 c/s, this maxima shifts to 2 c/d (Tolhurst, Sharpe & Hart, 1973).

E. *On-off vs counterphase presentation.* In on-off grating presentations, the stimulus is briefly presented and then replaced by a blank screen. In counterphase presentation, the second half of the cycle is not blank, but displays the same stimulus in the opposite spatial phase. Thus, the local luminance changes in a counterphased presentation are twice as great as in on-off. Correspondingly, visual sensitivity is twice as great for counterphase as opposed to on-off stimuli, but only when below 6 c/d (Kulikowski & Tolhurst, 1973).

IX. *Parallel Visual Pathways*

A. The results of the above studies strongly support the existence of two visual sub-systems (Breitmeyer, 1975; Breitmeyer & Ganz, 1976, 1977; Breitmeyer & Julesz, 1975; Keesey, 1966; Matin, 1975; Tolhurst, 1973, 1975a, 1975b; Weisstein. Ozoq & Szoz, 1975).

1. A *TRANSIENT system* which is sensitive to low spatial frequencies, particularly when associated with some element of change, such as flicker or movement (Kulikowski & Tolhurst, 1973; Tolhurst, 1973; Van Nes, Koenderink, Nas & Bauman, 1967). Brief stimuli are optimal for this system and "on" and "off" responses have been attributed to its influence (Tolhurst, 1975a, Breitmeyer & Julesz, 1975.)

2. A *SUSTAINED system* which is most sensitive to high spatial frequencies, particularly when steadily presented. (Keesey, 1966; Kulikowski & Tolhurst, 1973). The inability to detect rapid movement of high spatial frequency gratings, does not imply that the sustained system is insensitive to motion but rather that the perceptual experience of sustained activity is of form, regardless of the temporal parameters of the stimulus (Robson, 1966, Tolhurst, Sharpe & Hart, 1973). Interpretation of movement, is the other hand, is the contribution of the transient system (Robson, 1966).

B. The existence of separate form and movement detection systems is suggested by clinical reports of Riddoch's phenomenon (Bodis-Wollner, 1974; Riddoch 1917) and polyopsia (Bender, 1963). In Riddoch's phenomenon a patient who is form blind retains the ability to localize and grab flickering lights in an area of the visual field for which he has no conscious perceptual appreciation (Bodis- Wollner, 1974). Polyopsia, on the other hand, demonstrates the action of a form system in the absence of movement. In this condition, moving objects presented to the affected visual field appear to be multiply represented like a "string of pearls" rather than a single shifting image (Bender, 1963). If one presumes that abberant perceptions often reveal the nature of normal functioning, then a phenomenon such as polyopsia suggest that the normally operating movement system acts to inhibit the multiple perception of form.

C. _Electrophysiological evidence_ supports a duality at every level of the visual system (Enroth- Cugell & Robson, 1966; Cleland, Dubin & Levick, 1971; De Monasterio, 1978; Fukada, 1971; Ikeda & Wright, 1972, 1974; Hoffman, Stone & Sherman, 1972, Krantz, Webb & Sherman, 1978; Stone & Dreher, 1973) Although the same cell can show BOTH transient and sustained characteristics (Enroth-Cougell & Shapley, 1973; Hochstein & Shapley, 1976) certain features are more likely to be associated with one cell population or another. Transient-like (Y) cells, for example, have large non-linear summating receptive fields, are maximally responsive to movement, have short latency responses and fast conducting axons (Cleland & Levick, 1972; Enroth-Cugell & Robson, 1966, Hochstein & Shapley , 1976). Sustained-like (X) cells summate energy linearly (Hochstein & Shapley, 1976) and respond best to stimuli which either move or change slowly (Cleland et.al,1971). Secondly, being morphologically small and having thin axons, X cells have longer response latencies than Y cells and conduct information more slowly (Lennie, 1980).

Until recently, the X/Y dichotomy was relegated to animal physiology whereas in the human visual system, duality was distinguished psychophysically as transient or sustained. Despite similarities reported with the two methods, one could not presume a direct correspondence between animal and human function. However, in an extensive psychophysical study on rhesus monkeys (for which species the electrophysiology is known), Harwerth, Boltz and Smith (1980) presented bimodal reaction time data which is remarkably similar to that derived from human observers, strengthening the evidence that the underlying physiology is the same. Additionally, Miller, Pasik & Pasik (1980) showed that the psychophysically determined contrast sensitivity functions of rhesus monkeys were very similar to that obtained with human observers.

X. Masking with Gratings

When the test and mask are sinusoidal gratings, both the magnitude and timings of interactions vary with spatial frequency. Specifically, as spatial frequency increases,

A. The magnitude of masking decreases (Green, 1981; Tolhurst, 1975b) suggesting the importance of the low spatial frequency system.

B. The SOA of peak masking increases (Rogowitz, 1979).

3. The greater the spatial frequency DIFFERENCE between the test and mask the less the interaction between them (Watson & Nachmias, 1980; Blake & Levinson, 1977; Graham & Nachmias, 1971,Nachmias & Weber, 1975). This reduction in grating interaction between stimuli of widely discrepant spatial frequencies may occur either because the best mask for a test stimulus is one which is identical in spatial frequency (as might also be inferred from the findings of Battersby & Wagman, (1962) although they did not use harmonically pure stimuli) or because, as the difference between spatial frequency increases, the more likely it is for one of them to be high (above 10 c/d) and consequently associated with less masking. In specifically testing these hypotheses by varying either the spatial configuration or spatial frequency of the masking flanks, Growney (1976, 1978) failed to show that the optimal mask must be the same spatial frequency or size as the test. However, the grating masks used by Growney were confined in small rectangular visual windows and thus, contained additional spatial frequency components which probably confounded his results. In particular, he treated his 0 c/d mask as a uniform field,

although, being rectangularly shaped, it was likely to have its dominant spatial frequency at 5 c/d. It was indeed as effective a mask of a 5 c/d grating as was a sinusoid of that spatial frequency. In a previous study, Bodis-Wollner (1972) showed that 5 c/d, as opposed to any other frequency was the best mask of variously sized incremental patches, again suggesting that the dominant spatial frequency rather than the stimulus size is the more important factor in masking.

D. Changes in the phase relationship between the two stimuli affect the time course of masking (Watson & Nachmias, 1977). Brief gratings of the same spatial phase summate at very small SOAs, are independent by about 25 msec, and inhibitory at SOAs of 50 msec. The opposite behavior occurs between gratings which are 180° out-of-phase; that is, inhibition at small SOAs but summation at the SOA of 50 msec. Regardless of spatial phase relationship, the magnitude of inhibition is greater than that of summation.

Interestingly, the temporal delays associated with masking and facilitation of in- and out-of-phase gratings between 1.75 and 3 c/d are the same as those reported by Ikeda (1965) for like- and unlike-polarity pulse pairs respectively, suggesting that a common feature underlies the processing of both spatial phase and luminance polarity.

Phase related differences in masking revealed with the Crawford paradigm are as follows; In-phase test gratings are least detectable if presented after mask OFFSET, whereas test patterns which are 180° out-of-phase with the mask are least detectable just after mask ONSET (Tolhurst, 1975b). As was true in the Watson & Nachmais (1977) data, masking of one spatial phase occurs at the same SOAs as facilitation of the opposite phase, although, again, the magnitude of facilitation is less than that of inhibition.

In noting the opposing time courses of in- and out-of-phase masking, one may wonder if phase-related factors are responsible for the different temporal characterics of masking and metacontrast functions. This issue has not received attention possibly because the traditional masking stimuli are spatially complex and the phase relationships of the component frequencies are unknown. Additionally, changes in the time course of masking (e.g., the shift from a Type B to a Type A function) occur even for a fixed test-mask pair as their energy ratio is changed (Kahneman, 1968).

E. Finally, the magnitude of masking increases with the spatial complexity of the test and mask; that is, the greatest effect which occurs when the test and mask are uniform fields (and thereby contain all spatial frequencies at all orientations) the test threshold increase may be as great as 2.6 log units (Battersby & Wagman, 1962). For a sinusoidal test and a uniform field mask, threshold changes are smaller; about .6 log (Green, 1981). Finally, when the test and mask are both sinusoidal gratings threshold increments are even smaller; about .15 log (Tolhurst, 1975b). Whereas this estimate also depends upon the luminance level of the mask (Battersby & Wagman, 1962, Green, 1981) it is also likely that some reduction in masking reflects the more limited involvment of the visual elements as the spatial frequency content is restricted.

XI. Explanations of masking

Among the earliest theories that can be related to masking was Hecht's (1937) photochemical hypothesis of light adaptation which explains threshold changes in terms of photochemical availability. In terms of masking, this suggests that the long duration stimulus uses up the photochemicals necessary for the detection of the test stimulus. This theory is inadequate for many reasons. To begin with, it does not explain backward masking, e.g., the rise in test threshold before the onset of the mask (Battersby & Wagman, 1959) a time when photochemical availability is presumably at its maximum. Additionally, inhibition of the test by the mask occurs when these stimuli are are different colors (Foster, 1979) and therefore, deplete different photoreceptors of their pigments. Finally, since masking has been demonstrated to occur dichoptically (Battersby & Wagman, 1962, Schiller & Smith, 1965, Weisstein, 1971) it is obvious that neural as well as photochemical interactions are involved..

The task of explaining masking is quite formidable since the theory should account for a number of phenomena; for example, both forward and backward masking, as well Types A and B masking. In a herculean attempt to organize the metacontrast literature, Weisstein (1971) classified the various theories according to the types of functions they predict.

A. Theories which predict U-shaped (Type A) functions but not monotonic (Type B) masking are as follows:

1. Impossible Motion. Because the SOAs associated with masking are the same delays necessary for optimal apparant motion, Kahneman (1967) proposed that a common mechanism underlies both phenomena. According to Kahneman, test stimulus visibility is reduced by "motion" which causes it to blend with the mask or when it is forced to describe an "impossible" movement of going in two directions at once. However, others have shown that apparent movement occurs at spatial separations which are much greater than those which result in metacontrast (Weisstein, 1972) so that the two phenomena may be related but not identical.

2. Replacement from visual storage. This model assumes that stimulus information is temporarily stored before processing and that new information arriving before or during this time will disrupt this storage and prevent complete transmission. Although this model predicts a U-shaped masking function, it offers no insight about reasons why the SOA of maximal masking varies from forward to backward as the

spatial fit between the test and mask improves (Battersby & Osterreich & Sturr, 1964) or as mask energy decreases (Kahneman, 1967). Additionally, Weisstein (1972) has pointed out that the SOA of peak masking may sometimes be longer than the empirically estimated "read-in" times of other experiments. Finally, in situations involving the multiple presentation of test stimuli which had been masked in a single presentation may reappear (Schiller & Smith, 1966) suggesting that succeeding mask stimuli do not "steal" storage space.

B. Theories which predict monotonic but not U shaped functions

1. Adaptation. assumes that the neural elements responding to the mask are adapted so that they cannot respond to the test stimuli. This theory explains forward but not backward masking. An additional problem with this theory is the presumption that the mask restimulates the same neural elements as the test stimulus, which may be true in the masking situation but less likely for metacontrast when the flanks stimulate adjacent non-homotopic areas.

2. Lateral Inhibition - According to this theory, threshold changes in metacontrast, are accomplished by lateral inhibition originating from the retinal area stimulated by the mask flanks (Bridgeman, 1975).Because a longer time is required to pool inhibitory as opposed to excitatory neural. activity (Winters and Hamasaki, 1976) one would expect only

forward masking to occur. However, as already mentioned, most metacontrast masking is backward.

C. Theories which combine elements of the above theories.

Because of the difficulty in accounting for Type A and B masking in a single theory, Kahneman (1968) tentatively suggested that a combination of the above theories may be involved, each dealing with a different aspect of masking.

Opting for parsimony, Weisstein (1972) proposed a single-mechanism model to account for both Types A and B functions. Challenging the usual notion that inhibition is always longer in latency than excitation, Weisstein's model assumes the reverse and suggests that the inhibitory response to the later (mask) stimulus overtake and cancel the excitatory response to the (earlier) test. Since increases in the mask (but not test) energy would further speed the inhibitory component of the mask response, then the SOA associated with the test-mask interaction should be longer than that obtained with equal energy pulses. (In other words, masking should be more backwards as mask/test luminance ratios increases. However, exactly the opposite results are found in these circumstances; that is, Type B (backward functions) become Type A (SOA = 0; Kahneman, 1968).

To get around this problem, Weisstein (1972) proposed that as mask energy increases, its inhibitory response not only occurs earlier, but also persists for a longer time. Hence, under these circumstances, masking should occur for a more extended time period encompassing both earlier and later SOAs. Using a computer to simulate the possible latency changes in inhibition and excitation as the mask/ test (M/T) luminance ratio is increased, Weisstein tested her predicted masking functions against the empirical data using 16 msec tests and annular mask. As is typical of most metacontrast investigations backward sampling was conducted over an SOA range of approximately 300 msec whereas forward masking was explored for less than 150 msec. Fig. 1.1-1.5 show that for M/T ratios of 1 (equal test and mask energy) masking data resembles the typical Type B function, with maximal effect at about 50 msec before mask onset. At the highest M/T ratio (16/1) not only is the magnitude of masking considerably greater, but the function shows Type A characteristics; that is, the maximal masking effect occurs at the SOA = 0. Looking only at these two functions, the ostensible conclusion is that as mask energy increases, maximal masking shifts from later to earlier asynchronies. However, a different story is suggested by the intermediate M/T functions. These figures show that as mask energy increases, the backward trough (decrease in sensitivity) not only deepens, but also shifts to LONGER SOAs. Note that this shift to longer SOAs is the logical expectation if the latency of the mask inhibition is reduced. At the M/T ratio of 5, however, in addition to the backward effect, a new

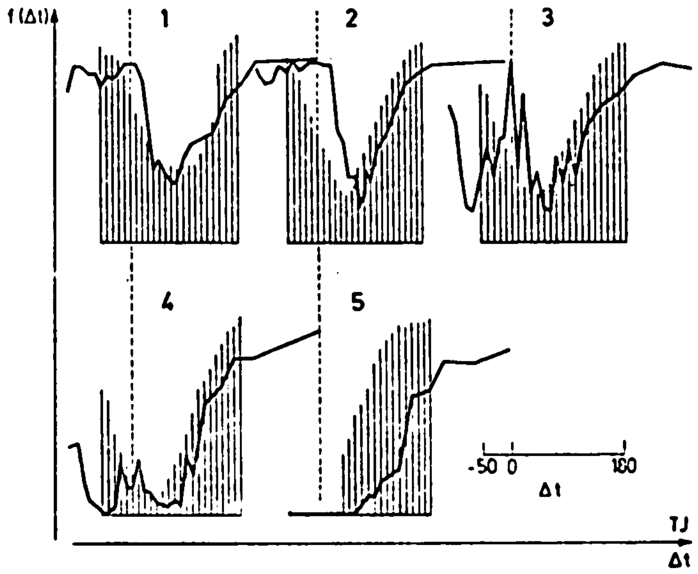

Fig 1. Weisstein's empirical masking data (solid lines) compared with her computer generated predictions (line slashes), In her figures, the test is a 1^0 disc of 16 msec duration. The mask is an annulus of $1^01'$ (inside diameter) and $1^023'$ (outer diameter) and 16 msec in duration. Fig 1.1-1.5 demonstrate changes in test thresholds as Mask/Target energy increases from 1,2,5,8 to 16 respectively.Time is represented on the X axis, sensitivity on the Y axis.

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FORWARD trough, equal in magnitude to the backward trough, appears approximately 80 msec after the mask onset, giving the masking function a W-shaped appearance. Since forward masking thresholds were not sampled at asynchronies much beyond 100 msec, it is not known if this "new" trough also occurred at the lower M/T ratios, but was not discovered due to insufficient sampling at the forward SOAs. With increases in the M/T ratio, this foward trough deepens and shifts closer to the origin completely swallowing up the backward trough by the highest M/T ratio (16/1) so that Type A characteristics prevail; that is, maximal masking at SOA = 0. Thus, discrete backward and forward troughs can no longer be demonstrated at high M/T ratios because the overall magnitude of masking is so great that the test stimulus is never seen. Thus, the masking function appears to represent a single phenomenon when, in fact it may be W-shaped, but out of the decision range of the magnitude estimation procedure. Therefore, although Weisstein tried to condense Types A and B masking into a unitary process, her empirical data are not in complete agreement with her theory, and, as will be argued later, the two functions probably do reflect the contributions of different neural mechanisms.

D. <u>Transient-Sustained Model</u>.

Although Types A and B masking cannot be jointly explained, one feature of Weisstein's model has gained considerable electrophysical support (Licker, 1969; Schiller, 1968; Singer & Bedworth, 1962), namely, the notion that fast neural inhibition generated by the mask stimulus overtakes and interferes with the slow excitatory response arising from the test. In recent years, the source of fast inhibition has been linked to the transient visual system, whereas slow excitation has been attributed to the sustained system (Breitmeyer & Ganz 1976). Additionally, a number of models which presume different transient and sustained interactions have been generated (Breitmeyer & Ganz, 1976; Matin, 1975; Weisstein, Ozog & Scoz, 1975).

Among the most popular is that of Breitmeyer & Ganz (1976) who sugggest that the neural response to every visual stimulus has several time-dependent components, the earliest of which (the transient response) signals the presence of the stimulus and the later of which (the sustained component) conveys information regarding its spatial characteristics. If the presentation of the test and mask is timed so that the early components of the second stimulus arrive at some neural locus at the same moment as the late components of the first, masking is presumed to occur.

Several testable hypotheses emerge from this theory of transient-sustained (T-S) interaction in masking.

1. If mask inhibition suppresses only the SUSTAINED response to the test stimulus, then the TRANSIENT test response should still occur in the nervous system. Since reaction time (RT) presumably measures the fast neural

response to a stimulus, then this value should not change even when the stimulus is masked and unseen. Such findings were obtained by Fehrer & Raab (1962). Additionally, the failure to see the test stimulus in the masked condition suggests that transient activity may not be accessible to conscious appreciation.

2. If masking involves the cancellation of the high spatial frequency components of the test stimulus, then a test stimulus which is blurred and hence has little high spatial frequency content to begin with, should not be appreciably masked. This was found to be true (Weisstein, Ozog & Scoz, 1975).

3. Blurring a subsequently presented MASK should NOT affect test sensitivity since the sustained response to the mask occurs too late to play a role in masking. The data regarding this point are conflicting. Weisstein et al., (1975) found the predicted results whereas Growney (1976) reported that even blurred masks are associated with reduced masking of the test stimulus. As will be presented later, the present results also suggest that the sustained response to the mask alters test sensitivity.

4. Fourthly, since the sustained response to the test is initiated at progressively longer latencies as spatial frequency increases, (Breitmeyer, 1975), the SOA of masking should also increase with spatial frequency. This prediction was supported by Rogowitz (1977).

5. Finally, if masking depends upon transient-sustained interactions, then, retinal placement of the stimuli should be an important variable. For example, it is known that as eccentricity increases, the receptive field sizes of both transient and sustained cells increases (Lennie, 1980). Therefore, the critical stimulus size necessary for masking should increase with eccentricity. This expectation was supported by Meijer, Wildt & Van der Brink (1978). (However, these authors explained their results in terms of inhibitory and excitatory areal summation; e.g., the small discs were likely to stimulate purely excitatory retinal loci whereas the larger discs would fall onto inhibitory areas).

Secondly, if activation of the transient system is a necessary requirement for masking, then peripheral masking should be greater in magnitude than foveal, since the relative concentration of transient cells'increases with retinal eccentricity (Lennie, 1980). Alpern's (1953) data support this interpretation.

An important limitation to the theory that the fast mask transient response overtakes and inhibits the slow sustained response is that it explains backwards masking only. Since forward masking theoretically involves the temporal coincidence of the mask-sustained and test-transient responses, Breitmeyer (1978) has proposed that these inhibitory interactions also occur. Indeed, this would be suggested by

Growney's (1978) finding that blurring of the mask which reduces its sustained component, also reduces the magnitude of masking. Similar conclusions were suggested in a study by Bodis-Wollner, Hendley & Kulikowski (1973) who investigated Weber's law using sinusoidal gratings rather than luminance fields. Specifically, these investigators asked, how great a contrast increment or decrement (delta C) is necessary to detect a difference in the contrast (C) of a given grating. In such a paradigm (called contrast modulation) it is helpful to think of the steady state contrast (C) as a sustained function, whereas change detection (delta C) is a transient operation. If the two systems are independent, then delta C = k at all values of C. If they interact, then delta C/C = K2 (Weber's law).

Independence of these two systems was observed at low steady level contrasts and low spatial frequencies, probably because the sustained contribution is minimal under these conditions (Legge, 1978; Keesey,1966; Kulikowski, 1974). As spatial frequency or mean contrast increased however, delta C/C = K2. Furthermore, since K2 is smaller than K, sustained activity must impair transient performance.

XII. Adaptation.

The possible link between the transient and sustained systems and visual masking provides an important approach for understanding, not only masking, but the transient and sustained systems as well. For example, if the offset peak in the masking function is due to the transient system activity (Tolhurst, 1975) does the failure to demonstrate a significant offset effect dichoptically (Battersby & Wagman, 1962) suggest that transient neural interactions at offset are monocular (possibly, although not necessarily, retinal) in origin?

One means of investigating the interaction between the transient and sustained systems is through the use of the adaptation techinque Briefly, adaptation involves a prolonged exposure (1-3 minutes) to a stimulus of some specified dimensions (Bodis-Wollner & Hendley, 1973; Blakemore & Campbell, 1968) such as spatial frequency, orientation, color, temporal characteristics, etc) followed by the measurement of sensitivity to test patterns which resemble or differ from the adapting stimulus along the same dimensions. If subsequent increases in thresholds'are limited to test stimuli which share a particular characteristic with the adapting stimulus, then a visual mechanism must exist which can be selectively influenced. If, on the other hand, adaptation ENHANCES sensitivity to a given feature, this would suggest a normally antagonsitic link between these two features which is released by adaptation.

The nature of adaptation is not clearly understood. Some investigators believe the procedure fatigues a normally excitatory cellular mechanism so that it cannot respond strongly to subsequently presented stimuli. However, others *have noted that the spatial frequency range of threshold suppression after adaptation (approximately one octave above and below the adapting frequency; Blakemore & Campbell, 1968) is considerably larger than their excitatory domain; that is, the range over which two gratings will summate (Sachs et al., 1971). For example, a 4 c/d adapting grating will elevate thresholds for spatial frequencies between 2-8 c/d although no summation will occur between 2 and 8 c/d. For this reason, Dealy & Tolhurst (1974) proposed that adaptation must involve INHIBITORY mechanisms which are different from excitatory ones. Low contrast gratings of different spatial frequencies do not summate (Sachs et al., 1971) because they fail to activate a common excitatory mechanism, whereas at high contrast, the same gratings will adapt one another (because they activate common inhibitory mechanisms (Dealy & Tolhurst, 1974).*

Since the aim of the present investigation is to study the contributions of the transient and sustained systems through the use of adaptation, a review of the variables associated with adaptatation is appropriate.

A.Kinds of adaptation

1.STEADY ADAPTATION- involves prolonged exposure to a stationary grating which is continuously present.

2. TRANSIENT ADAPTATION - is accomplished by either sweeping a fixation light across a steady grating, forcing the eyes to move (Tolhurst & Hart, 1972) or by temporally modulating the adapting pattern (by drifting it in a single direction; in two opposing directions simultaneously <counterphase> or by turning it on and off).

Adaptation effects are equal regardless of whether it is the stimulus field or the eye which is moving at a given speed (Tolhurst & Hart, 1972).

The advantage of counterphase adaptation is that it eliminates the bothersome afterimage which generally develops after unidirectional adaptation (Tolhurst, 1973).

B. Effects of Adaptation

Subsequent changes in test thresholds depend upon the temporal characteristics of both the TEST and ADAPTING stimuli.

1. Adapting and test stimuli BOTH steady:

a. Range of effect. Test sensitivity is depressed at spatial frequencies within one octave of the adapting spatial frequency, with the maximal effect being at the same test frequency as that of the adapting stimulus (Blakemore & Campbell, 1968, 1969; Blakemore, Muncey & Ridley, 1971, 1973; Graham, 1972).

b. Contrast- The greater the contrast of the adapting stimulus, the greater the elevating effect upon test threshold (Blakemore & Campbell, 1969; Stecher, Siegel & Lange, 1973). However, even low contrast adaptation can raise test thresholds (Stecher, Siegel & Lange, 1973; Bodis-Wollner &

Schenkein, unpublished data)

c. Adaptation time- The longer the time spent in adaptation the greater the depression of subsequent sensitivity to the same test stimulus (Blakemore & Campbell, 1969; Blakemore, Muncey & Ridely, 1971, 1973; Bodinger, 1978) Whereas Blakemore et al (1969, 1971, 1973) found that the adapting effect reached a maximum after a one minute exposure to a grating, Bodinger (1978) reports that an adapting period of about 10 minutes results in a threshold which is 2.5 times higher still than that following one minute of adaptation. Increasing the adapting contrast increases the magnitude of threshold elevation but not the time required for complete adaptation (about 60 sec.; Blakemore and Campbell, 1969).

d. The time course of recovery following adaptation varies with adaptation time (Blakemore, Muncey & Ridely, 1973; Bodinger, 1978) Following one minute of adaptation, the main effect, the raised threshold, tested psychophysically is lost within the first 30 sec (Bodinger, 1978). Three and 10 minuute adapting periods depress sensitivity for about one minute (Blakemore, Muncey & Ridley, 1973). When evoked potentials are used as a measure of recovery, effects can be seen for approximaely 5 minutes (Meccaci & Spinelli, 1976).

e. The orientation of the adapting grating can vary by no more than 12° from the test grating for an effect to occur (Campbell, Kulikowski & Levinson, 1966; Blakemore, Muncey & Ridley, 1973; Gilinsky, 1968).

f. Screen size- At least 7 cycles of an adapting grating are required for the maximal effect (Hoekstra, van der Brink & Bileson, 1974). Low spatial frequency stimuli, however, require a larger screen in order to achieve this effect and when the display size in increased, the lowest adaptable spatial frequency also decreases (Tolhurst, 1973).

g. Spatial frequency specificity- steady adaptation has a greater effect at high than low spatial frequencies. (Bodis-Wollner, Hendley & Kulikowski, 1972; Bodis-Wollner & Hendley, 1979; Kulikowski & Gorea, 1978). In fact, steady adaptation below 1.3 c/d has no effect upon subsequent sensitivity to steady gratings of any spatial frequency. For adapting stimuli between 1.3 and 3 c/d, the greatest test threshold elevation will always be around 2- 3 c/d. (Blakemore & Campbell, 1968; Tolhurst, 1973). Thus, there appears to be a lowest adaptable spatial frequency whose maximal sensitivity lies around 2-3 c/d but ranges from about 1.3 to probably 6 c/d. As long as the adapting stimulus is within the lower half of this range the most profound rise in threshold must occur at the test frequency of 3 c/d since there is no existing channel below it.Because both the adapting and test stimuli are stationary gratings, this lowest adaptable channel probably belongs to the sustained system.

2. When the adapting grating is steady and the test grating is temporally modulated adaptation effects are often found at spatial frequencies below 1.3 c/d, (De Valois, 1977a;

Mauderbocus & Ruddock 1973) going at least as low as .2 c/d (Kranda & Kulikowski 1976). However, threshold changes are smaller when the test stimulus is moving then when it is steady (Tolhurst, 1973).

After steady adaptation or under stabilized retinal conditions (both of which partial out steady state activity; Riggs et al., 1953) the ability to detect contrast modulation (change) becomes independent of mean contrast (steady state activity) and sensitivity improves (Bodis-Wollner, Hendley & Kulikowski, 1973, Bodis-Wollner & Keesey, Unpublished data) This finding supports the interpretation that the sustained system ordinarily inhibits the transients. Comparisons of steady adaptation and retinal stabilization as means of eliminating sustained influences, showed lower ABSOLUTE modulation thresholds under stabilized as opposed to steady conditions, suggesting that steady adaptation diminishes transient as well as sustained contributions.

3. *TRANSIENT* *adaptation*

a. An *unpatterned flickering field* as an adapting stimulus will lower subsequent sensitivity to test fields which are either flickering (Granit & Ammon, 1930; Ginsburg, 1966; Vega, Costiloe & Parsons, 1968) or stationary (Smith, 1970). The greatest reduction in threshold occurs when the test pattern is also flickering rather than stationary (Smith, 1970).

(1) *Drifting adaptation* patterns increase the thresh-

olds of COUNTERPHASE test gratings moving in the same direction as the adapting grating (Levinson & Sekuler, 1975) suggesting that transient encoding is directionally specific. Peak effects occur at the same spatial frequency as the adapting stimulus (Graham, 1972; Kranda & Kulikowski, 1976, Tolhurst, 1973) although the bandwidth of the depressive effect is broader than following steady adapation (Graham, 1972).

(2) Drifting adaptation gratings will also raise STEADY test thresholds, but less effectively than transient thresholds (Tolhurst, 1973). For low spatial freqency adaptation the maximal threshold change is never below 2-3 c/d (Tolhurst, 1973).

Comparing critical durations of various sinusoidal test gratings before and after transient masking, Legge (1978) confirmed the findings of others (Breitmeyer & Ganz, 1977; Nachmias, 1967; Spitzberg & Richards, 1975) that prior to masking, critical durations increase with spatial frequency for exposures as long as 200 msec. Beyond this interval, only high spatial frequency (above 1.5 c/d) sensitivity continues to increase (but at a somewhat slower rate so that the slope of the function relating threshold to stimulus duration has a kink). Adaptation to a brief, high contrast mask of the same spatial frequency increases, by a full log unit, the thresholds of low spatial frequency and briefly presented gratings (both of which are detected by transient mechanisms). This increase in threshold can be compensated *by increasing the test duration to 2-3 sec. However, the new function relating threshold to stimulus duration is monotonic (as opposed to the unadpated functions which kinks at 100 msec), indicating that adapted sensitivity is determined by a single, as opposed to two mechanisms.*

The persistence of low spatial frequency detection after transient adaptation suggests that the sustained system operates at these spatial frequencies although its contribution is usually hidden by the more sensitive transient system. Furthermore, the fact that transient adaptation can alter sensitivity to spatial frequencies as high as 12 c/d, suggests that the transient system operates at relatively high spatial frequencies. In addition, the dramatic increase in integration time constants when transient influences are reduced (Legge, 1978), suggests, either that the transient system ordinarily inhibits energy summation within the sustained system or that the short critical durations occur in the unadapted state simply because the transient system is more sensitive and requires less time to detect the stimulus than the sustained. In any case, these data suggest that both systems operate over a broad range of spatial frequencies with varying influences according to stimulus contrst, movement, duration, etc. Tolhurst (1975) has suggested that below .25 c/d, all patterns are detected by a purely transient system whereas those greater than 10 c/d are detected exclusively by the sustained system regardless of the temporal aspects of the stimuli. The findings of Bodis-

Wollner et al (1973, 1979) and Legge (1978) of a transient influence at 12 c/d raises the upper limit of the transient system slightly.

(3) A moving adaptation grating will raise the threshold of an ON-OFF test grating at two spatial frequencies; that of the adapting grating (a characteristic of the transient system) and also at about 3 c/d (a characteristic of the sustained system) (Tolhurst, 1973) indicating that on-off stimuli are detected by BOTH the transient and sustained systems.

Thus, steady or temporally modulated adaptation will affect BOTH transient and sustained peformance, although the most pronounced changes occur within the system whose preferred characteristics are the same as the adapting stimulus.

C. Conclusions based upon adaptation studies.

1. Psychophysical data show that selective adaptation of either the transient or sustained systems can be achieved (Bodis-Wollner et al. 1979; Legge, 1978) and that these effects are best revealed by TEST stimuli which have the SAME temporal characteristics as the adapting stimulus (Blakemore & Campbell, 1968). Thus, conclusions about the nature of adaptation should not be drawn without considering the temporal characteristics of BOTH the test and mask.

2. Cross-adaptation between systems can also be demon-

strated; that is, STEADY adaptation raises TRANSIENT test thresholds (Bodis-Wollner et al., 1979) and similarly, TRANSIENT adaptation raises STEADY test thresholds (Blakemore & Campbell, 1968). However, the cross-adaptation effect is smaller than the within-system effect. Selective adaptation, therefore, alters the BALANCE between the transient and sustained systems and suggests that there is a normally antagonistic relationship between them. Perceptual evidence also supports this interpretation. For example, spatial frequency doubling, (the perception of twice the true spatial frequency of a counterphasing low spatial frequency grating) can be increased by steady and decreased by transient adaptation (Kulikowski, 1973). Adaptation to a steady high contrast grating gives an afterimage of particles streaming at right angles to the adapting pattern (Georgeson, 1976; also seen in pop art, MacKay, 1961) whereas adaptation to rotary motion leads to the perception of lines perpendicular to the direction of motion (Georgeson, 1976).

3. Finally, electrophysiological evidence of selective adaptation has been demonstrated in the VER. Kulikowski (1974, 1978a, 1978b) showed that a low spatial frequency grating which is counterphasing below pattern threshold contains an early movement related component which can be reduced in amplitude by prior adaptation to a counterphasing but not steady grating. When the contrast is increased so that the pattern is seen, a later wave appears in the VER,

the amplitude of which can be reduced by preadaptation to a steady grating.

Thus, selective adaptation of one system can be used as a means of exaggerating the contribution of the other.

XIII. Ipsilateral vs Contralateral Adaptation

Given that perception is jointly influenced by the transient and sustained systems and that the two interact in the visual system, what is the neural locus of this interaction? An answer to this question might be achieved by adaptation of the contralateral eye.

A. As was already described, an adapting stimulus can be be either stationary or temporally modulated

1. Contralateral STEADY adaptation, STEADY test

As long as the test pattern is within one octave in spatial frequency and 12-15 degrees in orientation (Blakemore & Campbell, 1969; Blake & Fox, 1972; Bacon, 1976) of the adapting grating, adaptation of one eye to a steady grating will elevate thresholds in the contralateral eye. This transfer of adaptation however, is incomplete; the rise in threshold being 1.6 times less than when both adaptation and threshold measurement are confined to the same eye (Blakemore & Campbell, 1969). Despite the greater efficiency of monocular as opposed to dichoptic adaptation, most authors argue against the importance of local retinal factors in the monocular effect since subjects are encouraged to let their eyes wander over the pattern during the adaptation period. In fact, some investigators have slowly counterphased their low spatial frequency patterns (which would otherwise have required large eye movements) to reduce the effects of local fatigue (Stromeyer, Spillman, Klein & Dawson, 1977).

2. Contralateral TEMPORAL adaptation, TRANSIENT test

Interocular transfer of TEMPORAL adaptation was not found by Smith (1971) with flickering lights but was reported by Barlow and Hill (1963) who used moving stimuli. Pressure blinding of the adapted eye does not disrupt the transfer of this movement aftereffect to the unadapted eye. (Barlow & Brindley, 1963). Apparently, movement but not flicker adaptation transfers binocularly.

When the flickering adapting stimulus is a sinusoidal grating, contralateral transient adaptation has been reported at spatial frequencies below 2 c/d (Breitmeyer, Levi & Harwerth, 1977). This finding is in contrast to the ipsilateral transient adapting effect which occurs at least until 8 c/d (Breitmeyer et al., 1977). A possible explanation for this finding will be proposed in the discussion section.

B. Considerations

A problem in studying the binocularity of temporal processing is a confusion regarding the dependent variable. It *has previously been discussed that visual processing has two components, excitation and inhibition (Dealy & Tolhurst, 1974; Levi, Harwerth & Smith, 1979). Binocular EXCITATION can be studied via simultaneous dichoptic presentation of SUBTHRESHOLD stimuli to the two eyes. If a common binocular neuron is activated, then energy delivered independently to the two eyes, will summate and sensitivity should be greater that predicted by the independent detection of the two eyes (probability summation; Thorn & Boynton, 1974). In this situation, many studies have suggested independent processing of low spatial frequency (Blake & Cormak, 1979; Lema & Blake, 1977; Levi, Harwerth & Manny, 1979; Martens, Sloan & Blake, 1980, Rose, 1977) and movement information (Johnson & Enoch, 1976; Kaufman, 1974).*

Binocular INHIBITION, on the other hand, is best studied by adapting one eye and measuring sensitivity changes in the contralateral eye. In this situation, adapted thresholds not only reflect the excitability loss of the adapted units, but also the INCREASE in sensitivity of those neurons which have been temporarily released from inhibition (Dealy & Tolhurst, 1974; De Valois, 1977b). Hence, the Motion After Effect, (MAE), the experience of movement in the direction opposite that of adaptation, suggests the disinhibition of a normally antagonistic link between neurons detecting motion in opposing directions (Levine & Sekuler, 1975, Sekuler & Levinson, 1975). Because the MAE occurs dichoptically, it might be suggested that inhibition is binocular (Levi, Har-

werth & Manny, 1979).

In questioning the sources of inhibition and excitation, there is a growing but as yet, formally unstated impression that transient activity governs monocular excitation whereas sustained activity governs binocular inhibition and excitation. In a later section of this paper, additional evidence will be presented to support this theory and to suggest that the monocularity of the transient system is cortical if not also retinal.

CHAPTER 2

STATEMENT OF THE PROBLEM

The present experiments were designed to explore the interactions between the sustained and transient visual systems. Masking was chosen as the experimental paradigm based upon the evidence that masking results from either transient neural activity (Tolhurst, 1975b) or interactions between the transient and sustained systems (Matin, 1975; Breitmeyer & Ganz, 1976).

Because the influence of the transient system predominates at low spatial freqencies whereas the sustained system predominates at high sptial frequencies (Tolhurst, 1975a, Breitmeyer & Julesz, 1975; Arend, 1976; Tolhurst, Sharpe & Hart, 1973; Kulikowski & Tolhurst, 1973; Keesey, 1966), it is possible to vary the relative contribution of these two systems by controlling the spatial frequency content of test and mask stimuli through the use of sinusoidal gratings.

To help investigate the time-dependent changes in masking, (Battersby & Wagman, 1959; Crawford, 1947) the mask stimulus in the present experiment was relatively long in duration (725 msec) as compared to the traditionally brief (e.g., 10 msec) stimuli. The test stimulus, however, was brief since the SOA associated with masking is constant only for test stimuli less than 100 msec in duration (Kahneman, 1967).

In attempt to uncover parallels between masking and metacontrast, on one hand, and the processing of spatial phase, on the other, the test stimulus was set either in-phase or out-of-phase (180^0) with respect to the mask (Tolhurst, 1975b, Watson & Nachmias, 1977).

Separation of the transient and sustained systems was accomplished by selective adaptation; that is, prolonged exposure to a low contrast grating (Blakemore & Campbell, 1969; Keck, Paella & Pantle, 1976; Legge, 1978; Stecher, Siegel & Lange, 1973; Smith, 1970) which was either steadily presented or temporally modulated (Kulikowski, 1974; Tolhurst, 1973). However, it was expected that despite the specificity of the adapting stimuli, some cross-adaptation of the opposite system would occur, such that changes in sustained sensitivity would accompany transient adaptation and vice-versa (Blakemore & Campbell, 1969, Bodis-Wollner, Hendley & Kulikowski, 1972; Levinson & Sekuler, 1975; Tolhurst, 1973). Therefore, adaptation should alter the BALANCE between the two systems. If the inhibitory influence of the transient mask response is responsible for the elevation of test thresholds, then transient adaptation should reduce this effect. Adaptation of the sustained system however, should reduce the excitatory response to the test and make the masking effect even greater.

The ineffectiveness of a given type of adaptation upon the magnitude of masking would imply that either (1) the contrast of the adapting stimulus was too low to adapt the intended system or (2) the adapting stimulus affected both the transient and sustained systems equally so that no change in the balance between the systems was introduced. These two hypotheses can be tested by varying the contrasts of the adapting gratings since the two systems could not be affected equally by all contrasts of the same adapting stimuli (Kulikowski & Tolhurst, 1973). Other possible causes for a lack of adaptation effect on the masking functions are that (3) the adapted system has no role in masking or (4) masking occurs more peripherally in the visual system than the site affected by adaptation, so that it cannot be influenced. Decisions between these latter possibilities may reached by comparing test thresholds following adaptation of the ipsilateral and contralateral eyes. If only ipsilateral, but not contralateral adaptation alters thresholds, then the site of adaptation must be after that of masking. Additionally, different findings after ipsilateral and contralateral adaptation would suggest that the adapted system is not binocular since adaptation of binocular neurons which are directly involved in masking should yeild the same results as monocular adaptation.

Adaptation may also change the temporal delay of masking. For example, if adaptation delays the neural response of the adapted system with respect to the nonadapted system, then the SOA at which the two interact will change. Thus, transient or sustained adaptation could change either the magnitude or the time course of maximal masking or both.

In sum, the purpose of the present study was to investigate the roles of the transient and sustained systems in visual masking by selectively adapting either the same or the contralateral eye to stationary or temporally modulated gratings.

CHAPTER 3

EXPERIMENTS I AND II : GENERAL FEATURES

As already mentioned, this experiment was performed in two parts, the baseline condition (Experiment I) followed by adaptation (Experiment II). Apparatus and methods common to both conditions will be described first whereas those unique to each will be described under the appropriate subheading.

I. Methods

A. Subjects Two subjects, J.G. age 25 and J.C. age 30, both of whom were practiced in the present task, were studied. J.G's uncorrected and J.C.'s corrected acuities were 20/20.

B. Apparatus

All stimuli were sinusoidal patterns of variable contrast and spatial frequency. They were formed by multiplying the spatial signal, a high speed sine wave produced by a Wavetek 136 VCG/VCA generator by a slow, sweep-synchronized and modulated voltage of a 13 17A X-Y multiplier. The outputs of these multipliers were then connected to the z axes of either of two 11x11" Joyce display scopes.

The test stimulus was 8.32 msec in duration, which was the time required for a single raster sweep. The long duration mask represented several raster sweeps. Test and mask onsets were triggered independently and thus, their asynchronies could be varied in 8.32 msec increments. When these stimuli were presented simultaneously, the two signals added linearly. To create an out-of-phase grating, the amplitude of the test signal was phase inverted. Thus, the linear summation of the mask and the out-of-phase test stimulus was of lower contrast than the mask alone. The onsets of the test and mask patterns were square waved in time.

In Experiment I, a long duration mask and a brief test were always presented upon the same screen while the other was blank and maintained at the same mean luminance. A photo-diode and amplifier circuit, which measures local luminance distributions, was used to determine minimal and maximal levels on each screen so that the two could be equated. The average luminance level was 2.4 candelas/sq. meter, which is in the mesopic range.

In front of each display screen was a circular frame of 25.4 cm diameter, divided into four quadrants by hairline cross hatching. The two display scopes were placed on opposite sides of a partition and each reflected onto a 5 x 7" front surface mirror so that when the observer was positioned in the headrest, he could use the cross hatching as an aid for fusing the images (Fig. 2). From a distance of 120 cm, the stimulus field within the circular frame subtended a visual angle of 12°.

C. Stimuli The test and mask stimuli were vertically

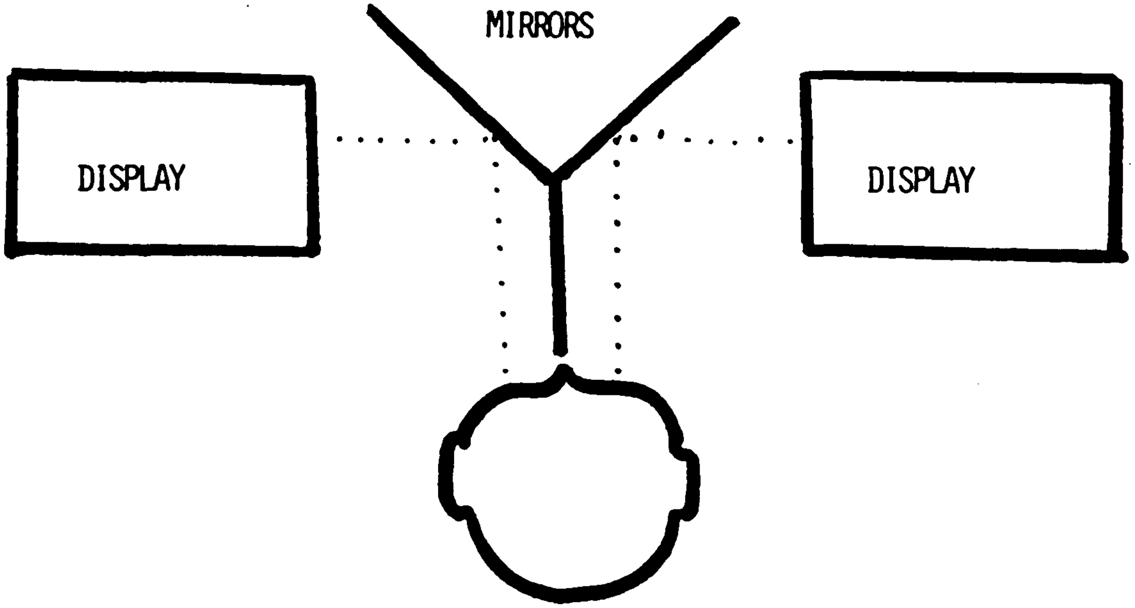


Fig 2. Illustration of the testing situation. The observer's head was positioned by a chinrest while he viewed the stimuli reflected from two front surface mirrors. A partition extending from his nose to the juncture of the two mirrors separated his two eyes.

oriented sinusoidal gratings of either .5 or 4 c/d, which are the spatial frequencies of peak sensitivity for the transient and sustained systems, respectively (Kulikowski & Tolhurst, 1973). It should be noted that although these spatial frequencies were chosen because they optimally EXCITE either the transient or sustained systems, BOTH spatial frequencies are within the detection range of both systems (Legge, 1978). The detectability of the stimuli by both systems is a necessary requirement for the study of the interaction between them. Some data were collected at 6 c/d. However, at this spatial frequency, performance by the observers was hampered by marked indecision, headaches, and impatience; a well known laxative effect which occurs above .5 c/d.

Within a given condition, the test and mask were the same spatial frequency. The masking stimulus was 725 msec in duration and was always set at 2.64% contrast where contrast is defined as (L <max> - L <min>)/ (L <max> + L <min>) where L is the luminance level of the screen. The 8.32 msec test stimulus was presented in either the SAME SPATIAL PHASE as the mask (in-phase) or SPATIALLY DISPLACED by 180° (out-of-phase). Simultaneous in-phase test-mask presentation resulted in a brief contrast increment (Fig. 3 above) whereas, depending upon its contrast, the out-of-phase test caused either a contrast decrement or a momentary counterphase (Fig. 3 below).

Data collection for experiments I and II required approx-

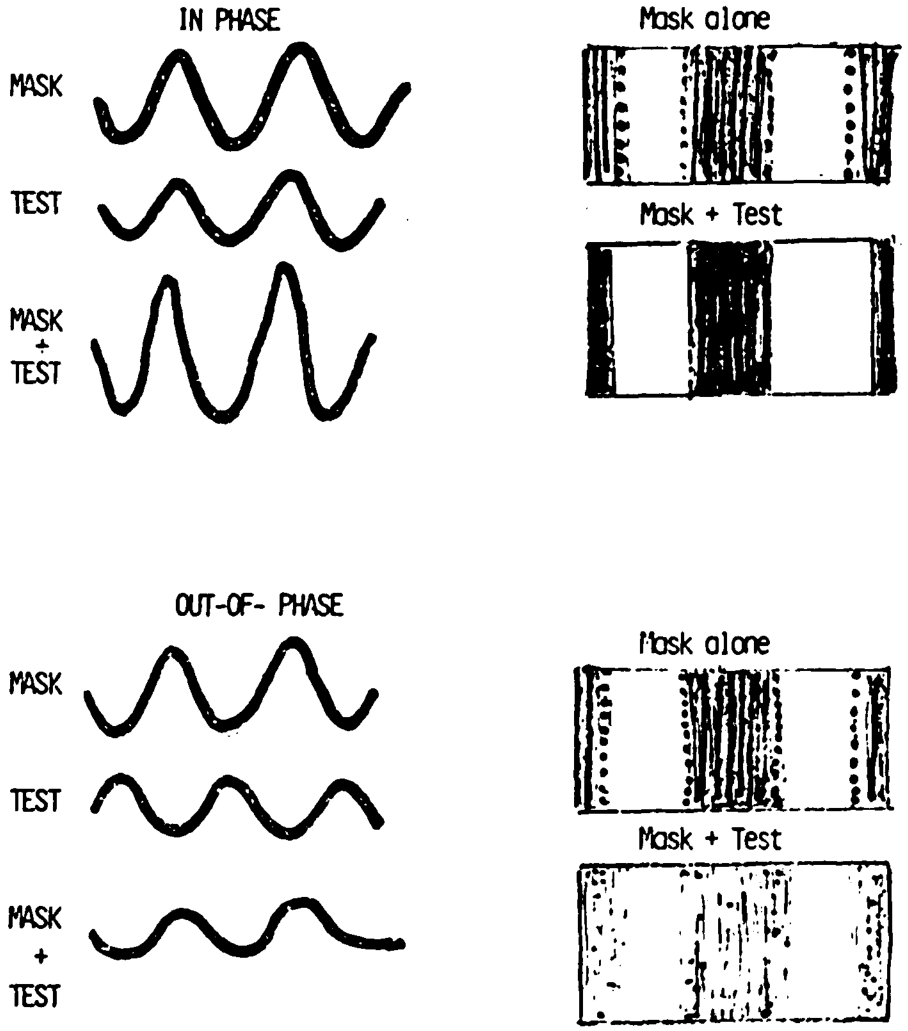


Fig 3. Spatial arrangement of the stimuli.

The test stimulus was either in-phase (above) or 180° out-of-phase (below) with the mask. Notice that the simultaneous presentation of the in-phase test with the mask results in a pattern of greater contrast than either the test or mask alone. The combined sum of an out-of-phase test and mask is of lower contrast than the mask alone.

imately 50 sessions of each subject and was conducted over the course of eight months. J.G was tested during the first five months and J.C., the remaining three.

II. Procedure: Experiment I

Because the mean luminance level used in this experiment was in the mesopic range, it was not considered necessary to fully dark adapt the subject. However, during the ten to fifteen minutes required to prepare the apparatus and data sheets, the subject sat in the room lit only by the phosphor of the display scopes. The trial format is shown in Fig. 4. The mask grating was presented on every trial and had a characteristic smoothness in the time course of its appearance. When the brief suprathreshold test grating was presented concurrently with the mask, this smoothness was disrupted and the pattern appeared to jerk momentarily. The observer was instructed to respond affirmatively when he detected this jerk. At the start of each session, several training trials were conducted in which the mask was presented alone (clear no) or simultaneously with a suprathreshold test (clear yes). When the observer felt he could confidently distinguish between the two, testing began. Clear yes and no trials were frequently included during the testing session, either at the observer's request, or to monitor his accuracy. Absent test pulses were almost never reported as seen. However, on the few occasions when this situation occurred, the observer was given several practice trials with feedback to help reestablish his criteria. Thresholds

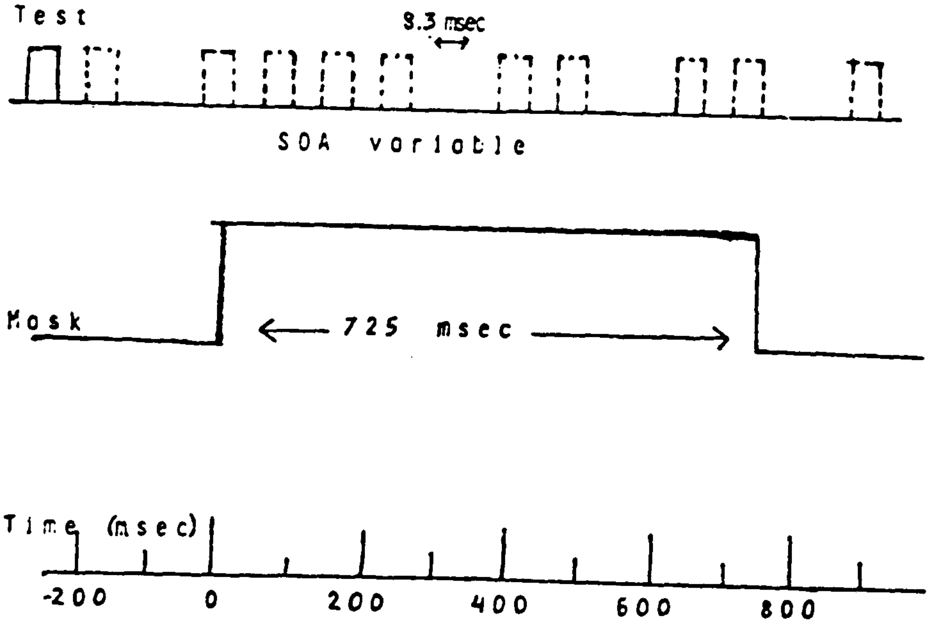


Fig 4. Temporal arrangement of the stimuli: Experiment I. The test and the mask were sinusoidal grating pairs of either .5, 4 or 6 c/d. The test stimulus was presented at varying asynchronies (SOAs) from approximately 100 msec before mask onset to approximately 200 msec after its offset. For the SOAs less than or equal to 80 msec from mask onset and offset, test thresholds were sampled at 8.3 msec intervals. For SOAs greater than 80 msec. from the temporal edges, sampling intervals were longer, ranging from 17-80 msec.

at these SOAs were then remeasured.

The observer was not asked to identify the spatial phase of the test stimulus (which, incidently, was impossible to do) but simply to detect any change in the appearance of the mask over time. Failure to detect any change in mask appearance indicated that the test stimulus was not seen.

There were three INDEPENDENT VARIABLES in Experiment 1; (1) The SPATIAL FREQUENCY of the test and mask pairs (.5 or 4 c/d). (2) The SPATIAL PHASE relationship between the test and mask (3) The TEMPORAL ASYNCHRONY (SOA) between test and mask presentation (ranging from about 150 msec before to 900 msec after mask onset).

The DEPENDENT VARIABLE was the percent contrast of the test stimulus at threshold.

In Experiment I, the trial length was 4.3 sec. About 1.5 sec before the onset of the mask, a 1 sec warning tone alerted the subject to the imminence of test presentation. After each mask and test presentation was a two second response period. Although the test stimulus could be presented at any SOA over a broad time span, the most frequent threshold sampling was conducted at the onset and offset of the mask (Battersby & Wagman, 1959; Tolhurst, 1975b). In a one hour session, in- and out-of-phase thresholds at approximately 25 SOAs were sampled. Since a complete function required many more trials than could be conducted in one session, a given session was restricted to a portion of either the onset or offset related SOAs.

Within a session, the different SOAs were tested in a quasirandom order with the constraint that, at a given SOA, in- and out-of-phase thresholds were always determined successively before the next SOA was selected. Contrast threshold ranges were grossly bracketed using the method of limits and then more finely explored over a contrast range some 2% above and below threshold (a span of about .5 log). This range was subdivided into .8% contrast steps and, using the method of constant stimului, detection was assessed 4-6 times for each contrast level. After approximately 16-30 trials, the contrast of 50% detection was determined from a psychometric template and defined as threshold. Most thresholds were determined during at least two sessions. However, thresholds at many of the peak and trough SOAs were measured at as many as nine different sessions.

Resting threshold, defined as the test threshold when no mask was presented, was determined at the start of every testing session.

In all parts of the experiment, the test and mask stimuli were presented to the left eye while the right eye viewed a blank screen of the same mean luminance.

Testing sessions were generally 60 minutes in duration, after which the subject was given at least an hour to rest before a second session began. One to three sessions were conducted on each testing day.

III. Reliability

At each spatial frequency and for each phase condition, sensitivity at approximately 60 SOAs were sampled. These measurements could not all be conducted in a single session and not every SOA could be repeatedly tested.

Assessment of reliability was handled in two ways:

1. Several SOAs were sampled at more than one session and standard errors of measurement were calculated.(An example of these are shown in Appendix i). Measures of the standard error (defined as the standard deviation divided by the square root of N) were very small and never exceeded .1 log.

2. Data Gestalt. after the thresholds at a number of SOAs were determined, a template was fitted to the data by eye. It was presumed that if subject performance was consistent, all subsequently measured thresholds should either fall along or deviate only a small amount from this approximation. Most data points conformed to this template.

IV. Results

Figures 5-8 show threshold functions at .5 (lower trace) and 4 c/d (upper trace) for each subject organized by spatial phase. Fig. 9 abstracts the essential features of these functions and includes the 6 c/d pilot data for comparison. From these data, it is immediatly obvious that the

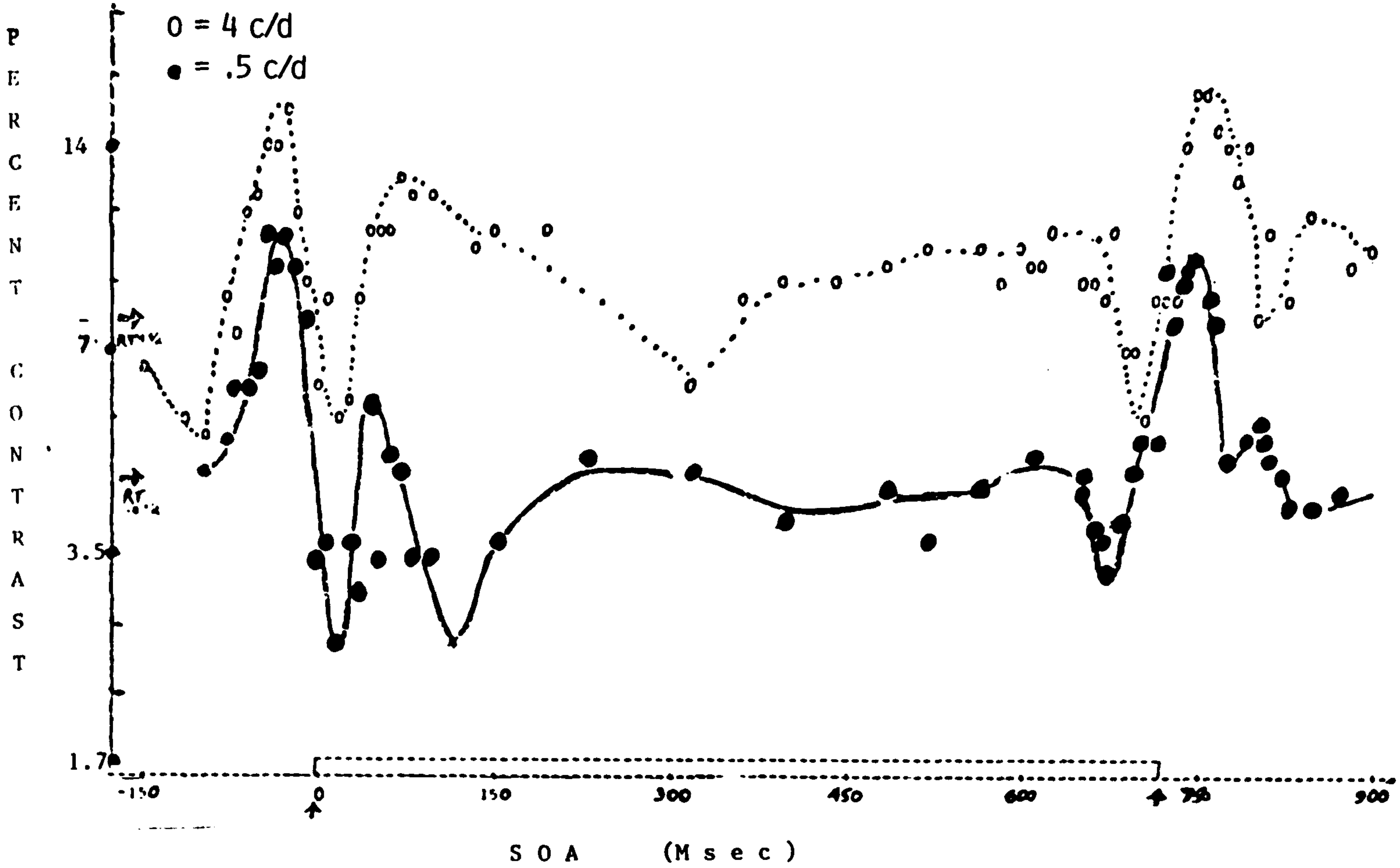


Fig 5. threshold as a function of stimulus onset asynchrony. J.G. .5 and 4 c/d comparison. In-phase condition.

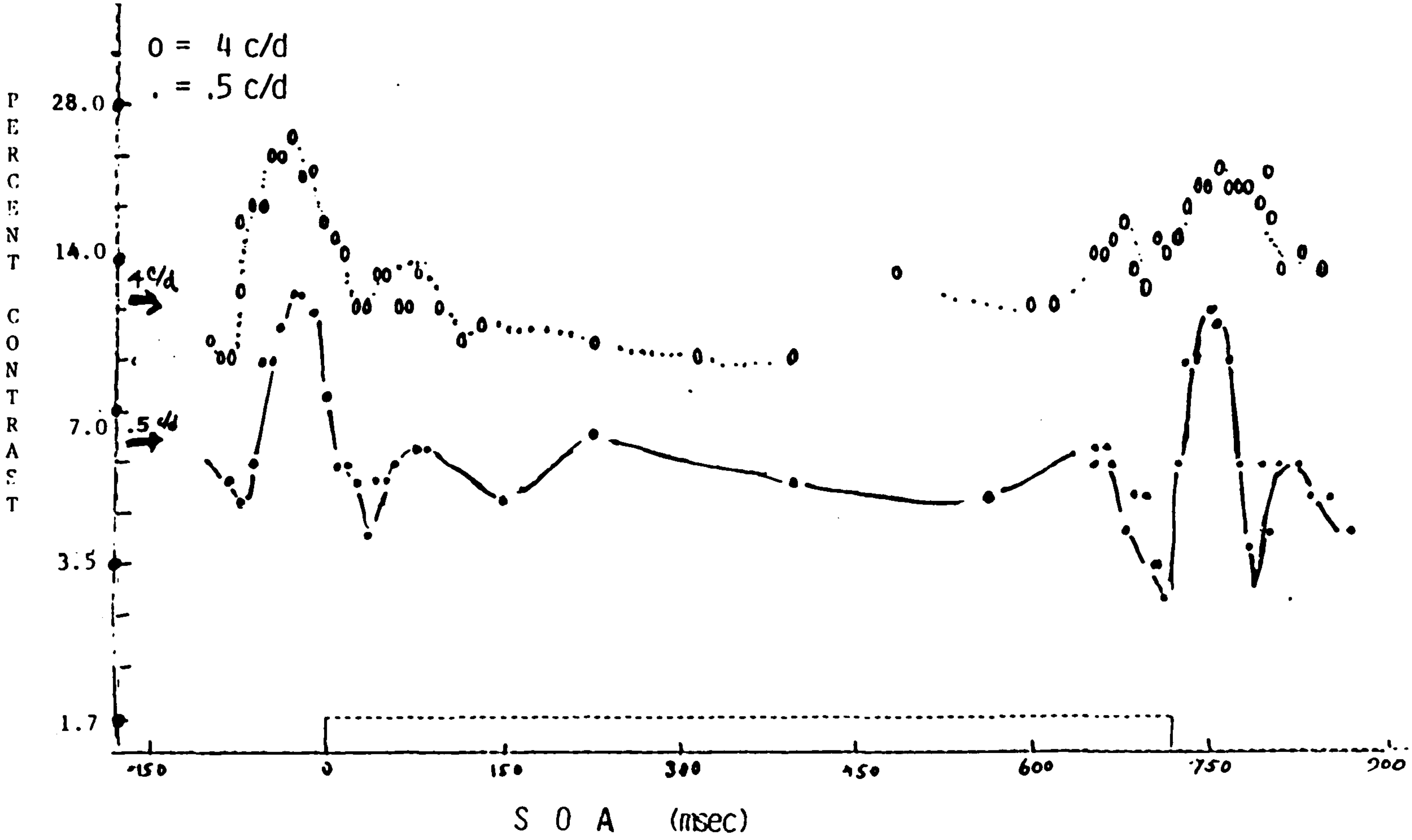


Fig 6. threshold as a function of stimulus onset asynchrony
J.C. .5 and 4 c/d comparison: In-Phase condition

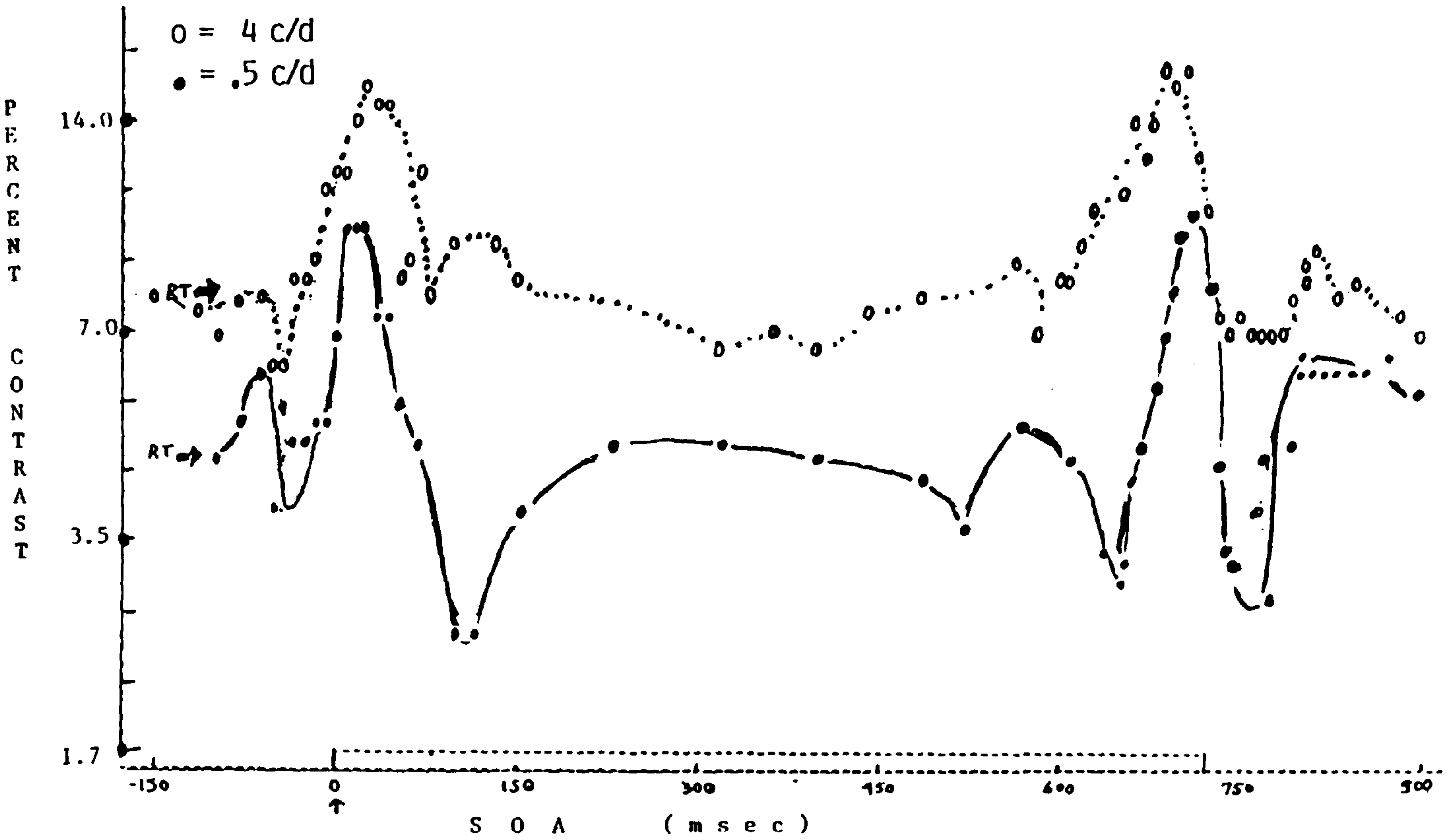


Fig 7. threshold as a function of SOA. Data for J.G. .5 and 4 c/d comparison. Same conditions as Fig 5 except that the spatial phase of the test stimulus was shifted 180° with respect to the mask.

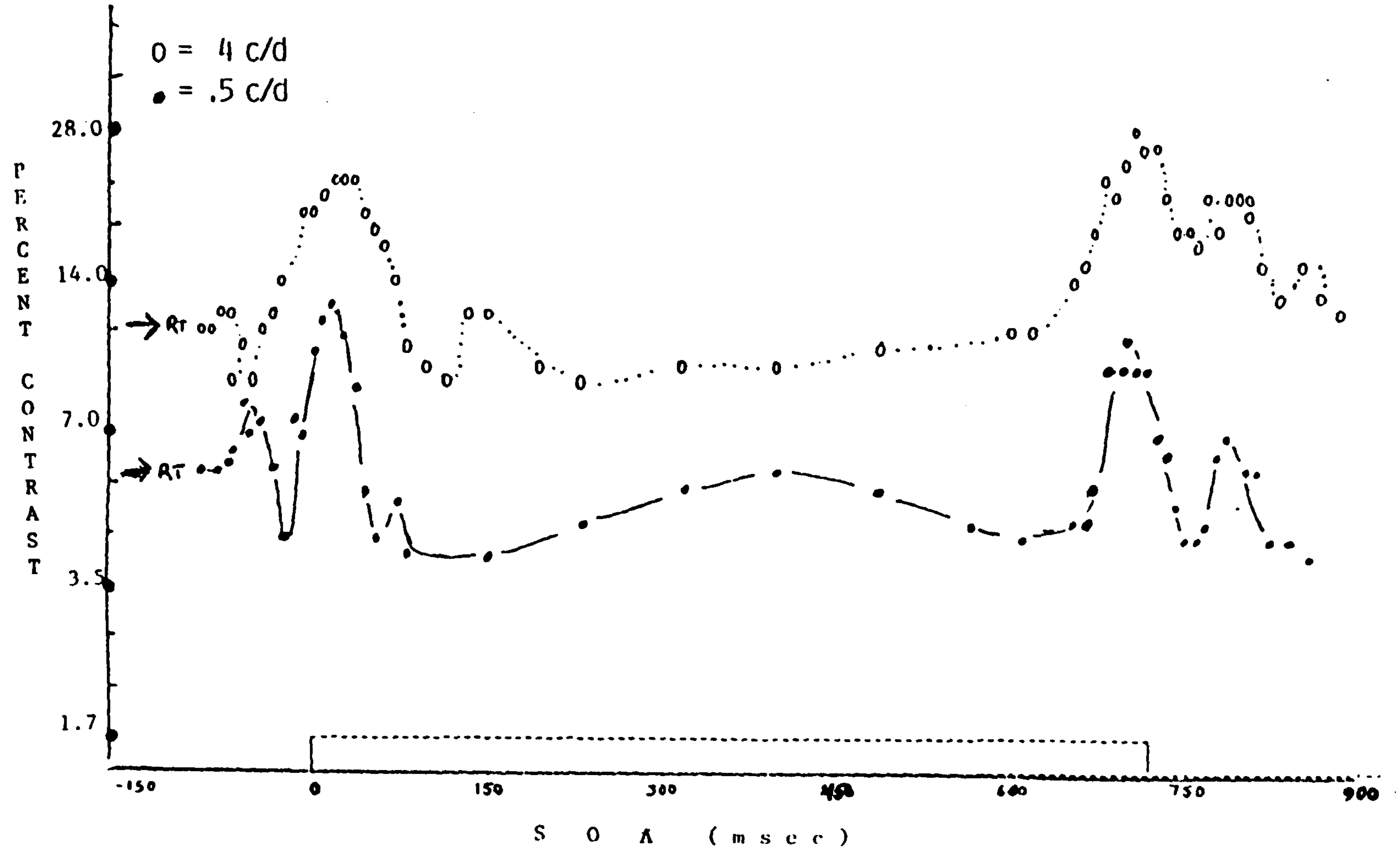


Fig 8. threshold as a function of SOA. Data for J.C. .5 and 4 c/d comparison. Same conditions as Fig 5 except that the test stimulus was shifted 180° with respect to the mask.

.5 c/d resting threshold (as well as the level of the masking function) are lower than those at 4 c/d by a magnitude of at least .25 log although, as will be discussed below, the difference between the two masked functions is not uniform at all SOAs. The finding of greater sensitivity at .5 c/d is theoretically significant. Recalling that maximal human sustained sensitivity occurs between 3-6 c/d (Nachmias, 1967; Robson, 1966; Schoeber & Hilz, 1965), whereas maximal transient sensitivity occurs between 0-5 c/d (Kulikowski & Tolhurst, 1973) it might be inferred that the superior performance at the lower spatial frequency indicates TRANSIENT mediated detection of the test stimulus, a likely consequence of both the brevity of and the abruptness in the test onset and offset. (Breitmeyer, 1975; Breitmeyer & Ganz, 1977; Breitmeyer & Julesz, 1977).

Threshold functions are characterized by several peaks (increases) and troughs (decreases) which occur with mirror-like symmetry around the temporal edges. At other SOAs, thresholds return to resting level, that is, it's threshold when no mask is presented.

A. The return to *resting threshold*, (which indicates that the mechanism detecting the test does not interact with that detecting the mask) occurs predominantly during the intermediate SOAs. At .5 c/d, the plateau formed by these resting thresholds is approximately 500 msec in duration. At 4 c/d, this duration is 400 msec for J.C. However, for J.G., the *intermediate portion of the function scoop-shaped indicating a small degree of test inhibition until about 300 msec after mask onset, the midpoint of the presentation period. Curiously, the resting threshold was obtained at the the SOAs when the test presentation was simultaneous with mask onset or offset (SOA =0, 725). This is interesting because precisely these SOAs are associated with the largest inhibitory effects in light masking (Kahneman, 1968).*

B. Types of peaks (Figs 5-9)

1. Primary

a. Timing The primary peaks occurred approximately 25 msec from the temporal edges and in no function, were more than 8 msec earlier or later than this estimate. This 25 msec delay was also noted in 6 c/d pilot data (Fig. 9), in which only the onset asynchronies were sampled.

b. Phase relationship. Although primary peak SOAs did not vary with spatial frequency, they were markedly affected by spatial phase. In-phase peaks preceded and followed the onset of the mask, whereas out-of-phase peaks occurred during mask presentation.

c. Magnitude- at .5 c/d these peaks were .25-.35 log above resting threshold. At 4 c/d, the increase over its resting threshold was similar, approximately .3 log for each subject. Interestingly, pilot data at 6 c/d show considerably smaller primary peaks, being only .15 - .2 log above threshold. Thus, there is a tendency for these peaks to

Fig. 9. Comparison of test thresholds at .5, 4 and 6 c/d. All functions are arbitrarily displaced on the Y-axis. Due to the mirror-symmetry in the timings of the peaks and troughs at mask onset and offset, only the onset data are shown here. Data points of the 6 c/d function are based upon the average of two determinations of threshold, whereas .5 and 4 c/d represent threshold averages based upon at least two and often, as many as nine independent determinations of threshold. Arrows indicate resting threshold. The number above each peak indicates the SOA (in milliseconds) at which that peak is greatest in magnitude. Notice that primary peaks remain at the same SOA for all three spatial frequencies. Secondary peaks, however, become more delayed as spatial frequency increases. Also, notice the changes in both the absolute and relative magnitudes of the primary and secondary peaks and troughs as spatial frequency increases.

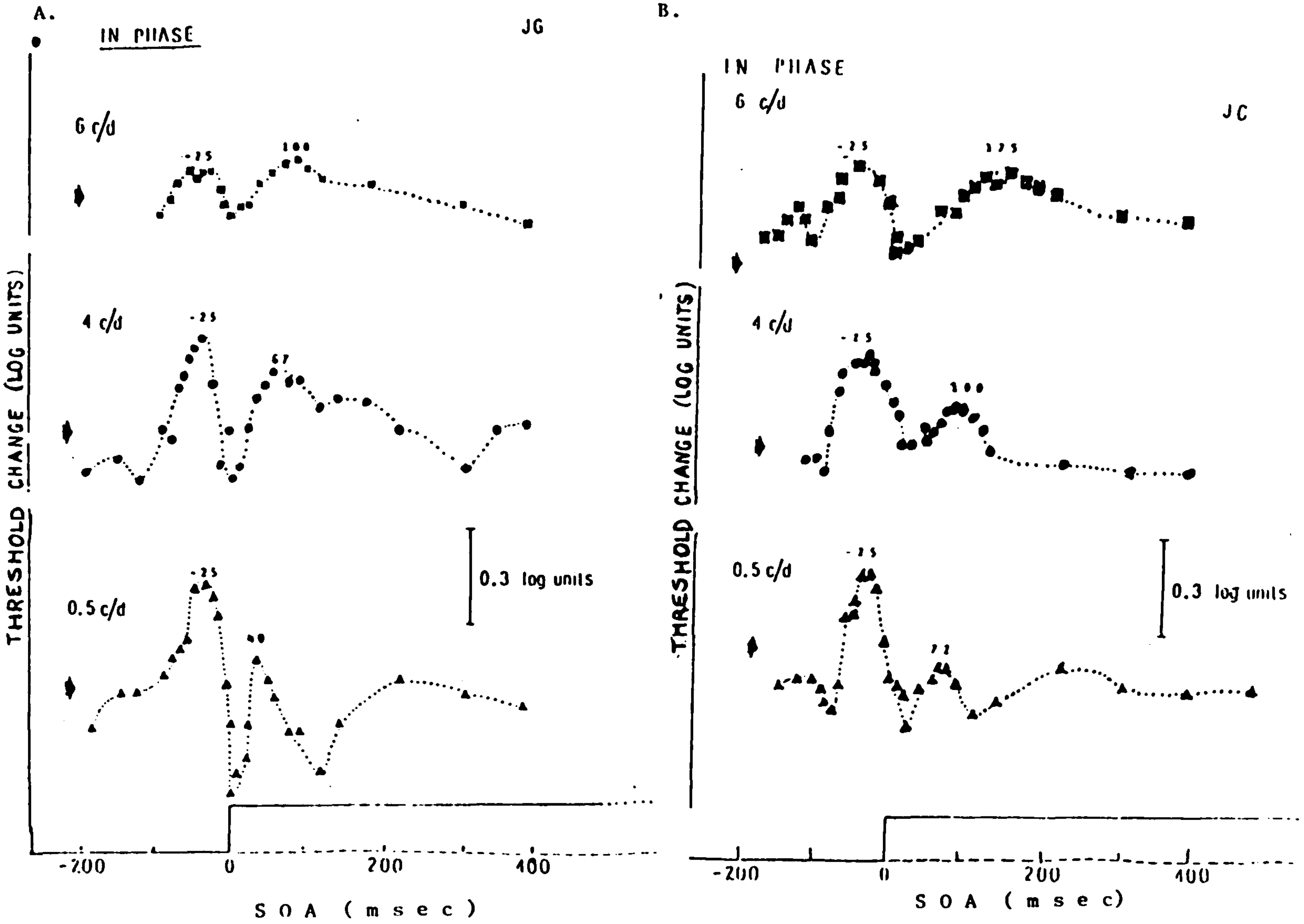

A.
IN PHASE
JG
6 c/d
-25
100
4 c/d
-25
67
0.5 c/d
-25
40
0.3 log units
THRESHOLD CHANGE (LOG UNITS)
-200
0
200
400
SOA (msec)
B.
IN PHASE
6 c/d
JC
-25
125
4 c/d
-25
100
0.5 c/d
-25
72
0.3 log units
THRESHOLD CHANGE (LOG UNITS)
-200
0
200
400
SOA (msec)

Fig. 9

diminish with increasing spatial frequency, although the trend is less obvious at these two relatively low spatial frequencies.

For both subjects at .5 c/d and J.G. at 4 c/d, the magnitudes of the in- and out-of-phase peaks were equal regardless of whether they were associated with mask onset or offset (Fig. 5,7). For J.C. however, (at 4 c/d) only the onset peaks were equal, both being .31 log unit above threshold (Fig. 6,8). At mask offset, J.C.'s primary out-of-phase peaks were .36 log ABOVE resting threshold, whereas the in-phase peaks exceeded resting threshold by only .27 log. Thus, the AVERAGE of J.C.'s in- and out-of-phase offset peaks (.31 log) was the same as that at onset, although there was relatively more masking of the out-of-phase stimulus at offset. Although this difference is small, it is not inconsistent with an assumption which·will be introduced in a later section.

An interesting phenomenon noted for J.G. at 4 c/d was the tendency for primary peaks to decrease over the course of the experiment, so that, for example, over a 5 week period,the in-phase threshold to a test stimulus presented 40 msec after mask offset, decreased from 2.1% contrast (N = 6, S.D. = .04) to 1.5% (N = 6, S.D. = .006). Corresponding changes in the resting threshold did not occur during this time and at the SOA of 400 msec, thresholds were .07% contrast (N = 11, S.D. = .01) and .07% (N = 5, S.D. = .01) during the first and second time periods respectively.

Despite these reductions in the primary peaks over time, the general shapes of the functions remained the same.

d. Duration of maximal inhibition was at least 8 msec, that is; the highest threshold estimates were obtained during either of two testing epochs, generally 16-24 msec from the temporal edges.

2. Secondary peaks

a. Timing. These peaks occurrred at longer SOAs from the temporal edges than primary peaks (approximatly 40-100 msec from onset and offset). For one subject, J.C., secondary peaks were temporally symmetrical about mask onset and offset. For J.G., the secondary onset peaks occurred in closer association to the temporal edge than those at offset. In almost all cases, secondary peaks at 4 c/d occurred at the same or a greater delay from the temporal edge than at .5 c/d (by 8 - 42 msec). In the 6 c/d pilot data, available only for the onset edge, secondary peaks were even further delayed from the temporal edge than at the lower spatial frequencies (Fig. 9).

Specifically, for J.G., the range of onset asynchronies of the secondary in-phase peaks was 40 msec at .5 c/d, 67 msec at 4 c/d and 108 msec at 6 c/d. For J.G., the respective SOAs were 72, 90 and 158 msec. Thus, spatial frequency is an important factor in determining the timings of these peaks.

b. Phase relationship- Secondary peaks always appeared on the opposite side of the temporal edge as the primary peaks; that is, if the primary peak preceded mask onset, the secondary peak followed it. In phase secondary peak occurred DURING whereas, out-of-phase secondary peaks occurred before or after mask presentation.

c. Magnitude- at .5 c/d, secondary peaks were approximately .1-.15 log above RT. At 4 c/d, these peaks were .2 log above resting threshold. Thus, secondary peaks were larger at 4 than .5 c/d. By 6 c/d secondary peaks were larger still, (approximately .2 -.25 log above resting threshold). As spatial frequency increased, not only did secondary peaks increase, but the heights of the primary and secondary peaks became more similar. In fact, at 6 c/d the two peaks were approximately equal, suggesting that the mechanism which determines secondary peaks is more effective at high spatial frequencies, whereas, the reverse is true of primary peaks.

C. Troughs. Brief decreases in threshold occurred on both sides of the primary peaks.

1. Primary troughs-

a. Timing. These troughs appeared between 17-50 msec from the temporal edges at approximately the same SOAs as the primary peaks. At a given temporal edge, the timings of the .5 and 4 c/d primary troughs were often equal. When differences occurred, the .5 c/d troughs were nearly always closer to the temporal edge than those at 4 c/d; the one exception being J.G.'s in-phase onset troughs, which were earlier at 4 c/d. In general, differences between the .5 and 4 c/d trough timings occurred at the onset of the in-phase and the offset of the out-of phase conditions.

b. *Phase relationship*. Primary troughs always appeared on the opposite side of the temporal edge as the primary peaks so that if the primary peak preceded onset, the primary trough followed it.

c. *Magnitude*- At .5 c/d, primary troughs were .15- .3 log below resting threshold, a change in sensitivity often equal in magnitude but opposite in direction to that observed at the primary peaks. At 4 c/d, primary troughs were shallower, being only .1- .2 log below resting threshold. The 6 c/d pilot data contain no troughs at all, suggesting that facilitory influences decrease with spatial frequency.

d. *The duration of facilitation* was less than 8 msec; that is, the lowest thresholds were never obtained in two temporally adjacent epochs. Thus, facilitation has a briefer time course than inhibition.

2. *Secondary troughs*

a. *Timing*. These troughs were 50-100 msec-from the temporal edge.

b. Magnitude was frequently comparable to the primary troughs, being .1- .3 log below resting threshold. There is no systematic trend to account for situations in which the the primary and secondary troughs differed in magnitude. It is indeed possible that, because facilitation was such a brief event, the 8 msec test stimulus was too long in duration for precise threshold measurement and that the brief moments of maximal sensitivity were haphazardly missed.

D. Onset vs offset differences: An important departure from the mirror-like symmetry in the magnitude and approximate timings of the peaks and troughs is that test-mask interactions at offset occurred for a longer time period (by 25-40 msec) than those at onset (Table 1).

A second difference is the previously mentioned assymetry in the offset peaks (J.C. 4 c/d) which were .09 log greater in the in- as opposed to out-of-phase condition. Onset peak magnitude was independent of spatial phase.

E. Phase-related differences. Figure 10A demonstrates the different timings of the peaks and troughs for test stimuli which are in- and out-of spatial phase with the mask. Superimpositions of these data are shown in Figs 10B-C for the two subjects at .5 c/d. The 4 c/d superimposions show the same trends and therefore, only the data for J.C. (Fig. 10D) is presented since it will be referred to later. The important features of these figures (Fig. 10 A-D) are as follows;

TABLE 1. SUMMARY OF SOAS (IN MSEC) ASSOCIATED WITH THE MAJOR MASKING EVENTS AT .5 AND 4 C/D.

Event	.5 c/d	4 c/d
In Phase:		
Primary Peak	-(21-25)	-(17-32)
Primary Trough	17-50	32-66
Primary Peak to Primary Trough	50	48
Secondary Peak	40-90	40-100
Out-of-Phase:		
Primary Peak	20	17-32
Primary Trough	-(25-50)	-(32-66)
Primary Peak to Primary Trough	39	55
Secondary Peak	(60-70)	(67-100)
Time delay from in- to out-of-phase peak	42	51
Primary Troughs: In- to Out-of-Phase	47	79
Duration of Phase specific response*:		
Onset	90	175
Offset	130	200

Note : Negative signs indicate that the interaction occurred either before or after mask presentation whereas unsigned numbers designate events which occurred after mask onset or before its offset. The data combine the results for both subjects.

*This expression refers to the total time period at either onset or offset when test thresholds depart from the resting level.

1. During the intermediate SOAs, thresholds for the in- and out-of-phase stimuli were identical. This was true not only for average threshold, but also true for the variability of the average threshold.

2. the heights of the peaks and troughs were independent of spatial phase

3. the TIMINGS of these events were not independent of spatial phase. Rather, the SOA associated with threshold increments in the detection of one spatial phase roughly

Fig 10A. Comparison of in- and out-of-phase thresholds graphed separately. The data on the opposite page are for J.G. at .5 c/d. The same relative timings of peaks and troughs occurred in the data for the second subject at .5 c/d as well as for both subjects at 4 c/d. Notice that, despite shifts in the timings of these peaks and troughs, their amplitudes are the same regardless of spatial phase.

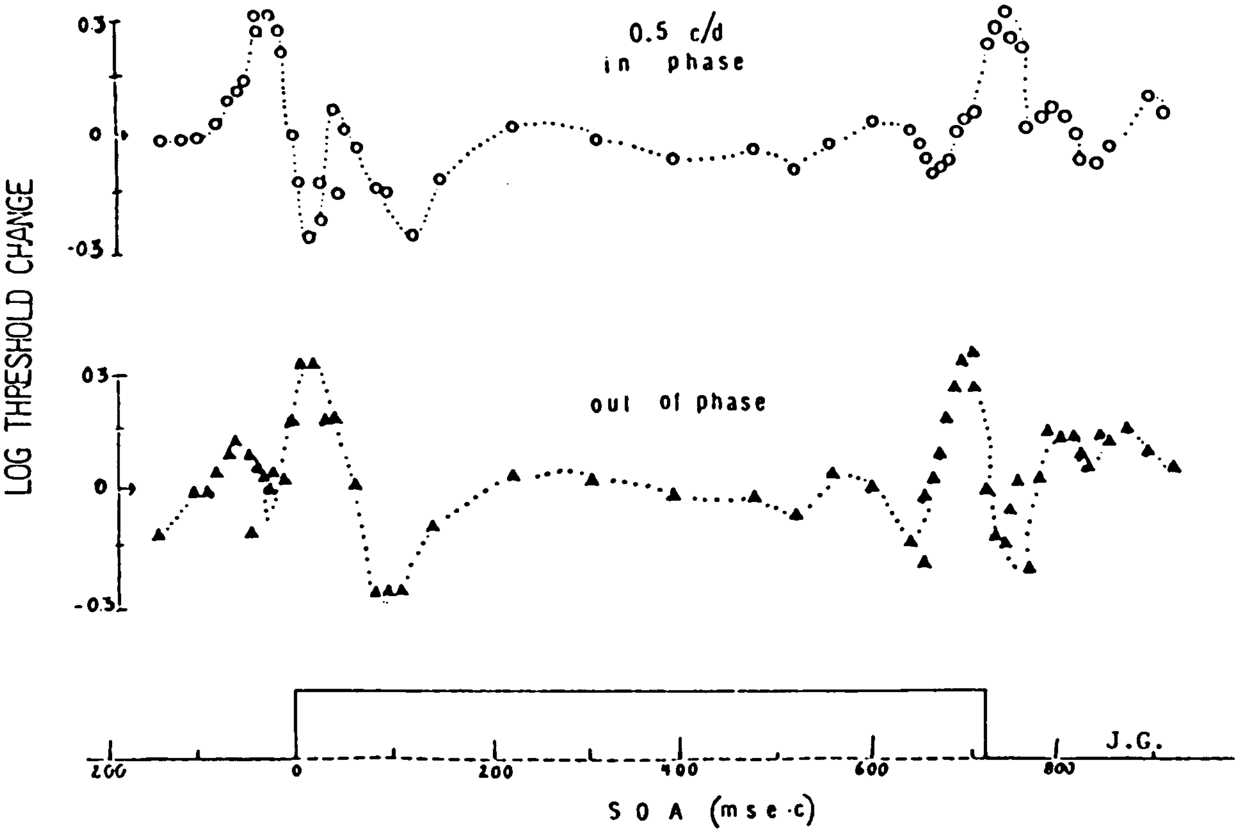

0.3
0
-0.3
0.5 c/d
in phase
LOG THRESHOLD CHANGE
0.3
out of phase
0
-0.3
J.G.
200
0
200
400
600
800
S O A (msec)

Fig 10A

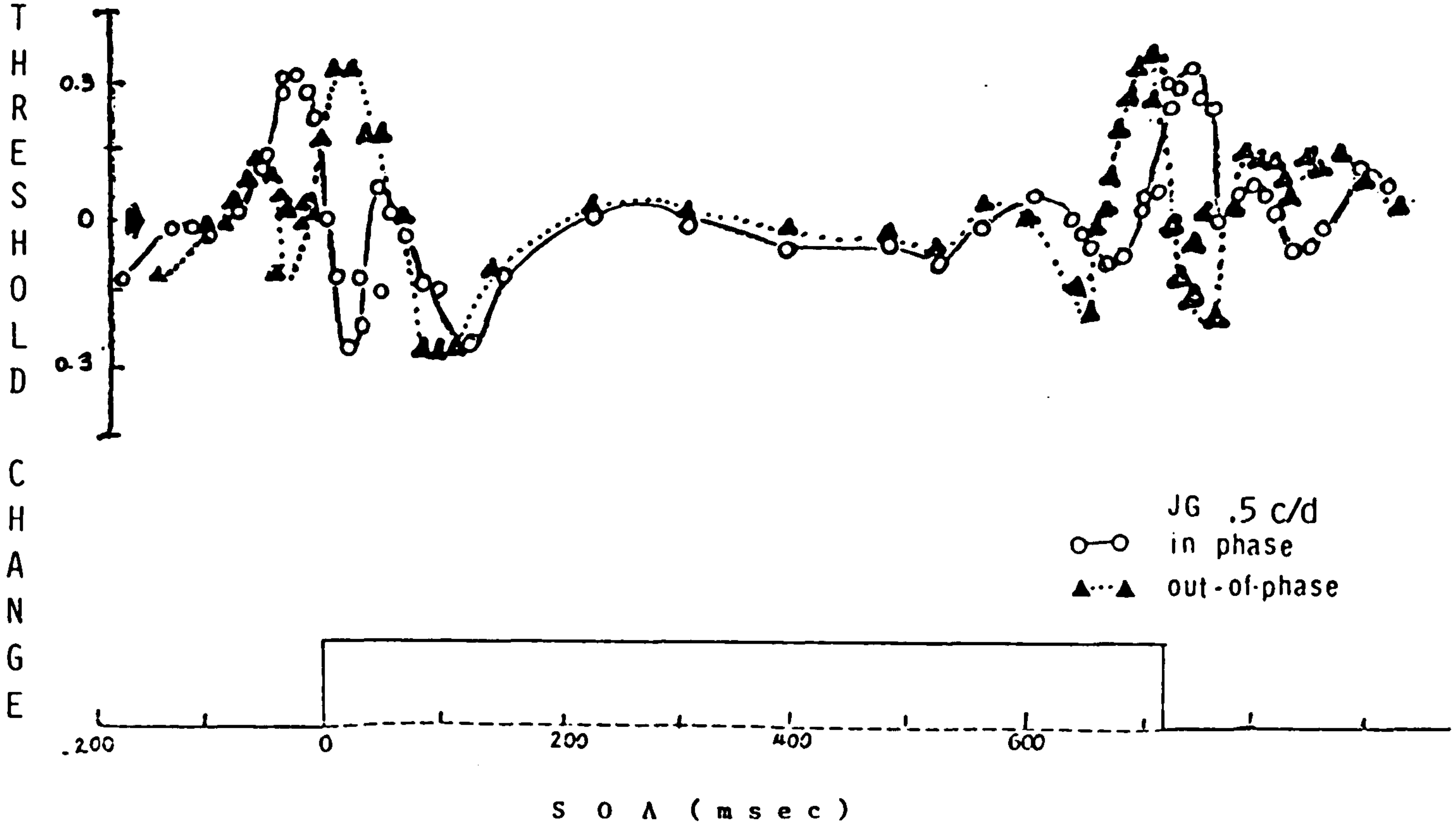


Fig 10B. Superimposition of the in- and out-of-phase threshold functions. Data for J.G., .5 c/d. Threshold change is plotted in log units.

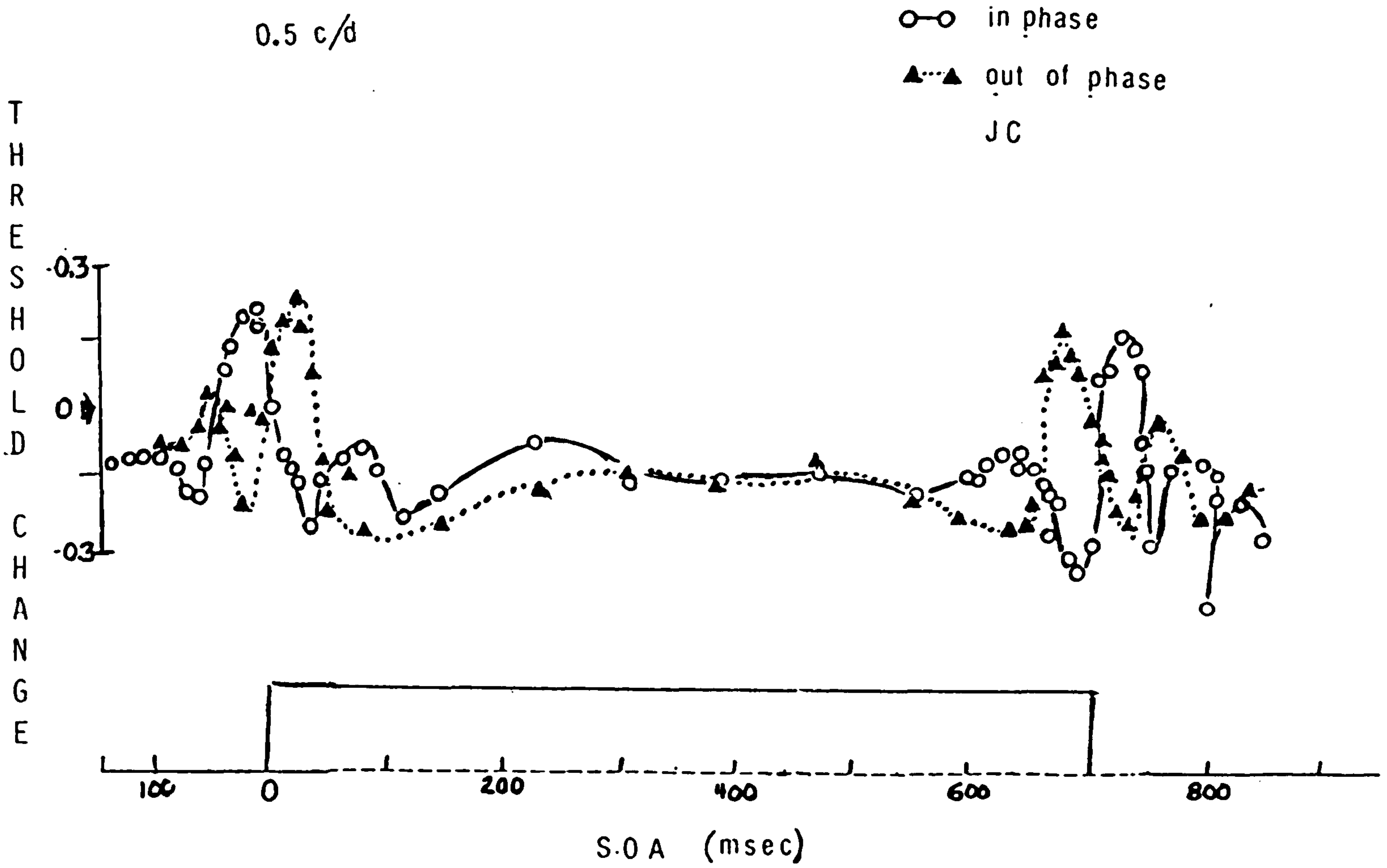


Fig 10C. Superimposition of the in- and out-of-phase threshold functions. Data for J.C. .5 c/d. Threshold change is in log units.

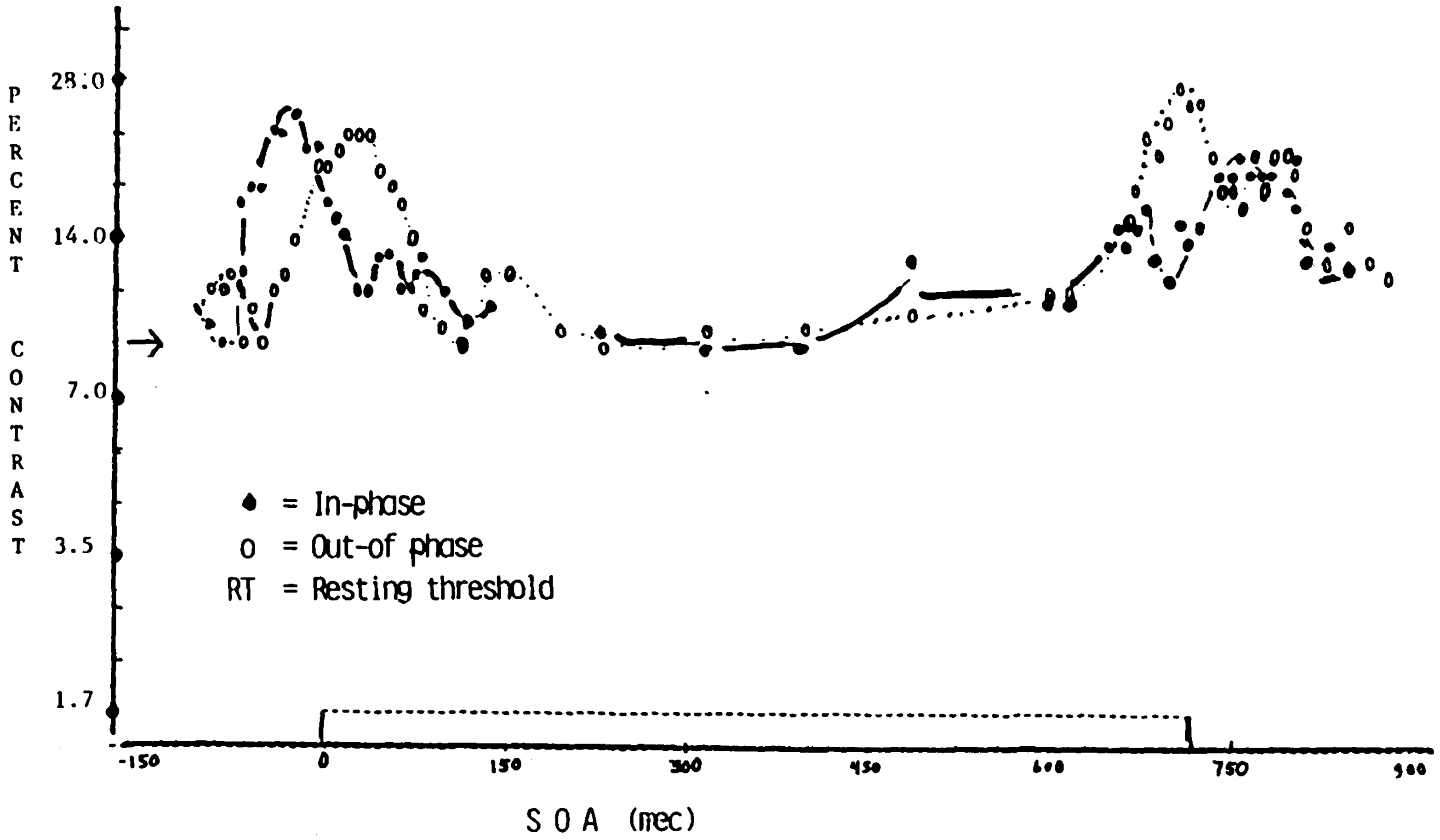


Fig 10D. Superimposition of the in- and out-of-phase threshold functions. J.C, 4/d.

corresponded to those associated with decrements in the detection of the opposite phase.

F. COMPARISON BETWEEN SUBJECTS

1. .5 c/d. Except that the total magnitude of masking and facilitation was slightly greater for J.G. than J.C. (peak to trough difference of .5 as opposed to .6 log), the data for the two subjects was nearly indistinguishable in terms of the shapes of the functions and even absolute sensitivities. The timings of the primary peaks never varied by more than 8 msec and were frequently identical. Differences in the timing of both the primary and secondary troughs and the secondary peaks were less than 35 msec.

2. 4 c/d. The 4 c/d functions for both subjects are similar in terms of the essential features but differ in their absolute thresholds, with J.G., the emmetrope, being the more sensitive at all SOAs. Interestingly, the superiority in detection was not uniform but was about .08 log for the resting level SOAs and approximately .17 log at the peaks, suggesting that J.C. was not only less sensitive to the unmasked test stimulus, but also more susceptible to masking.

3. 6 c/d. data were limited, but as can be seen from Fig 9, were quite similar for the two subjects.

V. Discussion: Nonadaptation data

In agreement with Tolhurst (1975b), the nonadaptated data show that both increases (peaks) and decreases (troughs) in the contrast threshold of a brief test grating occur as a function of onset delay with respect to a long lasting mask of the same spatial frequency. These threshold changes appear with mirror-like symmetry in magnitude and timing around mask onset and offset but not during the intermediate SOAs. However, in contrast to Tolhurst who only reported a single masking peak at onset or offset, two distinct types of peaks, designated as "Primary" and "Secondary", were observed.

A. Peaks.

1. Primary peaks occurred approximately 25 msec from the temporal edges. In-phase peaks preceded mask onset and followed offset, whereas out-of-phase peaks showed the reverse time course following onset and preceding offset. Similar peak timings were reported by Tolhurst (1975b) and Battersby & Wagman (1962) although, in the later investigation, this was true only when the test and mask were equal in size. Otherwise, maximal effects occurred at the SOA of 0.

For both subjects, the heights of these peaks were approximately the same at 4 c/d as at .5 c/d. However, in pilot data at 6 c/d, primary peaks were considerably smaller suggesting that masking decreases in magnitude with spatial frequency. This conclusion is comparable with the findings of others (Green, 1981; Tolhurst, 1975b; Watson & Nachmias, 1977).

Interestingly, for one subject (J.G.), 4 c/d peaks tended to decrease over the course of testing. These threshold decreases are not likely to have resulted from a shift in the apparatus since they occur only at the masking PEAKS and additionally, only at 4 c/d. On the other hand, the reduction in the variablity around these threshold estimates suggests that learning may have occurred during the course of testing. Progressive improvement in a grating discrimination task for a restricted range of spatial frequencies and orientations, was also reported by Fiorentini & Bernardi (1981) suggesting that learning does occur within so-called spatial frequency channels. The present finding suggests that this learning is more apparent at the temporal edges than during the plateau portion of the function.

J.C.'s failure to show similar evidence of learning may be a function of his shorter testing sessions which were less numerous and more widely distributed over time.

In all threshold functions, the duration of masking was at least 8 msec since maximum thresholds were frequently obtained at two adjacent SOAs (which were 8 msec apart).

The prominance of the primary peak at low spatial frequencies and its occurrence at a small temporal delay, suggests the involvment of a transient neural mechanism.

2. <u>Secondary peaks</u> - which occurred between 40-100 msec from mask onset and offset, always on the opposite "side" of

the temporal edge as the primary peaks. For example, if a primary peak occurred BEFORE mask onset, the secondary peak appeared at some longer delay AFTER the mask onset.

The SOAs associated with secondary peaks were more variable than those related to the primary peaks, but in general, secondary peaks tended to be further from the primary peaks at 4 c/d than at .5 c/d. The trend of increasing separation of the primary and secondary peaks with spatial frequency is further suggested by the pilot data at 6 c/d. Interestingly, Rogowitz (1977) found that the SOA of maximal metacontrast increases with spatial frequency. Thus, secondary peaks obtained in this study have a common feature with the single peak obtained in metacontrast studies. The significance of this finding will be discussed later.

The relative magnitude of the secondary peaks increased with spatial frequency. Thus, there was a change in the relative magnitude of the secondary peaks with respect to the primary peaks. At .5 c/d the primary peak was clearly larger than the secondary. By 4 c/d, the difference between the two peaks was smaller, and in the pilot data at 6 c/d, the primary and secondary peaks were about equal (Fig. 9).

Increase in both the prominance and delay of the secondary peaks with spatial frequency, suggests the influence of sustained neural mechanisms (Breitmeyer & Ganz, 1977; Spitzberg & Richards, 1975).

The existence of secondary peaks has not previously been reported, possibly because such peaks fail to occur when the test or mask are spatially uniform (Battersby & Wagman, 1962; Green, 1982) or because the appropriate asynchronies have not been sampled (Tolhurst, 1975b).

B. Troughs were decreases in threshold which occurred around the temporal edges and which were also designated as primary and secondary. Primary toughs occurred at approximately the same temporal delays as the primary peaks (17-32 msec from the temporal edges), but always appeared on the opposite side of the temporal edge, so that if the peak preceded onset, the trough followed it.

Secondary troughs occurred at longer delays from the temporal edges (50-100 msec) and were always on the same side as the primary peaks.

Except for the differences in timing, there were no obvious distinguishing features between the primary and secondary troughs. However, similaries were frequently noted in their durations and magnitudes. For example, primary and secondary troughs were always 8 msec or less in duration; that is, mimimum thresholds were never obtained for two temporally adjacent SOAs. Thus, facilitation may be shorter in duration than inhibition.

As was observed with the peaks, troughs also decreased with spatial frequency. However, peaks and troughs decreased at different rates; At .5 c/d these were approximately equal. By 4 c/d however, the peaks did not change appreciably whereas the troughs were greatly reduced. By 6 c/d, peaks were smaller, but troughs were virtually absent (Fig. 9). Therefore, the magnitudes of both inhibition and facilitation are inversely related to spatial frequency, although the decline in facilitation is more dramatic than that of inhibition. These findings are in agreement with others (Tolhurst, 1975b; Watson & Nachmias, 1977) and suggest that these two processes are not the inverses of each other. Another small difference between peaks and troughs was their timings from the temporal edges. Although the SOAs associated with the peaks for one spatial phase were similar to the troughs of the opposite phase, this correspondence was not exact and generally differed by about 8 msec.

As is clear from Figs 10 A-D, there is a noteworthy consistency in the data whereby all peaks and troughs of a given type (e.g., primary, secondary) tend to be identical in magnitude. However, in two conditions (J.G. .5 c/d and J.C. 4 c/d; Fig. 10B & D) facilitation for one spatial phase was .1 log greater than the other at onset, while, the opposite spatial phase was more facilitated by .1 log at offset. Similar inequalities did NOT occur at the peaks. Although these differences were relatively small, they support the following assumptions which will later be discussed in the context of a model; namely that (1) inhibition and facilitation are independent processes and (2) a common mechanism may facilitate gratings of one spatial phase at onset and the opposite phase at offset.

C.Mirror-symmetry in timing of peaks was noted about the presentation of the mask stimulus; that is, if maximal masking occurred 25 msec before the onset of the mask stimulus, it also occurred 25 msec after its offset. Similar observations have been reported by others (Battersby & Wagman, 1962, Crawford, 1947;

However, departures from mirror-symmetry occurred in the duration of offset masking, which was 45 msec longer than that at onset.

D. Mirror-symmetry in magnitude of onset and offset peaks.

At each spatial frequency, onset and offset peaks were usually equal in magnitude. This finding differs from those of others (Battersby et al., 1959, 1962, Crawford, 1947, Polous, 1980; Wagman & Battersby, 1959) whose assymetrical functions showed less masking at offset than onset. The absence or reduction of offset masking in these earlier studies may be a consequence of either the poor spatial fit between the test and the mask or due to the fact that they did not use patterned stimuli, since, offset masking increases both when the spatial fit between the test and mask is improved (Battersby & Wagman,1962; Battersby & Defenbaugh, 1969) but also when the spatial frequency com-

position of the test and mask is matched (Tolhurst, 1975b). Using a sinusoidal test and a uniform field as a mask, Green (1981) found symmetrical peaks using a forced choice procedure but not for the method of adjustment. Apparently, offset masking is sensitive to several experimental parameters.

Interestingly, a departure from the symmetry of peak magnitudes did occur in J.C.'s 4 c/d data (Fig. 10D). In this situation, offset thresholds of the out-of-phase test stimulus were .1 log greater than those of the in-phase test. Onset peaks, however, were equal regardless of spatial phase. Although the data were limited, they do suggest that (1) onset masking is different from offset and raises the possibility that (2) the mechanism responsible for in- and out-of-phase masking may be antagonistically linked so that the increase in the inhibitory advantage over one spatial phase equals the decrease in inhibition of the opposite spatial phase.

The interpretation that different mechanisms operate at onset and offset is supported by the electrophysiological discovery of discrete cell populations which signal either light onset or offset (Hartline, 1938; limulus) or by the existence of on- and off-center cells (Kuffler, 1954) distinguishable morphologically (in terms of the retinal layer of synaptic contacts <cat>; Wassle et al., 1982), pharmacologically (Ikeda & Sheardon, 1982 <cat>, Schiller, 1982 <monkey>) and electrohysiologically in terms of the differ-

ing variability in the time course of the neural responses (<goldfish>, Levine & Sheffner, 1977). In the human, various psychophysical studies show differences in performance at onset and offset; for example, low spatial frequency detection is more greatly enhanced by abruptness of onset than of offset (Breitmeyer & Julesz, 1975). Furthermore, the onset and offset of masking patterns differentally affects the perception of appearance and dissappearance of a test pattern (Phillips & Singer, 1974). Finally, several investigators (Battersby & Wagman, 1962; Polous & Makous, 1980) have shown that onset masking occurs both monocularly and dichoptically whereas offset masking is only dichoptic.

E. Phase Effects. Another important and obvious feature of the masking data was the different timing of the in- and out-of-phase peaks. Primary in-phase peaks always occurred before or after mask presentation whereas the primary out-of-phase peaks occurred DURING the mask presentation. Interestingly, the SOA at which the test stimulus was most readily detected depended upon whether it added to or subtracted from the contrast of the simultaneously occurring mask. Any test stimulus which ADDS to the contrast of the mask (that is, increases the amount of change associated with the transition from the blank field to the mask onset) is facilitated, whereas a test stimulus which SUBTRACTS from it is inhibited. For example, an in-phase grating presented either just after mask onset or before its offset adds to the contrast of the mask and exaggerate the magnitude of change at the temporal edges. Similarly, an 180% out-of-phase grating presented just before onset or after offset of the mask, alters field luminance in a fashion exactly opposite to that which will be caused by the mask. Thus, in these relative temporal positions, in- and out-of-phase gratings are more detectable than at any other SOAs. On the other hand, presenting an in-phase grating just before the mask onset or after its offset, is similar to creating a "step" of contrast which reduces the transition between the mask and the backround. Similarly, an out-of-phase grating which follows mask onset and precedes its offset, subtracts from the mask contrast pedestal, again reducing the total change. At these asynchronies, these two stimuli are masked.

Although the TIMING of masking differed according to the spatial phase of the test stimulus, the MAGNITUDE did not (this finding is in agreement with Tolhurst (1975b) and Watson & Nachmias (1977)).#herefore, it is inappropriate to use criteria such as the magnitude of threshold change to determine whether or not phase encoding occurs in the visual system. Nevertheless, several investigators have done this and have suggested that, because there is no difference in the contrast thresholds of complex gratings when the components are in the peak-add vs the peak-subtract position, that phase encoding does not occur (Graham & Nachmias, 1971; Graham, Robson & Nachmias, 1978). The more accurate conclusion, however, is that there is no superiority for detection of in- as opposed to out-of-phase gratings. Similarly, when

Watson & Weber (1978) showed that the phase relationship between the fundamental and the third harmonic (F and 3F) of a complex grating cannot be identified when the components are at threshold, their finding should be interpreted to mean only that the threshold for phase discrimination is DIFFERENT from that for spatial frequency detection and not that phase difference is indiscriminable at any contrast. Indeed, a replication of the Watson & Weber study using a higher contrast 3F stimulus showed discrimination for phase differences greater than 30° (Burr, 1980).

Additionally, when different experimental designs are used, it is clear that spatial phase discrimination does occur. For example, multistable perceptions occur more readily at some phase relationships than others (Atkinson & Campbell, 1974). Secondly, there are differences in the subsequent appearance of a flickering test grating according to the spatial phase of the adapting grating (Jones & Tulaney-Keesey, 1980) and finally, during adaptation, it has been found that the eyes cannot wander randomly across the adapting field; rather subjects typically adopt a particular phase angle in which they position their eyes more frequently than any other (Jones & Tulaney-Keesey, 1980).

With regard to spatial frequency and phase encoding, the data show in-and out-of-phase peaks to be more pronounced at the lower spatial frequencies of .5 and 4 c/d than at 6 c/d (for which only pilot data are available). Regardless of *spatial frequency, however, phase effects occurred at onset and offset but not during the intermediate SOAs. Since low spatial frequency channels are associated with sensitivity changes at stimulus onsets and offsets (Tolhurst, 1975a) and since the magnitude of onset and offset masking decreases with increases in spatial frequency, (Tolhurst (1975b) these data suggest that phase processing is more strongly associated with low, as opposed to high spatial frequencies. Similar conclusions might be drawn from other phase encoding studies in which phase-related interactions are most frequently reported when the stimuli are of low spatial frequency, for example, 1 and 3 c/d (Atkinson & Campbell, 1974) or less than 1 c/d (Ross & Johnston, 1980). Grating pairs which are widely separated (more than four octaves; Stromeyer, Lange & Ganz, 1972) or are relatively high in spatial frequency (3 and 9 c/d; Nachmias & Weber, 1978, Holt & Ross, 1980) do not show phase sensitive effects. Indeed, Burr (1980) showed that significantly more contrast is needed to discriminate phase differences between pairs of high spatial frequency, as opposed to pairs of low spatial frequency gratings.*

Finally, whereas the data clearly demonstrated the occurrence of phase discrimination, the subject was never able to specify the test phase when asked. This was true for suprathreshold as well as subthreshold test stimuli and suggests that the processing of spatial phase of brief stimuli does not reach conscious perception.

F. Differences between the .5 and 4 c/d functions

Finally, it was noted that all thresholds, whether masked or unmasked, were lower at .5 c/d. This finding must be interpreted to mean that detection was mediated by the transient system since it is maximally sensitive at low spatial frequencies. The significance of this finding will be considered later.

CHAPTER 4

EXPERIMENT II: ADAPTATION CONDITION

I. Rationale

Before the design of the adaptation condition is presented, it is worthwhile to consider in detail, the types of information which can be derived from such a procedure.

From Experiment I, it was proposed that detection of the test stimulus was mediated by the transient system. This conclusion was based upon the observation that performance at .5 c/d was superior to that at 4 c/d at every SOA, a finding which is consistent with both the abruptness and brevity of the test stimulus. Note that this proposition does not exclude the possibility of a sustained response to the test. However, it is proposed that detection is mediated by the transient system.

POSTULATE (1) The transient neural response to the test must be subject to one of the three following outcomes. Either it can be inhibited or facilitated by the neural response to the mask, or it can fail to interact with the response to the mask. An obvious situation in which the test and mask fail to interact is during the determination of the resting threshold, since in this condition, the test is presented in the absence of the mask. However, if resting threshold is also obtained at some SOAs when the test and mask are presented concurrently, then the absence of interaction between the neural responses to the test and mask is a reasonable inference. Since test thresholds measured during the intermediate SOAs were the same as at resting level, it will be presumed that the test and mask did not interact at these SOAs and that these thresholds are determined exlusively by transient cells activated by the test.

POSTULATE (2) When the transient mechanism which is detecting the test is either inhibited or facilitated by the neural resonse to the mask, threshold will depart from the resting level. Peaks represent inhibition whereas troughs represent facilitation.

POSTULATE (3) Inhibition of the test transient response can result from interactions with either:

(a) the transient response to the mask or (b) the sustained response to the mask.

Facilitation of the test transient response can result from interactions with either

(a) transient response to the mask or (b) the sustained response to the mask.

The results of adaptation can help uncover which of these neural interactions are occurring at which temporal delays; for example,

1. If thresholds during the intermediate SOAs are deter-

mined soley by a transient mechanism, then, transient ADAPTATION should REDUCE the excitability of this mechanism and RAISE THRESHOLDS at these SOAs. The magnitude of this change should vary with the contrast of the adapting stimulus.

Steady adaptation, on the other hand should NOT affect transient excitability at SOAs when the threshold is at the resting level, such as at the intermediate SOAs.

2. At peaks caused by inhibition between the transient response components of the test and mask (T-T interactions), transient adaptation may reduce the excitability of the neural elements responding to the two stimuli, but it should not change the balance between them. Thus, thresholds should increase due to adaptation, but the inhibitory influences represented by the peaks should be preserved. Furthermore, changes in the timing of these adapted T-T peaks should not occur, since any increases in the latency of the neural responses which might be caused by adaptation should be equal for both the test and mask mechanisms. Thus, at T-T inhibited SOAs, peaks should increase but remain at the same SOAs.

STEADY adaptation, again, should have NO effect upon thresholds at SOAs determined soley by T-T inhibition.

4. At peaks which are caused by SUSTAINED inhibition due to the mask, transient adaptation should decrease the TEST

response without altering the magnitude of inhibition. In this situation, the test detector must overcome the adversive effect of two conditions; one due to adaptation, and the other due to the relatively greater antagonism of the mask. Therefore, at SOAs characterized by S-T inhibition, threshold rises should be LARGER than those associated with T-T inhibition. Furthermore, the response latency of the ADAPTED transient response should be longer than the nonadapted. Since the sustained system is not adapted, latency changes should not occur within this sytem. Thus, a shift in the timing of test-mask interactions can be predicted. (The same logic applies for steady adaptation except that changes in the SOA of interaction should be in the temporally opposite direction).

For reasons which will be explained later, peaks which result from transient-sustained interactions should shift CLOSER to the temporal edge after TRANSIENT adaptation and FURTHER from this edge after STEADY adaptation.

4. To predict adapted threshold changes at the troughs, a logic similar to the above applies. Suppose, for example, that FACILITATION results when the transient responses to the test and mask summate within the same mechanism. In this situation, the transient system is exclusively responsible for detection and facilitation. Thus, transient adaptation should impair detection and eliminate facilitation. Therefore, troughs characterized by T-T facilitation,

thresholds should diminish.

If the sustained system does not contribute to T-T troughs, then steady adaptation would have no effect.

5. Finally, in the condition in which the sustained response to the mask facilitates the transient response to the test, transient adaptation should attenuate the test DETECTOR but NOT THE FACILITATOR. Thus, transient excitability would be reduced by one route but partially restored by another. The net result of this circumstance should be a smaller reduction in T-S troughs than that associated with T-T facilitation. Additionally, latency changes as a consequence of adaptation should shift the SOA of this effect closer to the temporal edge.

Steady adaptation, on the other hand, should eliminate facilitation and reduce the troughs.

A summary of these predictions is presented in Table 2. In a binocular system, these results should be identical regardless of which eye is adapted. On the other hand, this would not be true if a given system is monocular. It should be noted, however, the term monocular does not automatically imply retinal origin, since cells which are either predominantly or exclusively monocular have been described at cortical as well as subcortical levels (Hubel & Weisel, 1962).

II. Method: Experiment II

1. The transient response to the TEST (T_t) determines threshold
2. Peaks and troughs indicate INHIBITION or FACILITATION of T_t.
3. Sources of this inhibition and facilitation are:

Inhibition by	TRANSIENT response to the MASK (T_m) SUSTAINED response to the MASK (S_m)
Facilitation by	TRANSIENT response to the MASK (T_m) SUSTAINED response to the MASK (S_m)

AT SOAS DETERMINED BY	TRANSIENT ADAPTATION SHOULD	PREDICTED THRESHOLD CHANGE
T_t alone	Reduce excitability of T_t	Increase
T_m x T_t inhibition	Reduce excitability of T_t Reduce both excitability and inhibition of T_m	Increase
Sm x T_t inhibition	Reduce excitability of and delay T_t with respect to S_m Fail to alter S_m	Large threshold increase Shift in peak asynchronies
Tm x T_t facilitation	Reduce excitability of test detector and mask facilitator	Reduction or loss of troughs
Sm x T_t facilitation	Reduce and delay excitability of T_t Preserve facilitation of S_m	Reduction and temporal shift of troughs
	SUSTAINED ADAPTATION SHOULD	
Either T_t alone OR T_t x T_m interactions	have no effect	None
S_m x T_t inhibition	reduce and delay S_m inhibtion	Decrease and temporal shift of peaks
S_m x T_t facilitation	reduce and delay S_m facilitation	Troughs should decrease and temporally shift

TABLE 2. Predicted outcomes of transient and sustained adaptation

The subjects, apparatus and test and mask stimuli were the same as in Experiment I and, as was true in that condition, the test and mask were presented to the same eye.

A. Stimuli

Adapting stimuli were the same spatial frequency as the test and mask.

1. The SUSTAINED adapting stimulus was a stationary grating in the same spatial phase as the mask. To avoid sharp temporal edges, this grating was always ramped on and off over a period of 260 msec and thus, was presented at full contrast for 3.7 sec. Temporal ramping was achieved by modulating a signal through an R-C integrater network which causes its amplitude to rise slowly. Two back-to-back zenor diodes maintained the signal at the desired amplitude. At stimulus offset, a downward ramp resulted.

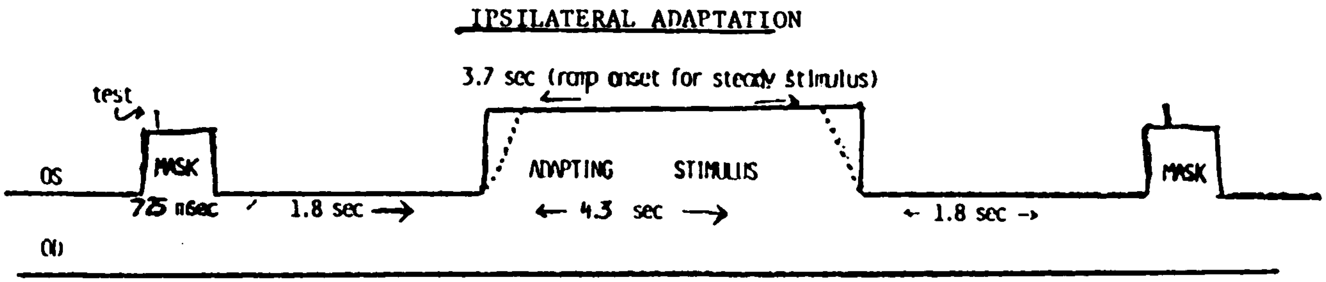
2. The TRANSIENT adapting stimulus was counterphase modulated in a square-wave fashion at the rate of 8.6 Hz (Kelly, 1972; Koenderik & Van Doren, 1979; Kulikowski & Tolhurst, 1973). This signal was created by alternating the polarity of the modulating signal.

Pilot studies were done to select the appropriate adaptation contrast. During a session, this contrast was held steady, although, over the course of the study, several adaptation contrasts were explored. Because there was no prior knowledge as to which SOAs would be affected by what contrast or how to equate adapting contrasts for the two subjects, it was frequently necessary to generate an entire adapted function simply to conclude that the contrast was ineffective.

B. Procedure

Adaptation sessions began with a 3 minute exposure to the adapting grating and were identical to the nonadapted condition except that adaptation was refreshed for 4.3 sec before each trial. Thus, adaptation trials were somewhat longer than the nonadapted (Fig. 11). As in Experiment I, the test and mask were presented monocularly to the left eye. In the ipsilateral adaptation condition, the left (tested) eye was also adapted. In the contralateral adaptation condition, the right eye was adpated and the left eye tested. On days when multiple sessions were conducted, the morning adaptation condition was the same as that of the afternoon. Contralateral adaptation experiments were never performed on the same day as ipsilateral studies. (Note: the term "contralateral" is preferred to "dichoptic" in describing the adaptation condition, since dichoptic term often implies that two stimuli are simultaneous although independently presented to the two eyes. In the present study, adaptation preceded and was never simultaneous with the test and mask presentation).

For each spatial frequency, the adaptation data were collected several weeks after the nonadaptation data (control) since a foreknowledge of the basic shape of the function was



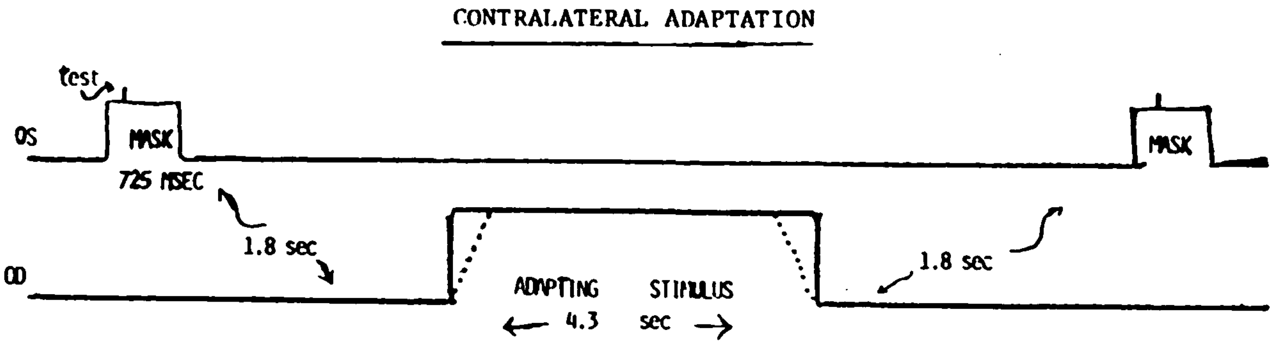


Fig 11 TEMPORAL ARRANGEMENT: EXPERIMENT II (ADAPTATION)

In the ipsilateral condition, (Fig 11 A. the test, mask and adapting stimuli were all presented to the same eye while the contralateral eye viewed a blank screen of the same mean luminance.

In the contralateral condition (Fig 11B), the test and mask were presented to the same eye, but adaptation was of the contralateral eye. The adapting stimulus was never presented simultaneously with the test or mask.

necessary in order to select those SOAs at which adaptation might demonstrate an effect. Fewer adapted SOAs were sampled than nonadapted. Of the two troughs which appeared at each temporal edge, only the earliest (primary troughs) were repeatedly measured.

Over the several months of data collection, stability of thresholds was assessed by measuring the nonadapted thresholds at the SOAs of -25, 25 and 400 msec. For J.G. at 4 c/d peaks showed a steady decrease over time. For this reason, the entire function was later reevaluated and a composite baseline which contained both early (high estimates) and later (lower estimates) data was established. However, this the composite baseline was still somewhat elevated as compared to the threshold values at the time of adaptation. Therefore, in comparing the nonadaptation and adaptation data, one should keep in mind that 'any observed threshold INCREASE in the adaptation condition runs COUNTER to the general trend of a threshold decrease over time, and should not only be regarded as real, but probably underestimated with respect to the true magnitude of the effect. However, a decrease in threshold may be spurious. For this reason, all adapted thresholds which were lower than the baseline were compared with nonadaptation data collected at approximately the same time period to determine if the effect was real. Only those adapted thresholds which were consistently below nonadapted thresholds measured around the same time period, are reported here.

C. Reliability of the adaptation data were not determined by repeated measures since the amount of testing time involved made this approach prohibitive. To help distinguish real adaptation effects from those due to shifts in motivation, accomodation or fixation, the only features which are emphasized are those which either occur at both .5 and 4 c/d, or are the same for both subjects, occurred at more than one adapting contrast, or at more than one peak, etc.

III. Results

At .5 c/d, the adaptation results for both subjects were very similar and both will be discussed. However, at 4 c/d, the adaptation contrasts explored had no effect upon J.C.'s thresholds. Therefore, at this spatial frequency, only J.G.'s data will be discussed.

A. Ipsilateral Transient Adaptation

1. .5 c/d function

For J.G., an entire adapted masking function was generated using 2.6% contrast (Fig. 12A-B). Selected asynchronies were explored using 4.6% contrast. Because there was no difference in the effects of these two different contrasts, only 2.6% (Fig. 12C-D) was explored for J.C. It can be seen from Fig. 12A-D that, although all adapted thresholds were raised, the shape of each masking function was preserved.

To facilitate data analysis, transparencies of the baseline functions were made and shifted along the Y axis until the resting levels of the adapted and nonadapted functions

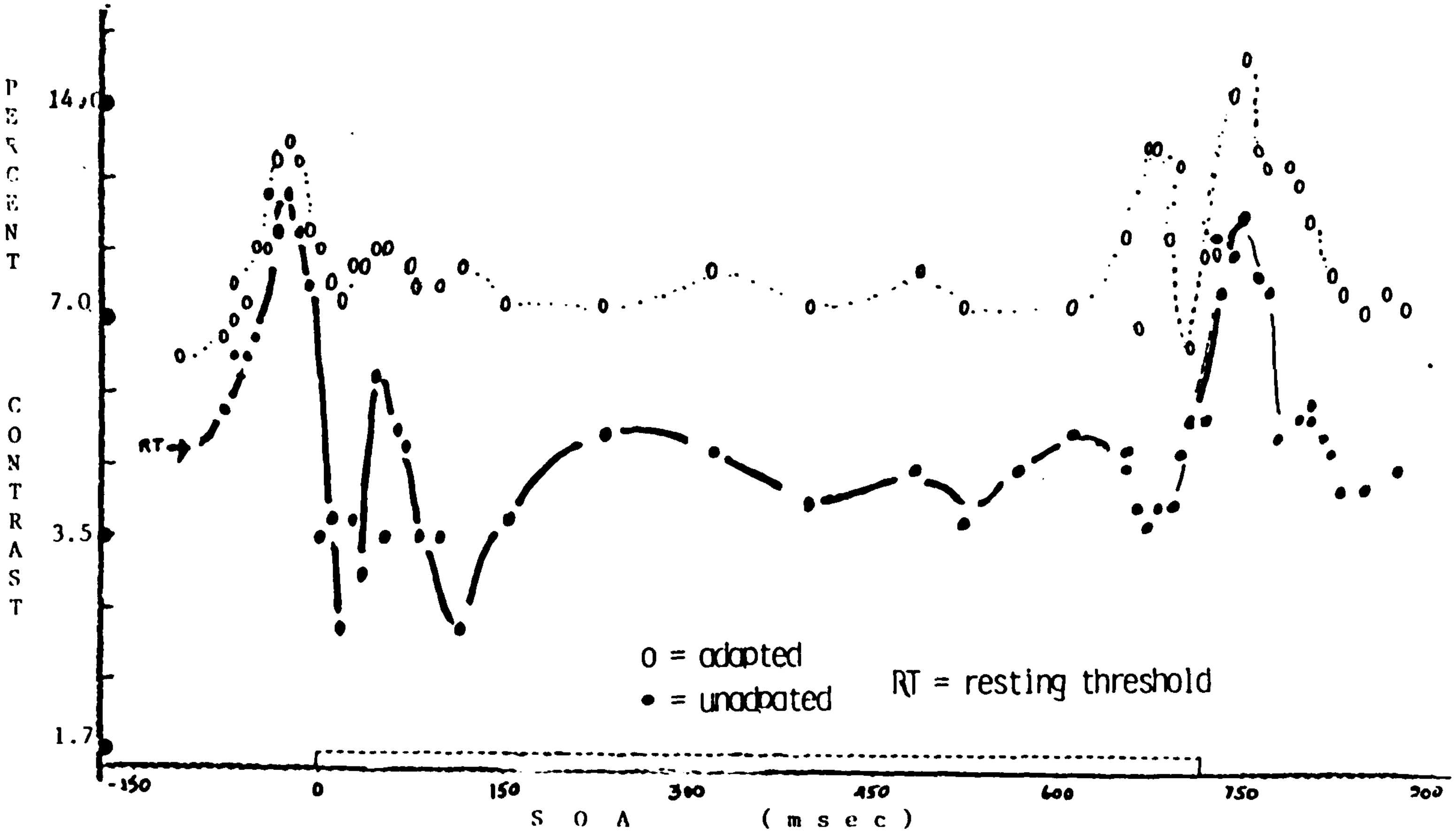


Fig 12A. Ipsilateral transient adaptation: The test and mask were in the same spatial phase. The adapting contrast was 2.6%. Data for J.G. .5 c/d.

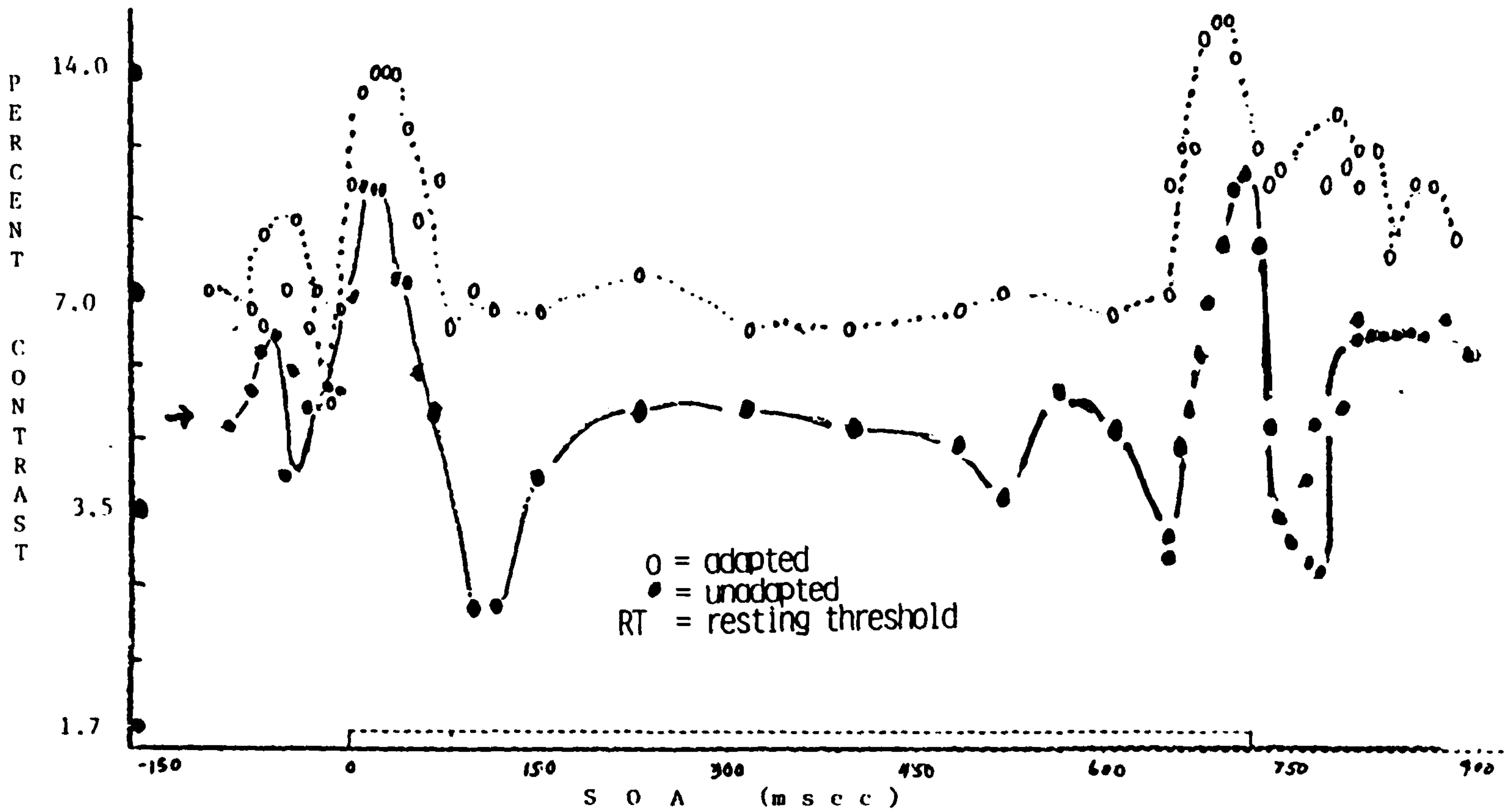


Fig 12B. Ipsilateral transient adaptation; The test and mask 180^0 out-of-phase. The adapting contrast was 2.6%. Data is for J.G. .5 c/d.

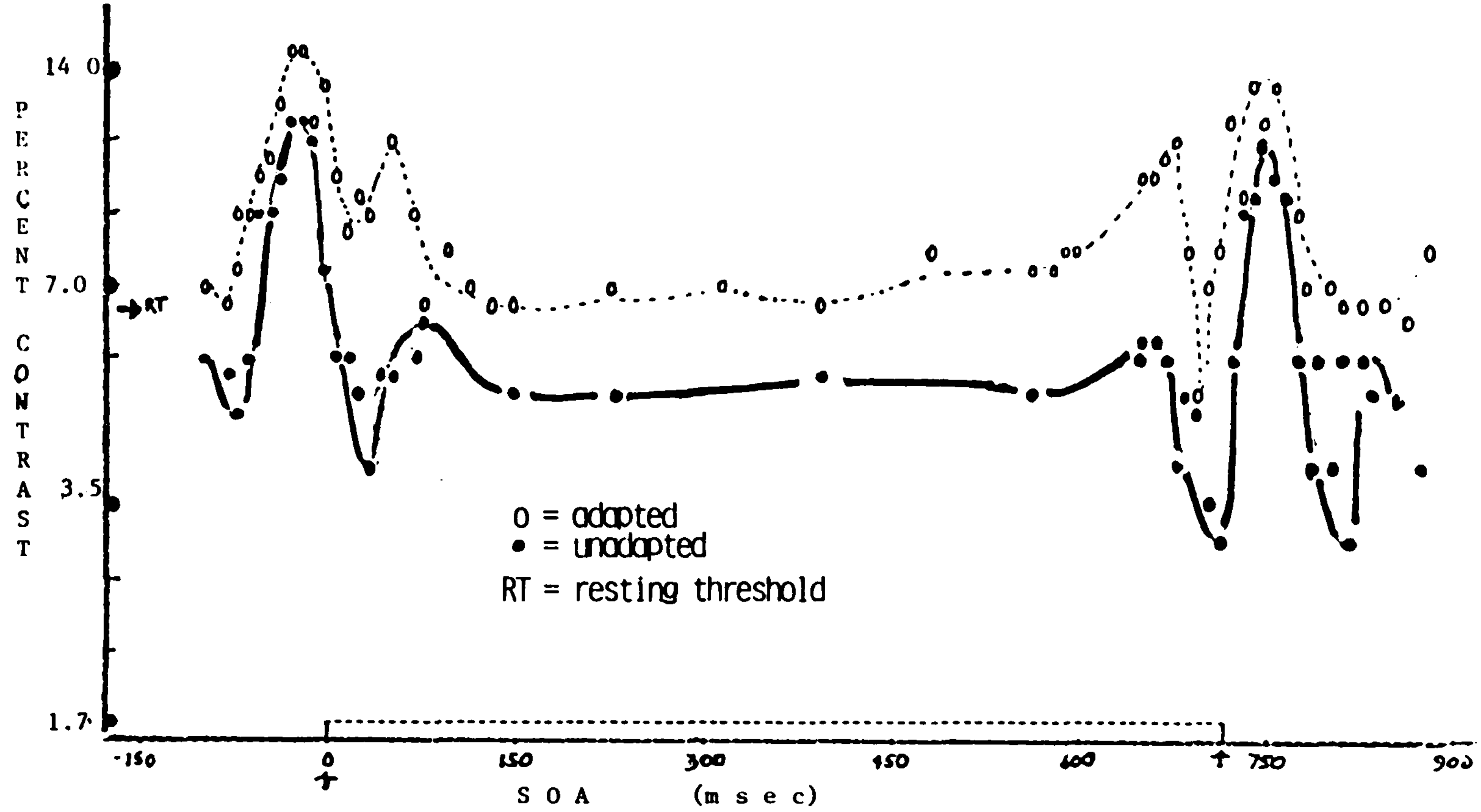


Fig 12C. Ipsilateral transient adaptation: The test and mask were in the same spatial phase. The adapting contrast was 2.6% Data is J.C. at .5 c/d

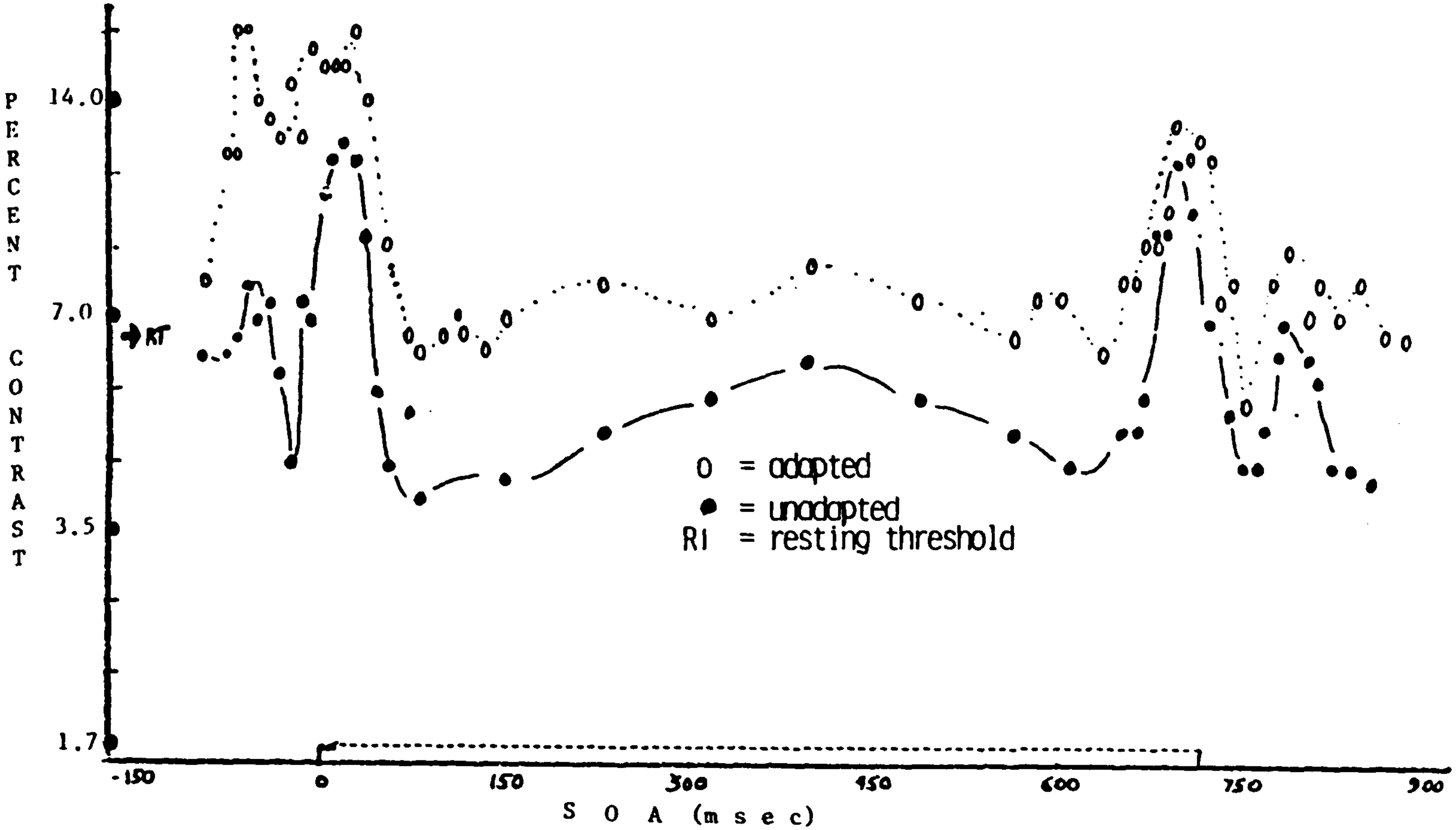


Fig 12D. Ipsilateral transient adaptation; The test and mask were out -of-phase. The adapting contrast was 2.6%. Data for J.C., .5 c/d coincided. The average shift in the baselines required for this overlap, was from .09- .15 log. Interestingly, when the resting levels of the masking functions were aligned, the primary peaks nearly coincided, suggesting that contrasts, .5 c/d primary peaks and the intermediate SOAs were equally affected by adaptation in the explored range. According to earlier reasoning, this suggests that T-T inhibition normally occurs at the primary peaks.

Differences between the adaptation and nonadaptation functions were as follows;

a. Nearly every secondary peak was disproportionately elevated by adaptation, imposing an additional .1 to .3 log increase upon the already higher adapted thresholds.

b. Secondly, four of the eight adapted secondary peaks that were shifted, appeared closer to the temporal edge. In one case, the magnitude of this shift was 46 msec. Three more of the secondary adapted peaks remained at the same SOA and one occurred at a longer delay from the temporal edge.(There was no consistent relationship between the direction of temporal shift and any other experimental parameter). The finding of an additional threshold increase at the secondary peaks plus a shift toward the temporal edge suggests that sustained inhition of the transient response to the test (S-T) normally occurs at this temporal asynchrony. Interestingly, when the adapting contrast was raised to 4.6%, there was no further threshold rise at either the primary peaks or the intermediate SOAs. However, the secondary peaks continued to increase. Thus, the effectiveness of adaptation effect is different at the two types of peaks.

c. Troughs were reduced by .1 to .3 logs following adaptation. For some functions, this meant a nearly complete elimination of the troughs as would be expected if the source of facilitation were a transient mechanism. However, at these same SOAs, there were small (8-17 msec) shifts in trough timing, suggesting that sustained influences also occur at these SOAs.

2. <u>The 4 c/d ipsilateral transient adaptation</u> data support the conclusions drawn at .5 c/d. Several adapting contrasts (.96, 1.5, 2.0, 2.6 and 4.6%) were explored. Because changes in test thresholds were independent of spatial phase, only the out-of-phase data are shown here (Fig. 13A-D). The lowest adapting contrast, .96%, was subthreshold for J.G. but was investigated based upon Smith's (1965) finding that transient adaptation can occur with subthreshold gratings.

<u>The results were as follows</u>;

a. All thresholds were raised by adaptation, as is expected if detection is mediated by the transient system. The magnitude of the threshold increase was contrast dependent, but a given adapting contrast did not equally affect all SOAs.

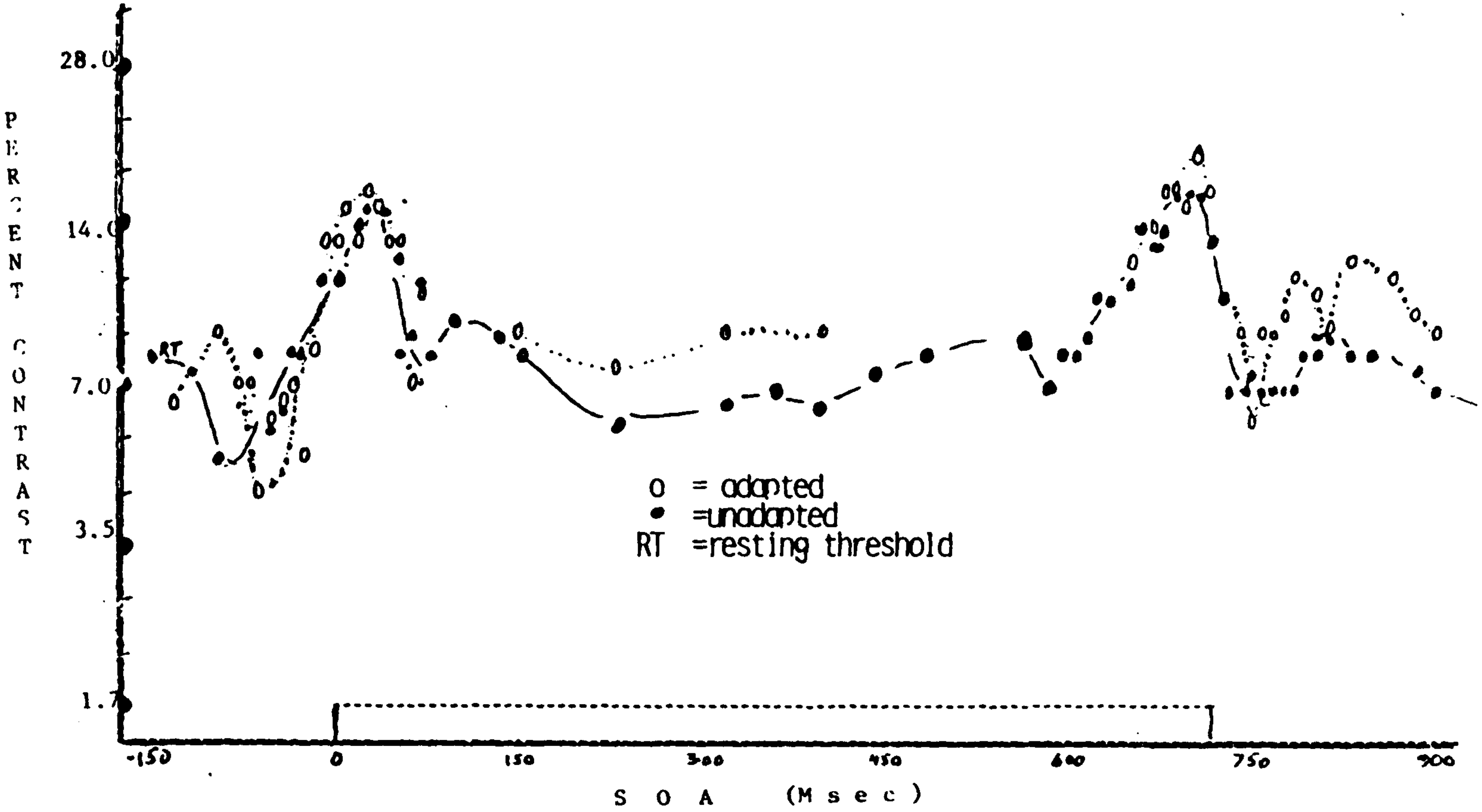


Fig 13A. Ipsilateral transient adaptation. The test and mask were out-of-phase. The adapting contrast was .96%. Data is for J.G., 4 c/d.

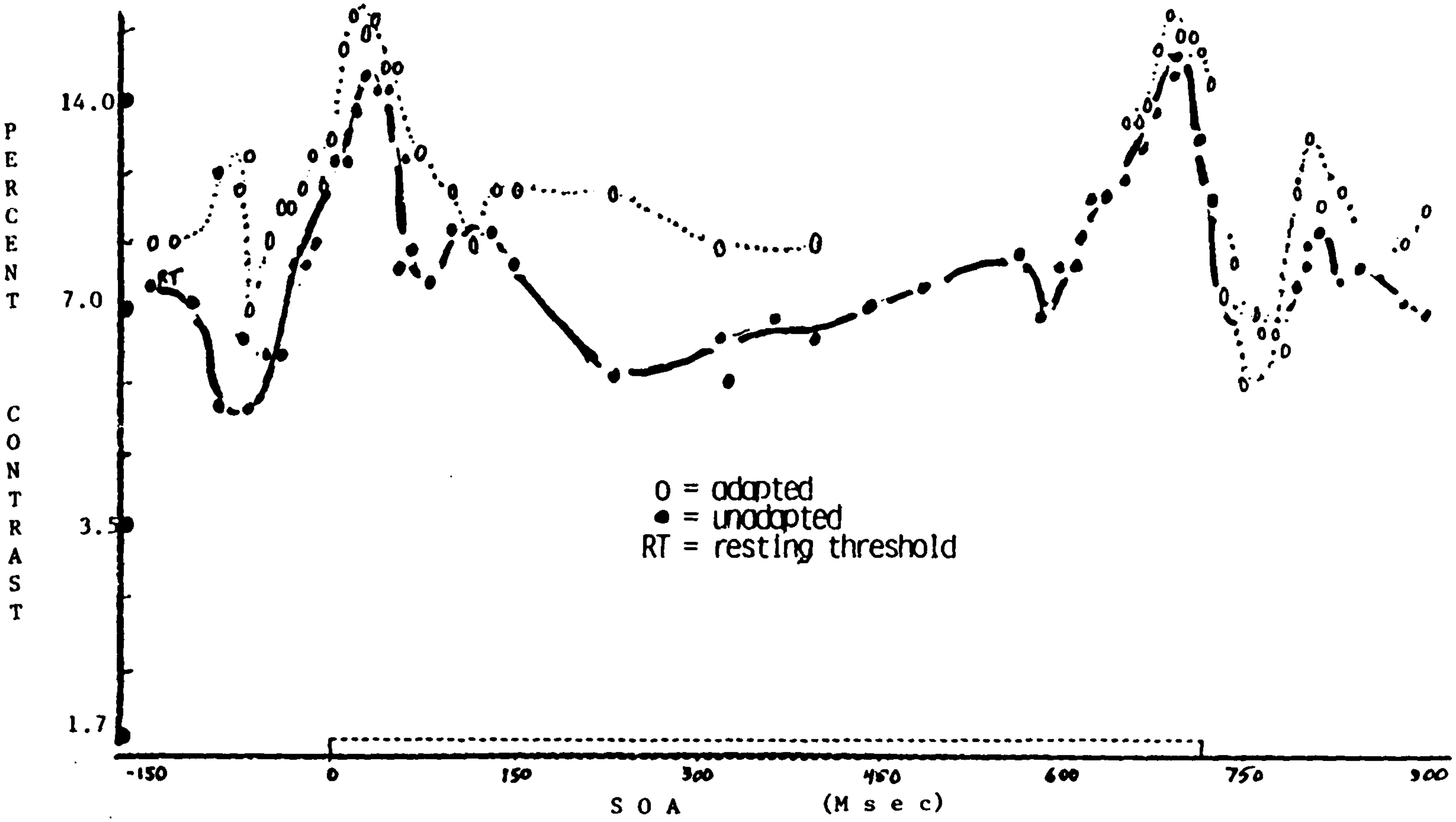


Fig 13B. Ipsilateral transient adaptation. The test and mask were out-of-phase. The adapting contrast was 1.5%. Data is for J.G. at 4 c/d.

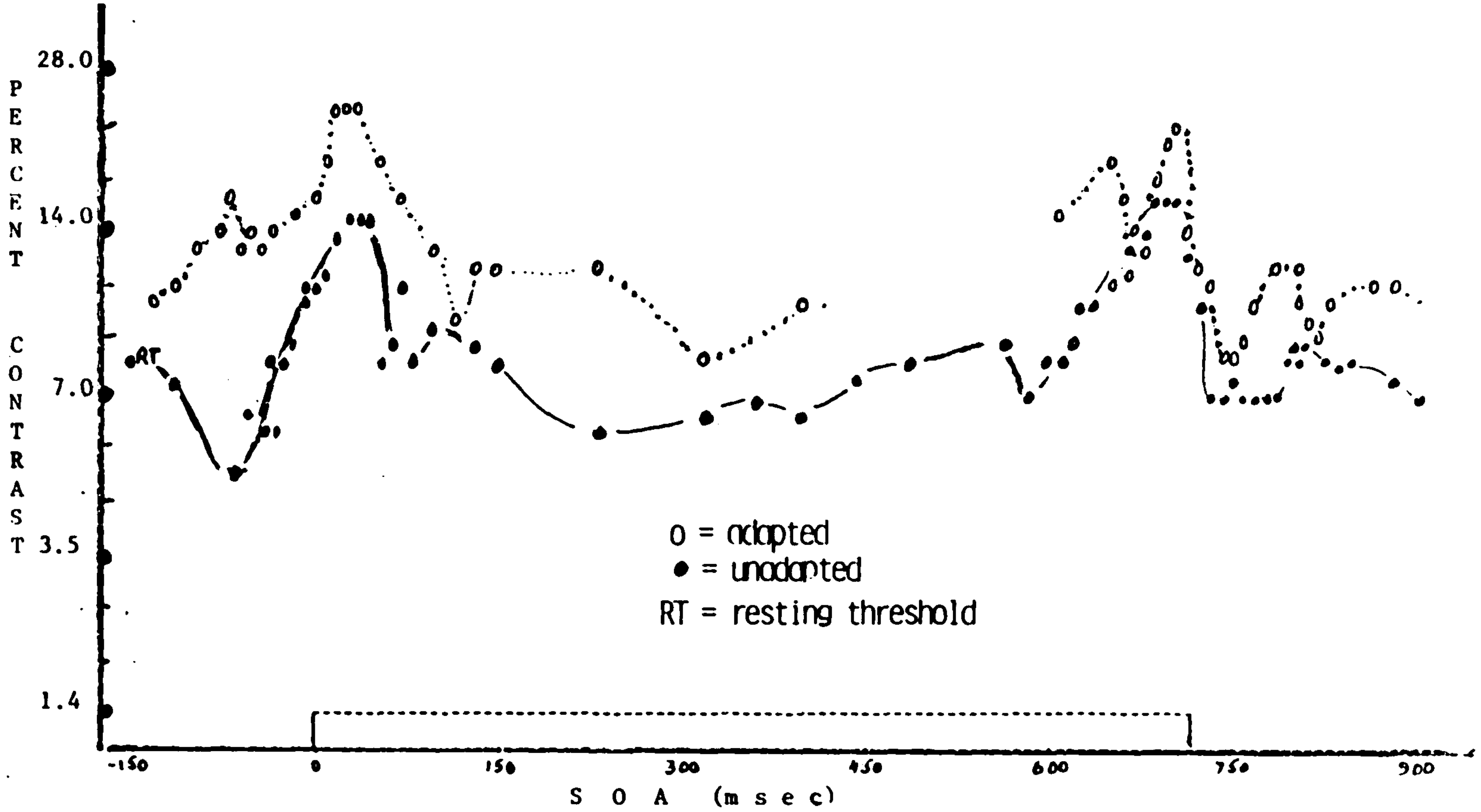


Fig 13C. Ipsilateral transient adaptation. The test and mask were out-of-phase. The adapting contrast was 2.6%. Data is for J.G. at 4 c/d.

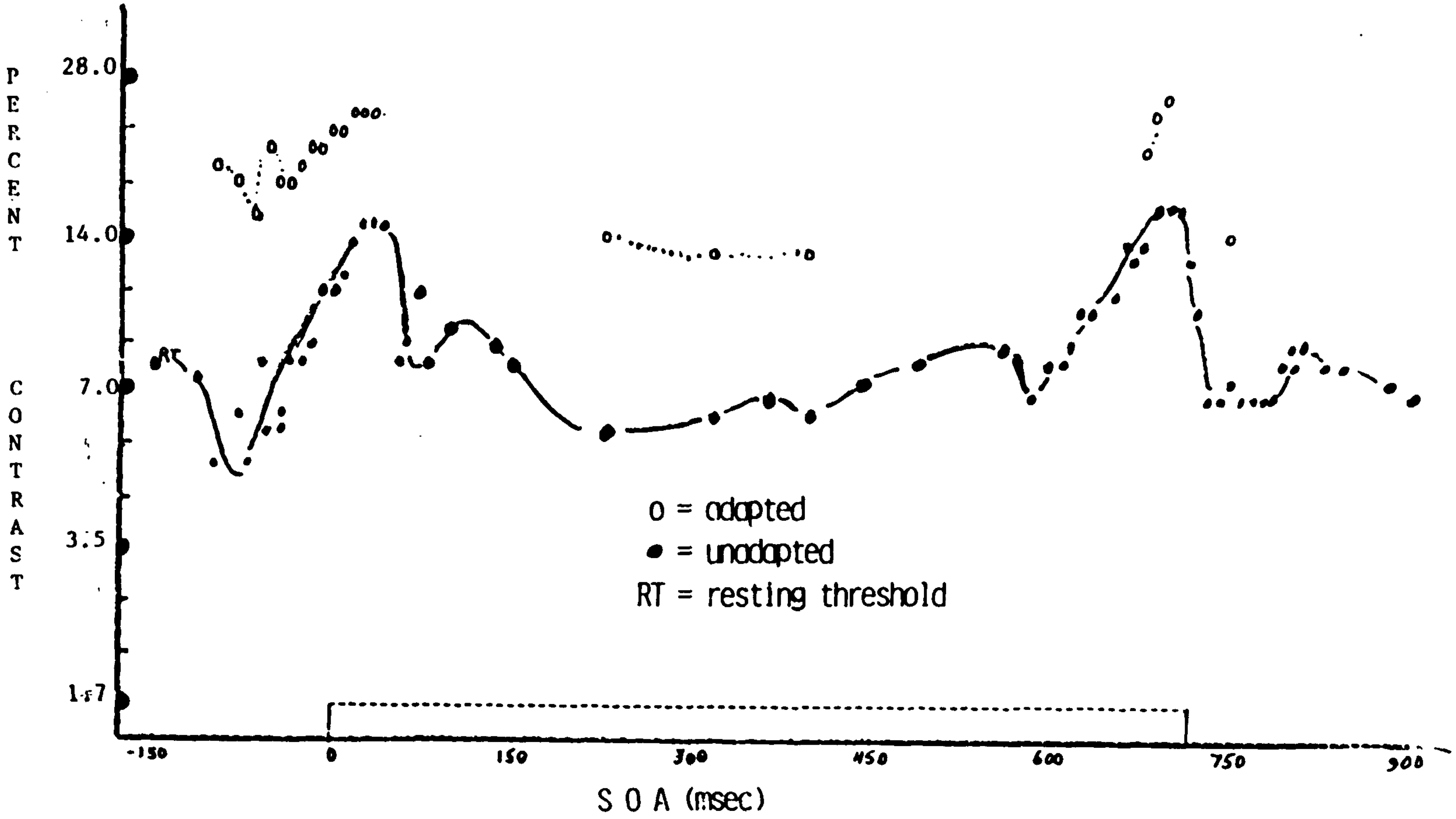


Fig 13D. Ipsilateral transient adaptation: The test and mask were out-of-phase. Adaptatation was at 4.6% contrast. Data is for J.G. at 4 c/d.

b. At the intermediate SOAs, thresholds increased linearly with adapting contrast. (This was determined by averaging thresholds at the plateau of each function and calculating the regression equations as a function of adapting contrast. For J.G. this equation was $y = .0134\ C + .078;\ r = .99$, where Y is the average contrast of the adapted function and C is the adapting contrast).

The lowest adapting contrast had no effect at the intermediate SOAs other than flattening out the scoop shape in the function (Fig. 13A) whereas at the highest adapting contrast, these thresholds also increased by about .2 log.

c. The lowest adapting contrast did not affect the primary peaks. However, as adapting contrast increased, these peaks rose by a SMALLER factor than the intermediate SOAs, being only .15 log higher after 4.6% (the greatest) contrast. A similar effect was reported at .5 c/d.

d. Secondary peaks, however, were elevated by .05 - .15 log units after adaptation to the subthreshold contrast. With higher adaptation contrast, the rise in the secondary peaks was more marked that at the primaries. Additionally, secondary peaks were also shifted closer to the temporal edge, by as much as 66 msec.

Consistent with the .5 c/d data, these findings suggest that S-T inhibition occurs at the secondary peaks and that T-T inhibition occurs at the primaries.

e. Finally, transient adaptation diminished troughs by about .4 log after 4.6% contrast, suggesting that T-T facilitation normally occurred at this SOA. Small temporal shifts of about 17 msec were also observed at the troughs, but the temporal direction of these changes differed, being towards the temporal edge for out-of-phase stimuli and away for in-phase stimuli.

B.Ipsilateral steady adaptation

Since secondary peaks were selectively RAISED and shifted to EARLIER SOAs by TRANSIENT adaptation, the reverse effects, namely, a decrease of these peaks and shift to LATER SOAs would be predicted for steady adaptation. No threshold change would be expected during the intermediate SOAs.

The actual findings were as follows;

1. At .5 c/d, PEAK thresholds did NOT change for either subject. This conclusion was reached after pilot explorations with several adapting contrasts (2.6, 3.5, 4.6 and 6%) and after extensively exploring 4.6% contrast. This contrast was chosen because it appeared to be effective during the pilot study. Unfortunately, this was not apparant later on.

Among the threshold changes which DID occur after ipsilateral steady adaptation was a .1-.15 log threshold decrease for out-of-phase stimuli presented during the intermediate SOAs (J.G.;Fig. 14A &B). This finding is particularly interesting since the steady adapting stimulus was in the same spatial phase as the mask. If phase contingent adapta-

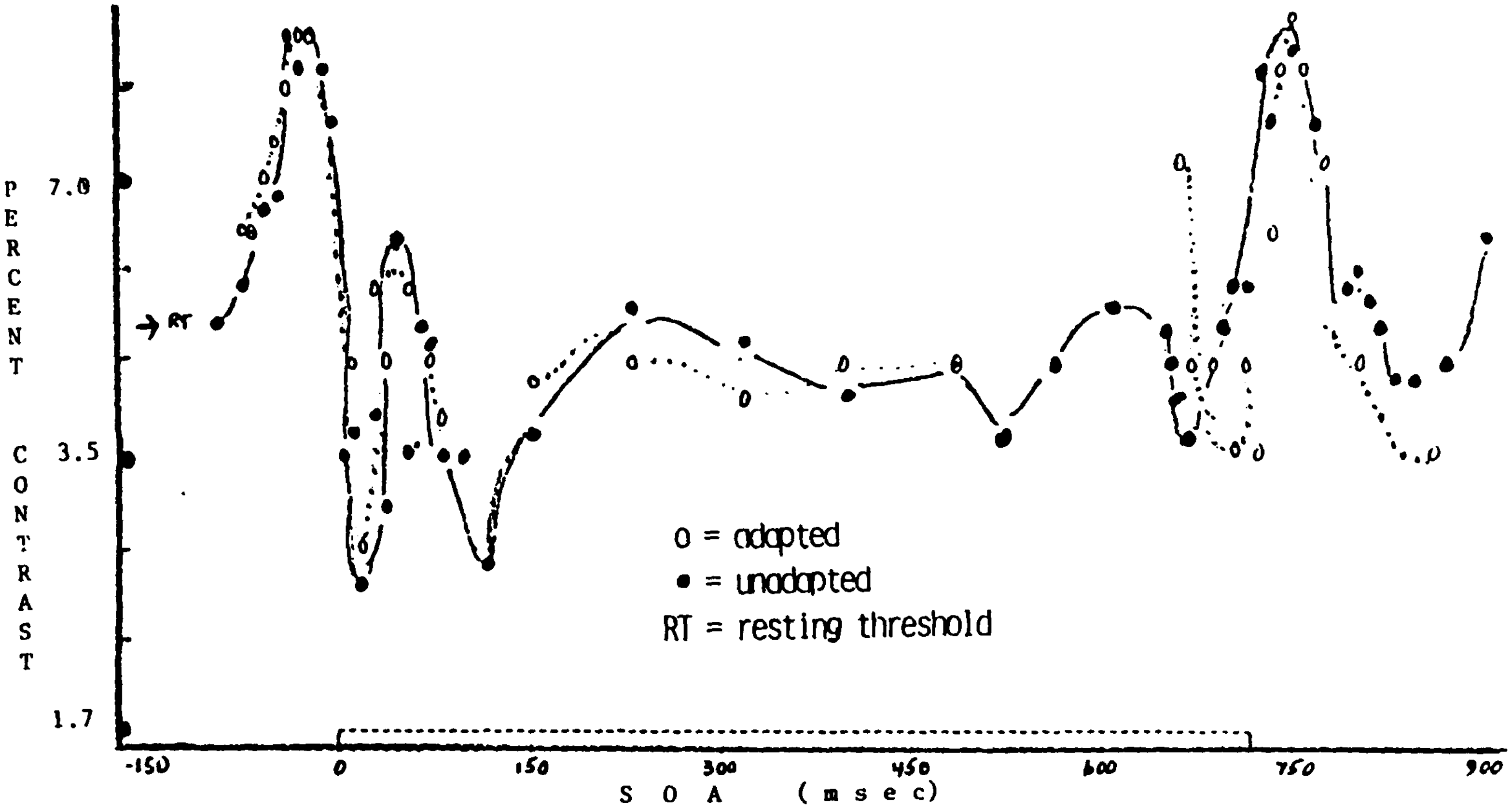


Fig 14A. Ipsilateral steady adaptation. The test and mask were in-phase. Adaptation was at 3.5% contrast. Data is for J.G. at .5 c/d.

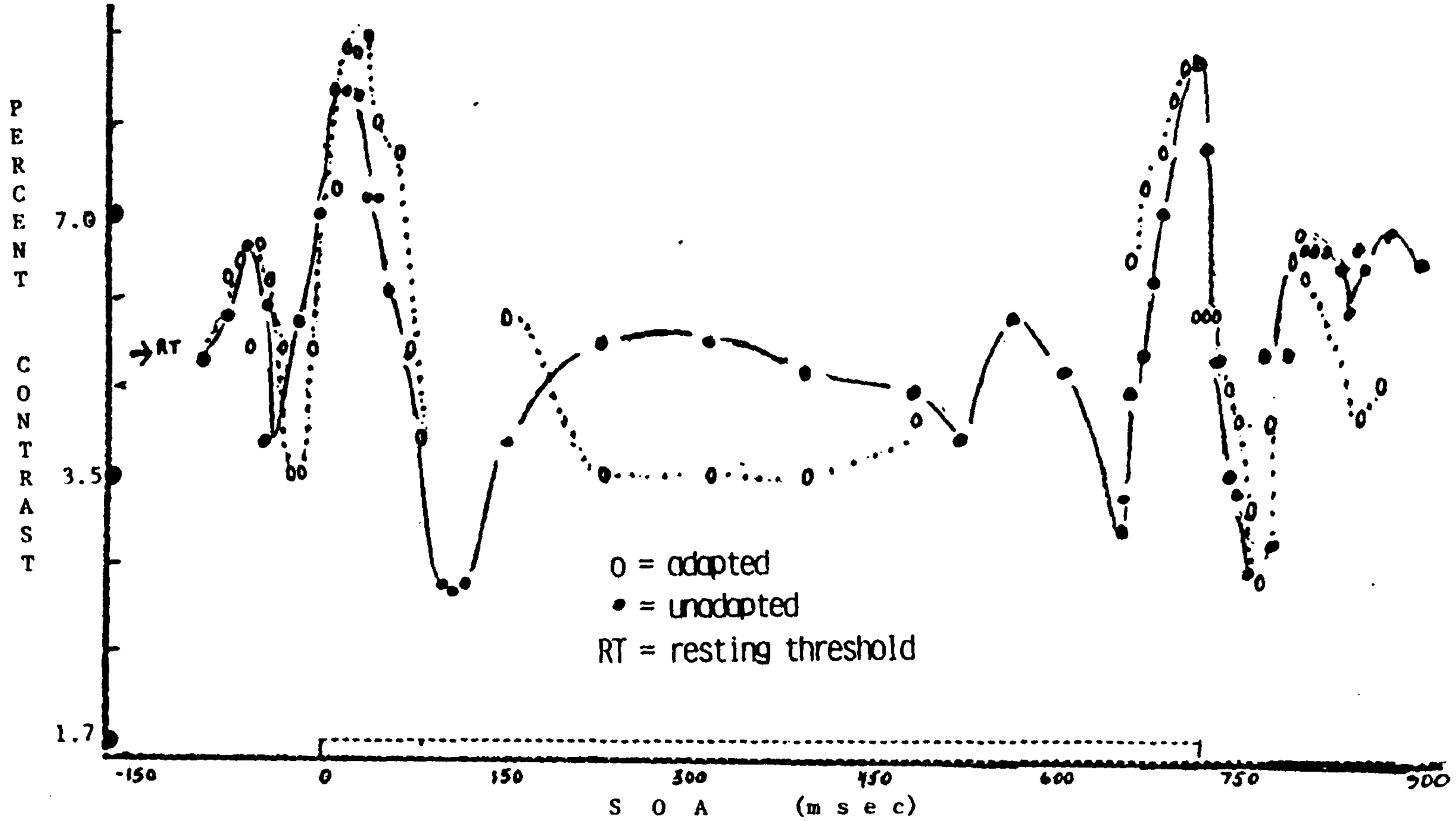


Fig 14B. Ipsilateral steady adaptation. The test and mask were out-of-phase. Adaptation was at 3.5% contrast. Data is for J.G. at .5 c/d.

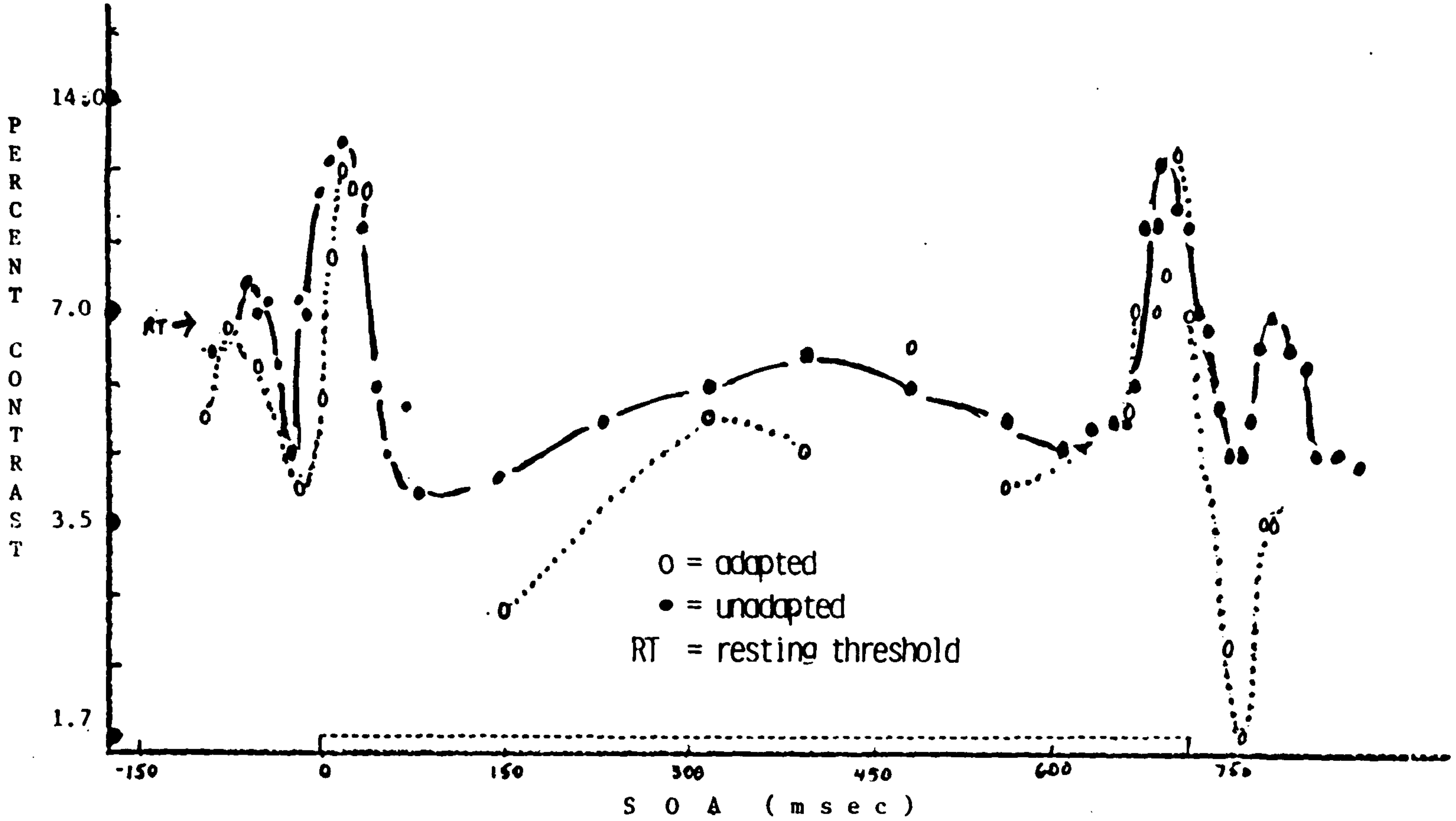


Fig 14C. Ipsilateral steady adaptation. The test and mask were out-of-phase. Adaptation was at 3.8% contrast. Data is for J.C. at .5 c/d.

tion occurs, then some sort of IMPAIRMENT in IN-phase detection might have resulted. Instead, an IMPROVEMENT in OUT-of-phase detection occurred with NO impairment in in-phase detection. There is no apparant exlanation for this finding although, it is possible that phase dependent changes did occur within the sustained system but were not revealed by a stimulus which taps only the performance of the transient system.

Peaks for the second subject, J.C. were also resistent to .5 c/d steady adaptation (at 3.8% contrast; Fig. 14C) The only threshold change noted in this condition was a marked deepening of the out-of-phase troughs by approximately .4 log. As will be described, similar changes occurred at 4 c/d.

2. At 4 c/d, two steady adapting contrasts were explored. The lower of these two, 2.6%, altered thresholds in the the same way as ipsilateral TRANSIENT adaptation (Fig. 15A-B); that is, (1) Primary peaks were slightly (.1 log) elevated. Recall that since nonadapted 4 c/d thresholds tended to fall during the course of the experiment, this suggests that the effect was not only real, but probably greater than that implied by comparison.

(2) Out-of-phase secondary peaks and primary troughs were closer to the temporal edge wherease primary troughs and in-phase secondary peaks were shifted away. The significance of these phase-related changes in timing is not clear,

but are the same as those reported after transient adaptation. Changes in peak and trough timing PER SE, suggests that sustained influences occur during these events.

(3) Thirdly, adapted secondary peaks were slightly elevated in comparison to the nonadapted state.

(4) Finally, 3 out of 4 troughs were deepened by as much as .3 log units. Recall the earlier hypothesis that if troughs are created by mask-sustained facilitation of test-transients, then they should be REDUCED or ELIMINATED by sustained adaptation. On the contrary, thresholds during these SOAs DECREASED. The fact that sustained adaptation had ANY affect upon troughs indicates that the sustained mechanism must operate at these SOAs. However, the route through which it acts to decrease test threshold can not be as straightforward as originally proposed. In a later section, a model will be presented to account for this finding.

Because these threshold changes were so similar to those reported after transient adaptation, it is probable that, at this spatial frequency, the low contrast adaptation stimulus, although STEADY, actually adapted the transient system.

After adaptation at a higher contrast (3.2%), thresholds changed in accordance with earlier predictions for steady adaptation (Fig. 15C-D); that is, secondary peaks DECREASED (by .1-.3 log) with the greatest change occuring at the in-phase onset and out-of-phase offset. The same temporal shifts of the troughs reported after 2.6% adaptation also

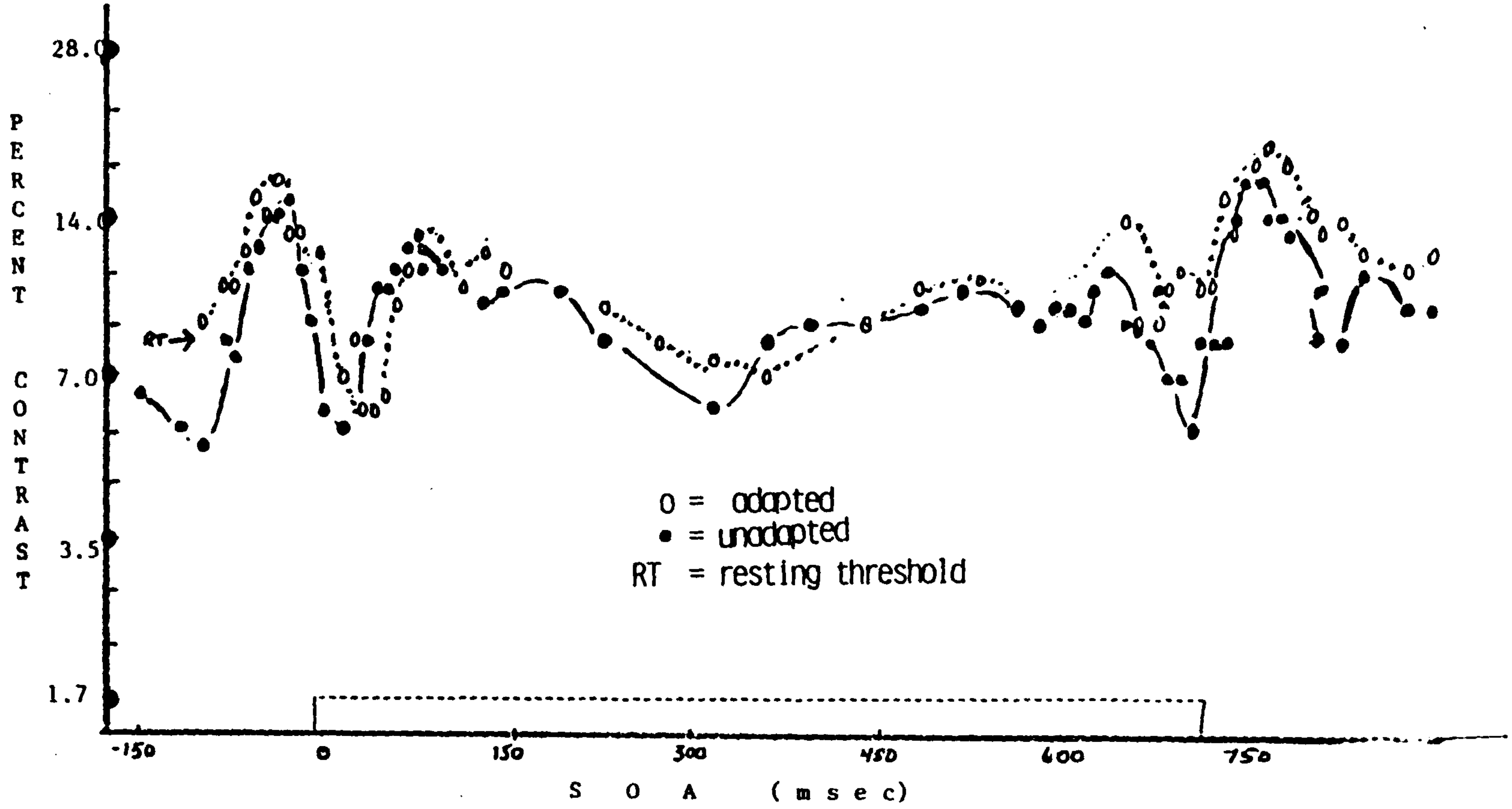


Fig 15A. Ipsilateral steady adaptation. The test and mask were in-phase. Adaptation was at 2.6% contrast. Data is for J.G. at 4 c/d.

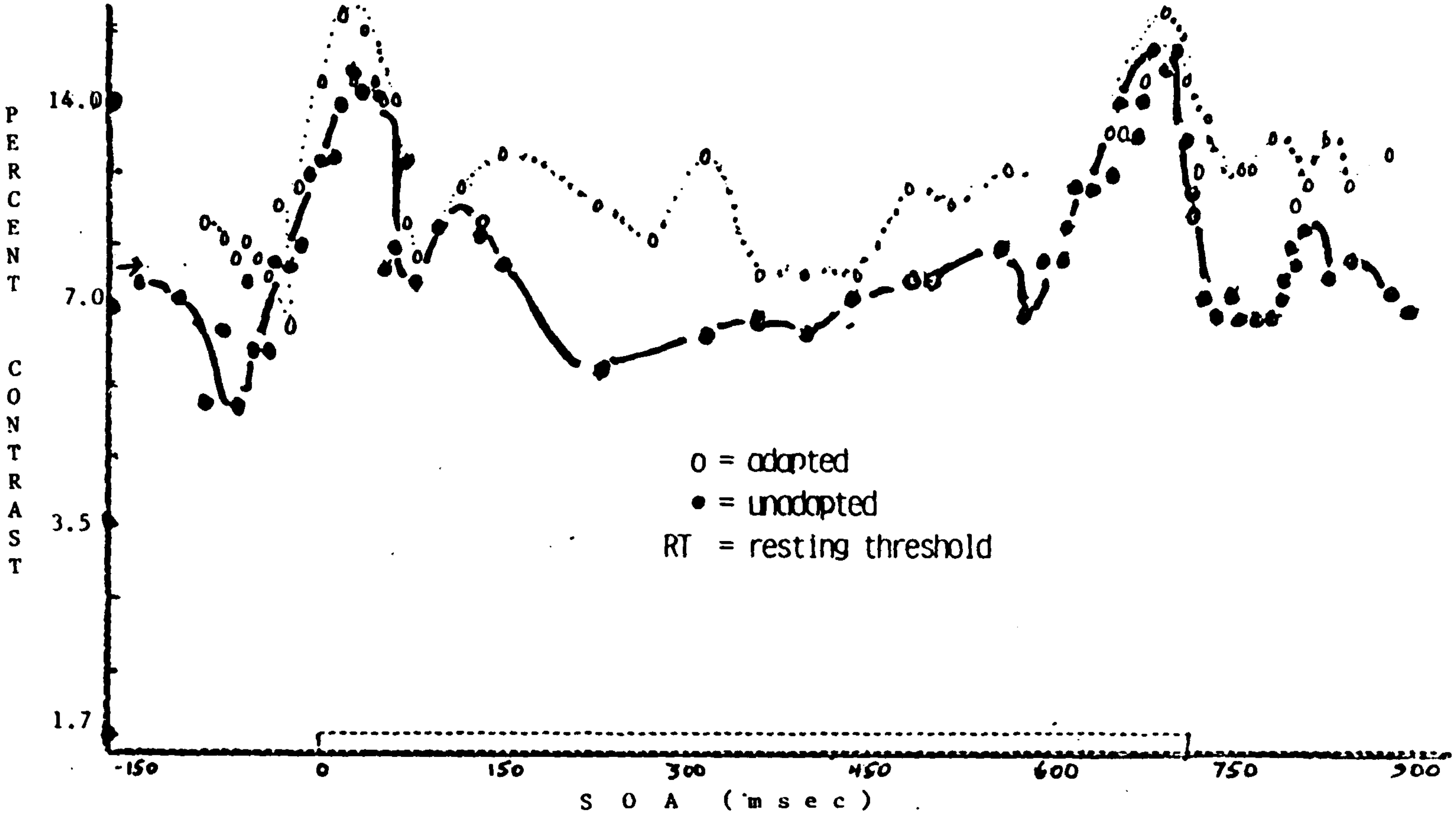


Fig 15B. Ipsilateral steady adaptation. The test and mask were out-of-phase. Adaptation was at 2.6% contrast. Data is for J.G. at 4 c/d.

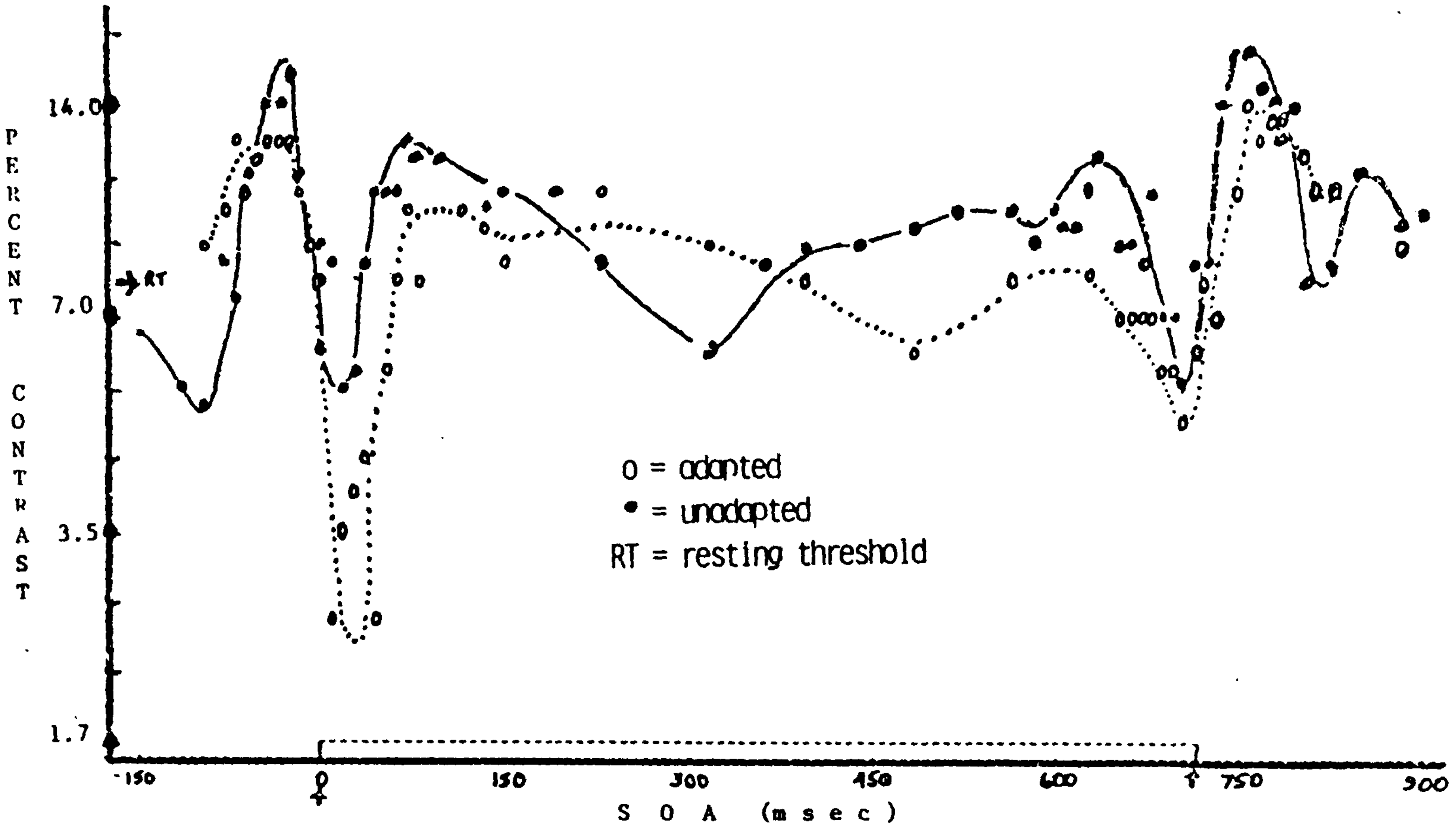


Fig 15C. Ipsilateral steady adaptation. The test and mask were in phase. Adaptation was at 3.2% contrast. Data is for J.G. at 4 c/d.

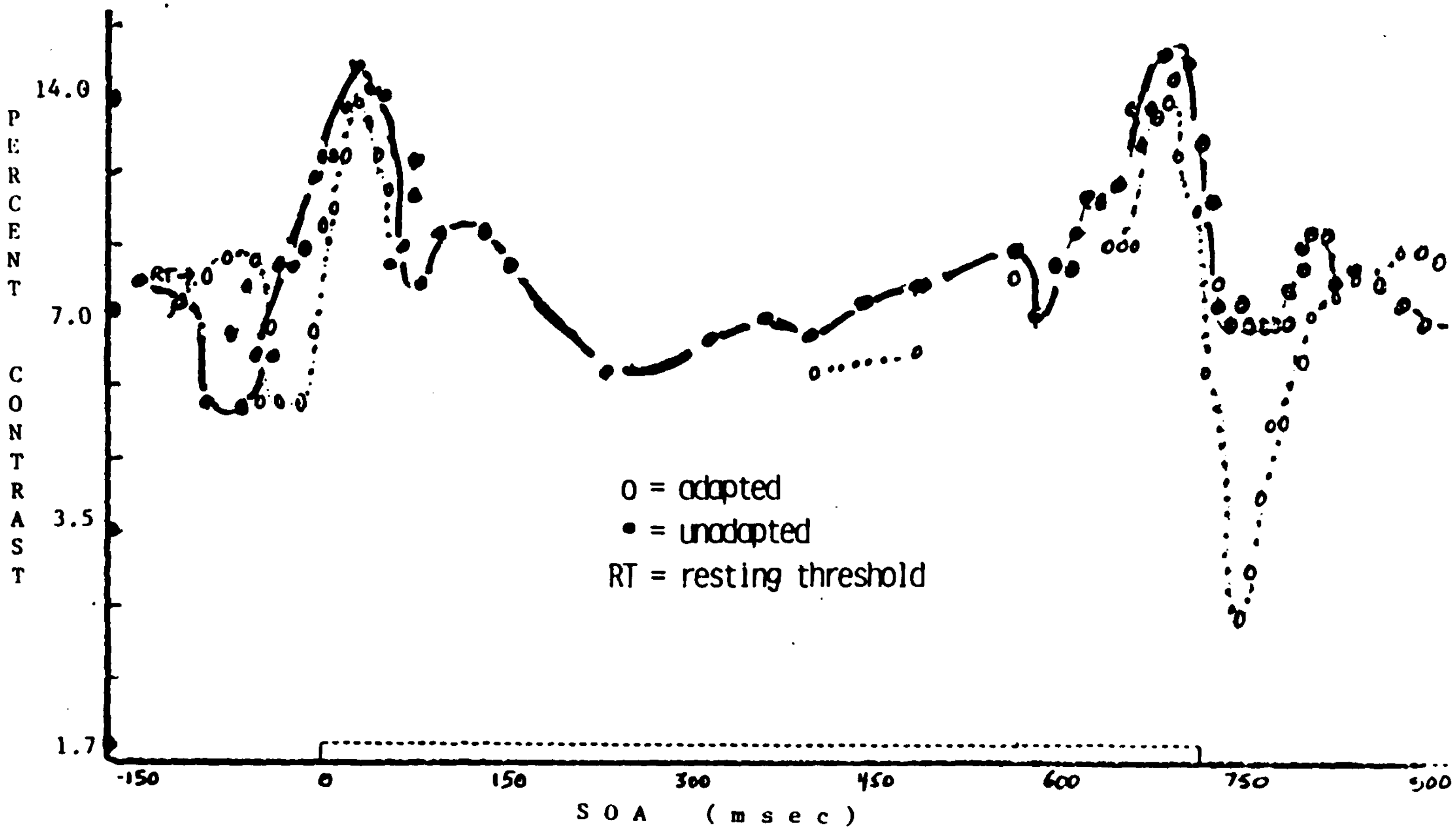


Fig. 15D. Ipsilateral steady adaptation. The test and mask were out-of-phase. Adaptation was at 3.2%. Data is for J.G at 4 c/d.

occurred after 3.2% contrast adaptation.

A threshold DECREASE of the same magnitude as described at the SECONDARY peaks also occurred at the PRIMARY peaks, indicating not only that sustained inhibition of the test transient normally occurs at this time, but that it must be as great as that occurring at the secondary peaks.

Thirdly, the paradoxical deepening in the troughs, noted at .5 c/d, appeared at 4 c/d, being about .1-.3 log in magnitude and greatest during in-phase onset and out-of-phase offset. Shifts in the timing of these troughs were also observed and were the same as those reported for 2.6% steady adaptation.

There were no differences noted in the in- and out-of-phase steady adapted thresholds during the intermediate SOAs.

C. Comparison of ipsilateral and contralateral adaptation

1. Because ipsilateral steady adaptation had no effect at .5 c/d contralateral data were not collected at this spatial frequency so comparisons cannot be made. However, the data at 4 c/d show that STEADY adaptation had the same effects regardless of which eye was adapted (Fig. 16A-D), that is;

a. Threshold INCREASES similar to those associated with transient adaptation following LOW contrast (2.6%) adaptation at 4 c/d (Fig. 16A-B) but

b. a REDUCTION in threshold at the peaks and troughs

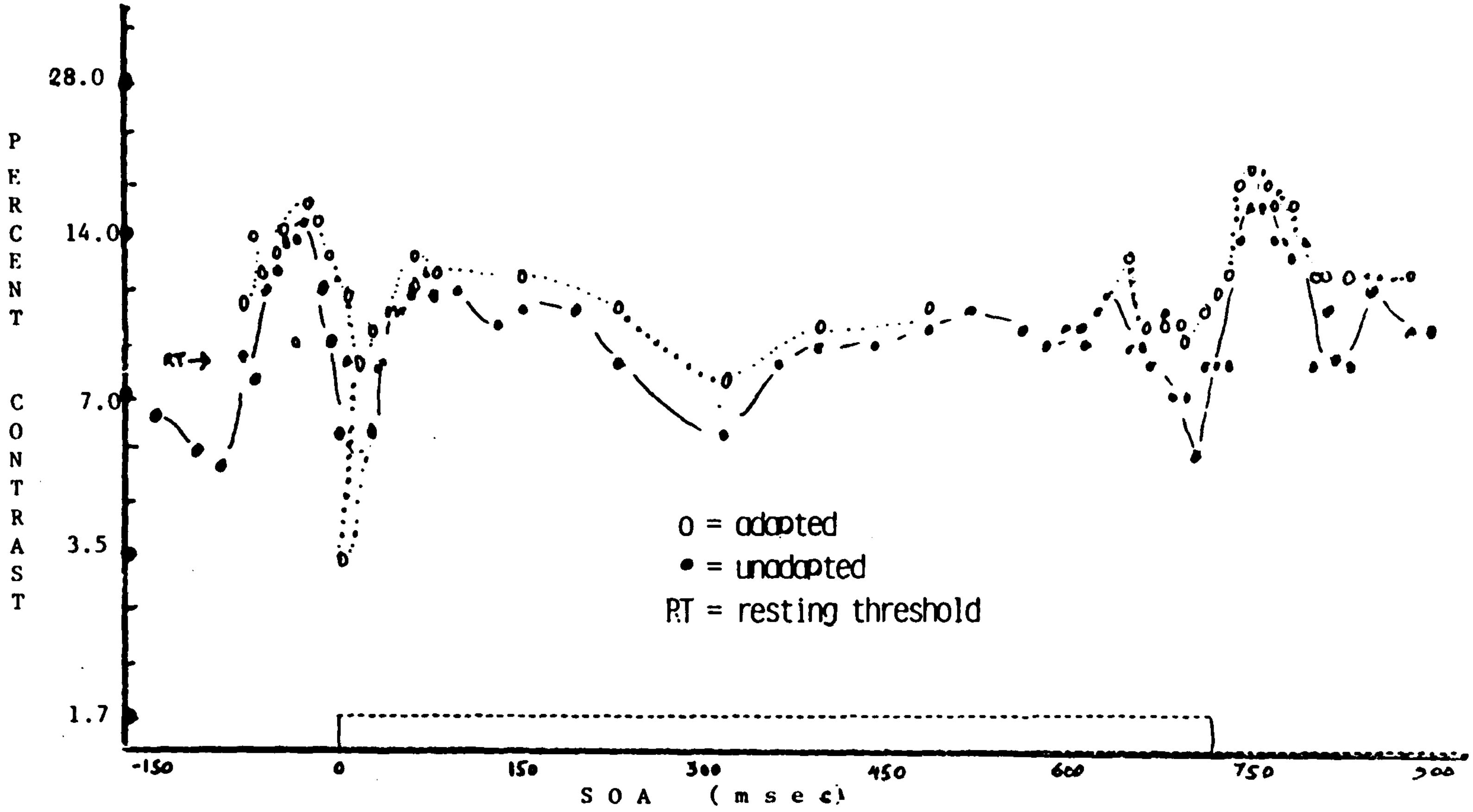


Fig. 16A. Contralateral steady adaptation. The test and mask were in-phase. Adaptation was at 2.6% contrast. Data is for J.G. 4 c/d.

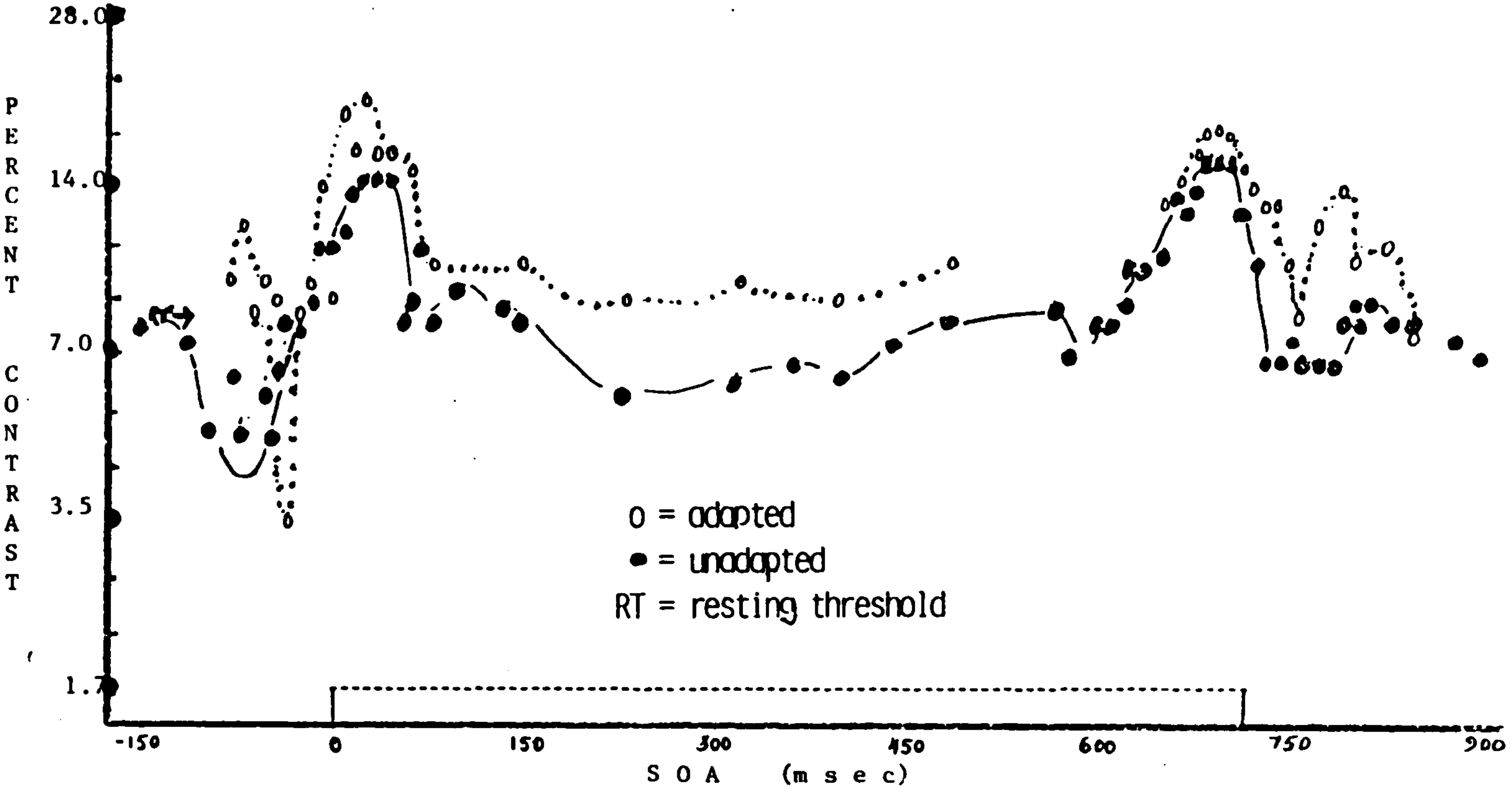


Fig 16B. Contralateral steady adaptation. The test and mask were out-of-phase. Adaptation was at 2.6% contrast. Data is for J.G. at 4 c/d.

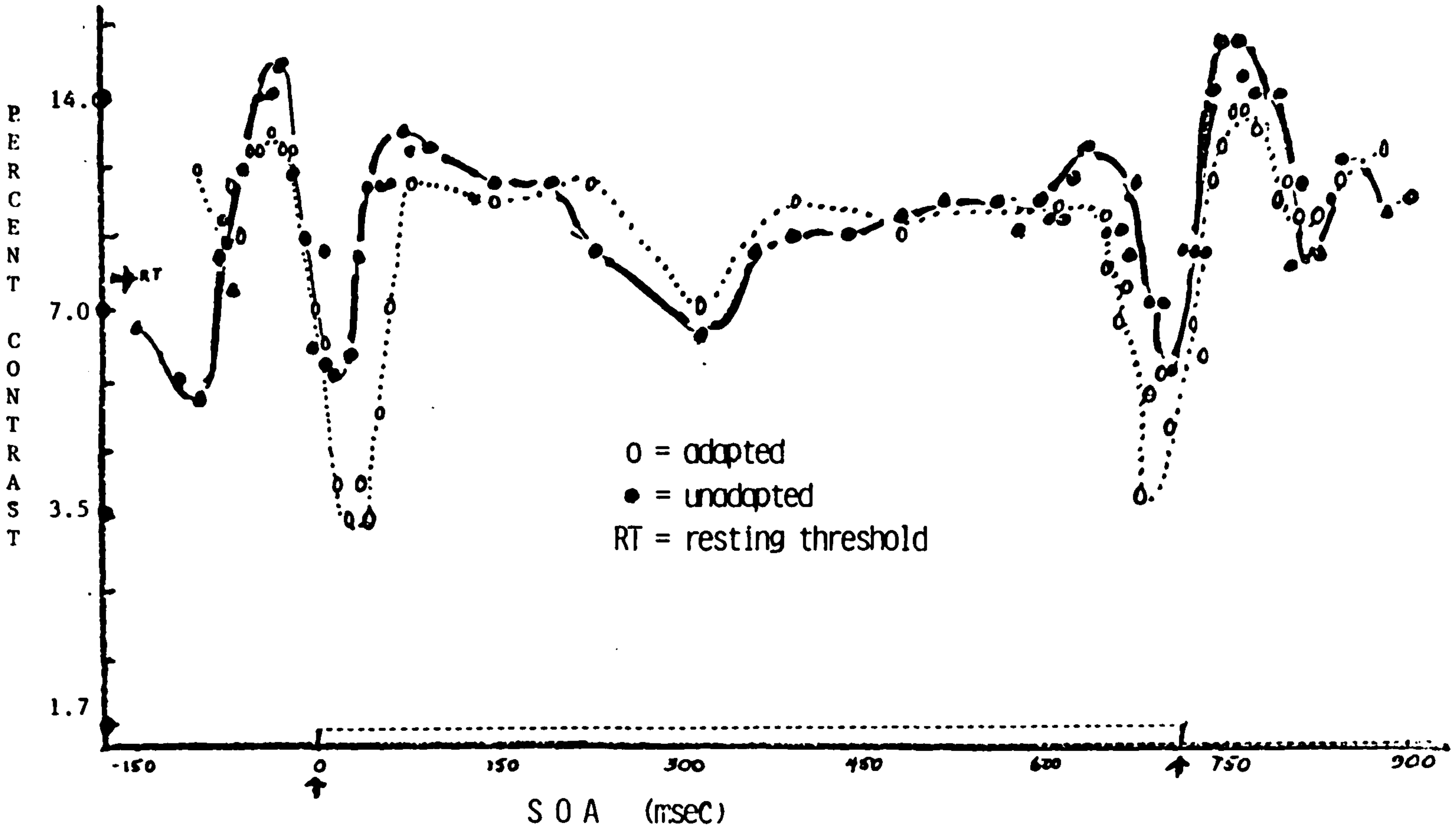


Fig 16C. Contralateral steady adaptation. The test and mask were in phase. Adaptation was at 3.2% contrast. Data is for J.G. at 4 c/d.

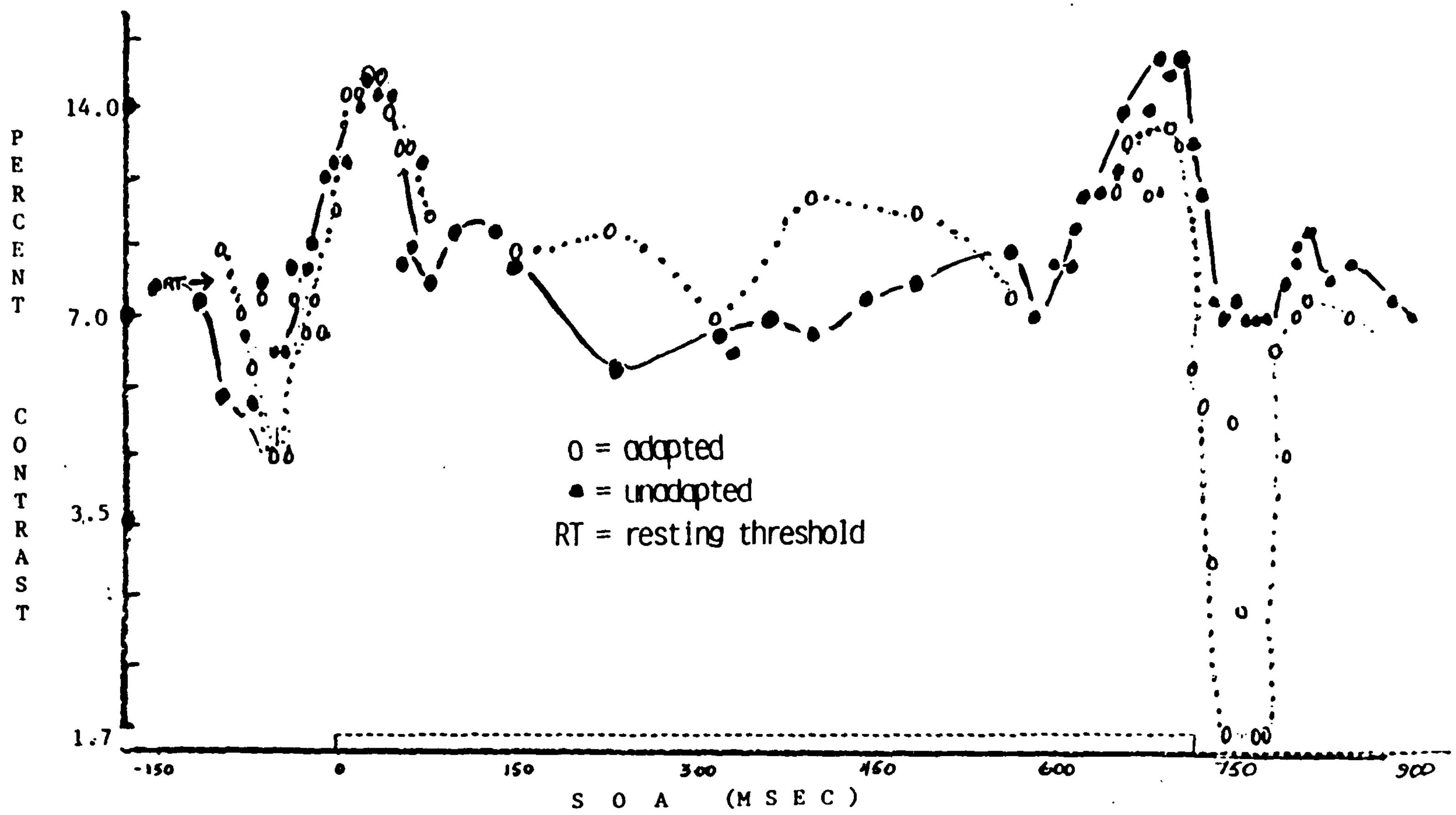


Fig 16D. Contralateral steady adaptation. The test and mask were out-of-phase. Adaptation was at 3.2% contrast. Data is for J.G. at 4 c/d.

after HIGHER contrast (3.2%) adaptation (Fig. 16C-D).

Because the ipsilateral and contralateral results were QUANTITATIVELY and QUALITATIVELY identical, it may be suggested that (1) the sustained cells which are involved in determining thresholds are susceptible to binocular influence and that (2) these cells may be at the LGN (Pasik, personal communication) or more likely, beyond, since binocular interactions do not occur more peripherally. As a point of interest, contralateral steady adaptation altered both onset AND OFFSET peaks, in contrast to the conclusions of several investigators (Baker, 1958; Battersby & Wagman, 1962) that offset masking only occurs monocularly.

2. The effects of TRANSIENT adaptation were NOT the same in both eyes. Specifically, for J.G. at .5 c/d, CONTRALATERAL transient adaptation at .5 c/d, was ineffective at both 3.2 and 4.6% contrasts. Recall that in the ipsilateral condition, these contrasts had pronounced effects. The highest contralateral adapting contrast, 5.4%, raised primary and secondary peaks by the same amount (.15 log; Fig. 17A-B), but did not alter thresholds during the intermediate SOAs.

Finally, changes in the time course of masking (a shift in the secondary peaks to earlier temporal delays), occurred in the contralateral condition, with shifts ranging from 8-48 msec.

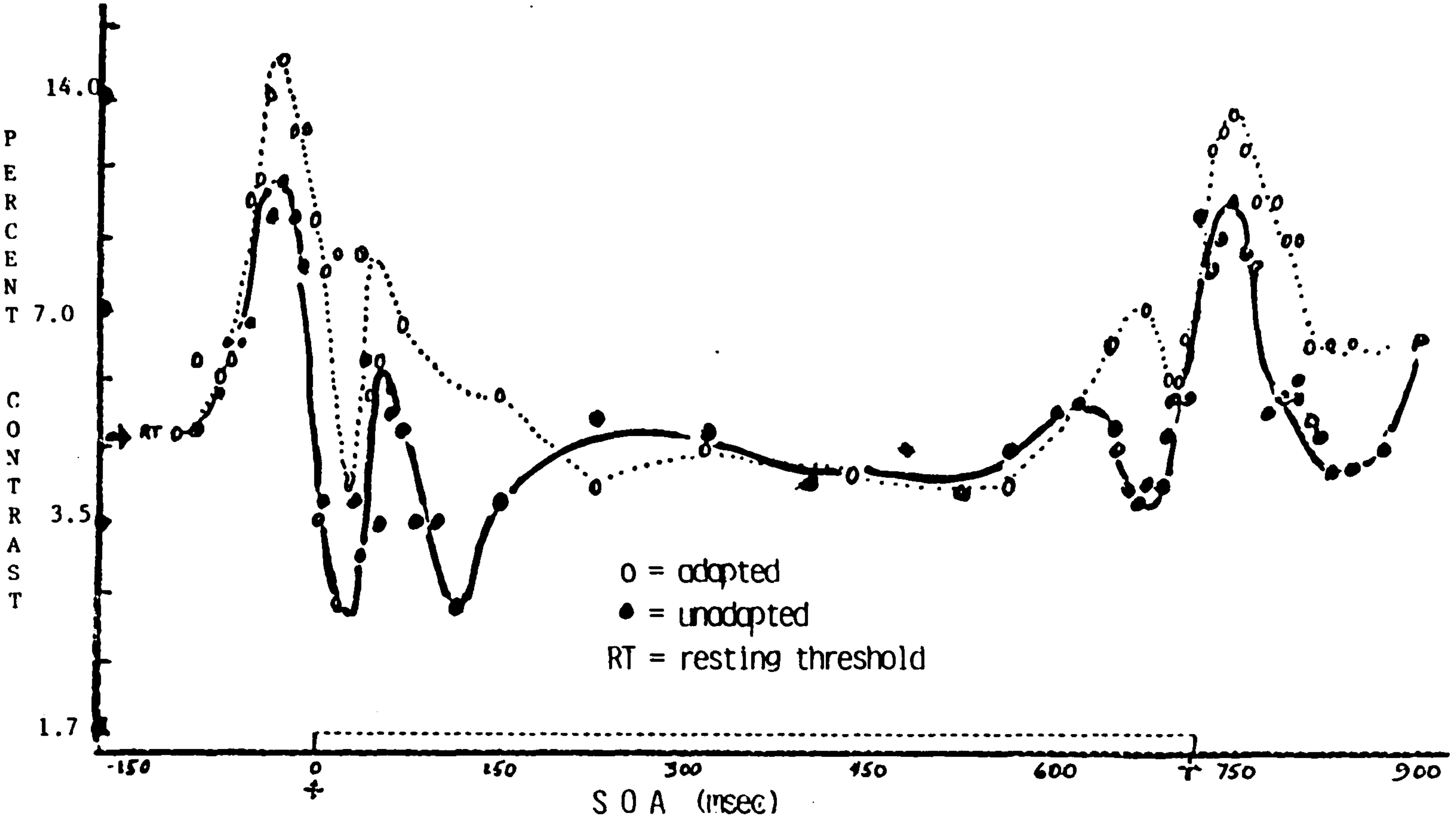


Fig 17A. Contralateral transient adaptation. The test and mask were in-phase. Adaptation was at 5.4% contrast. Data is for J.G. at .5 c/d.

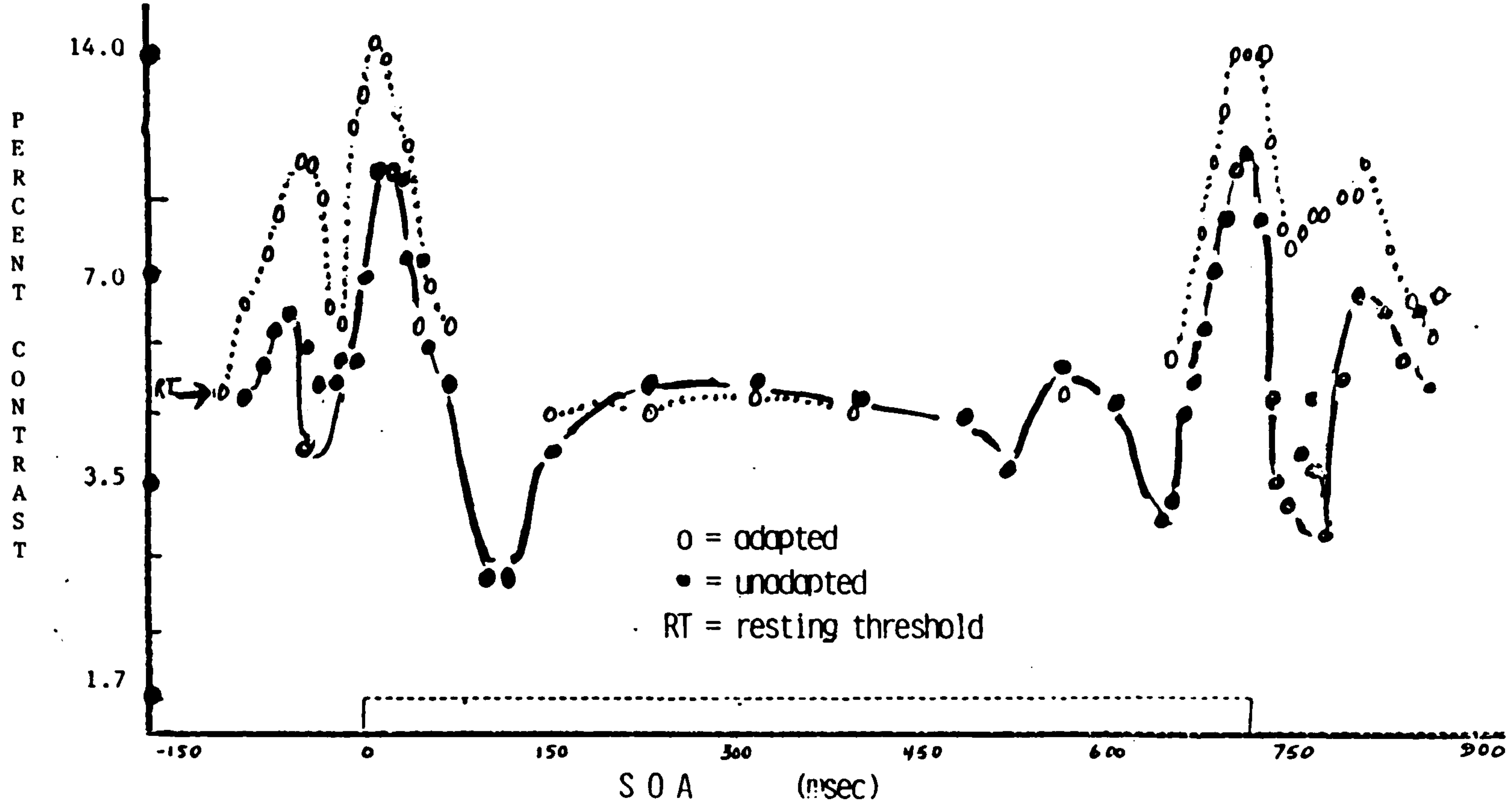


Fig. 17B. Contralateral transient adaptation. The test and mask were out-of-phase. Adaptation was at 5.4% contrast. Data is for J.G. at .5 c/d.

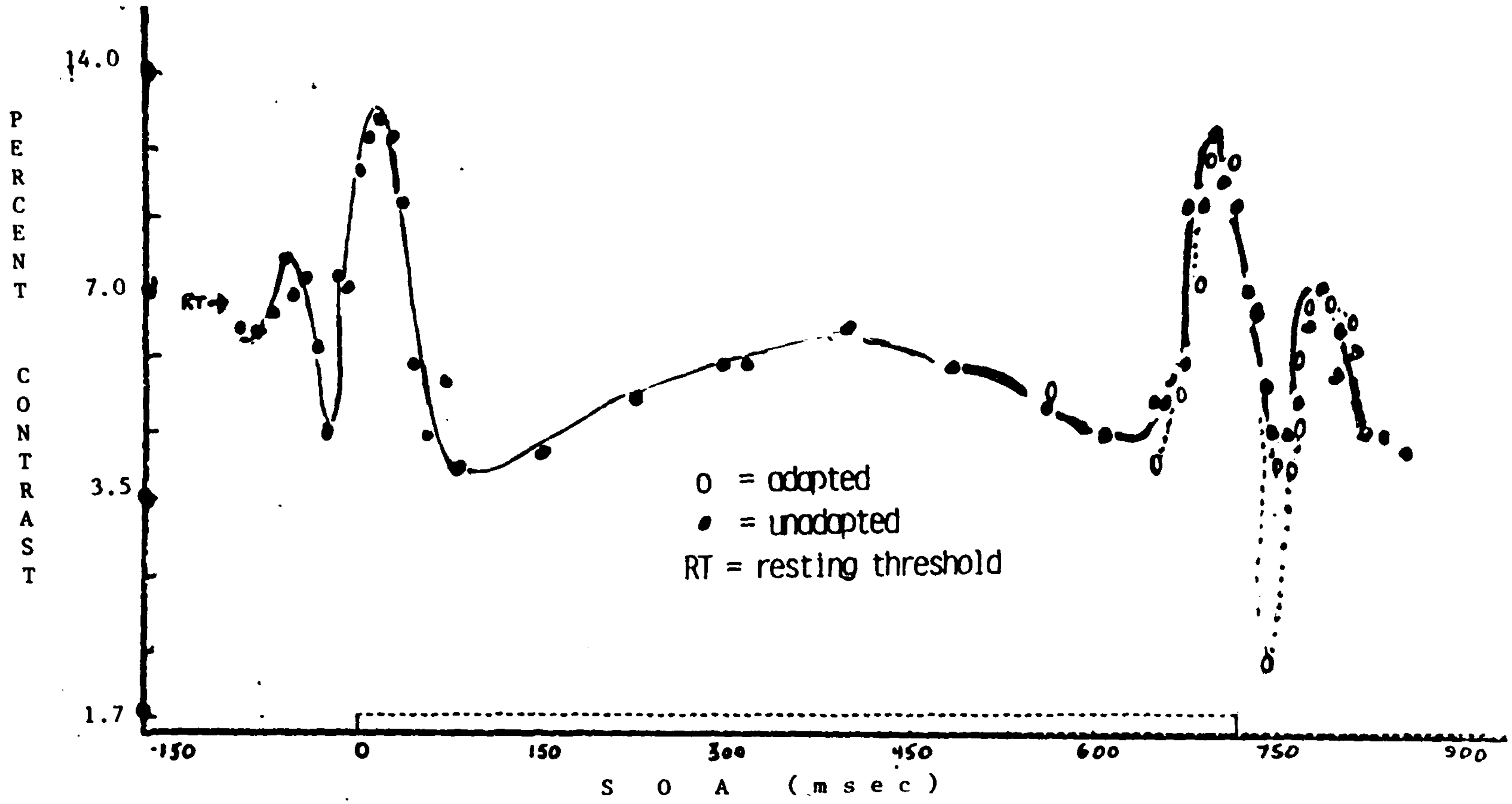


Fig 17C. Contraiateral transient adaptation. The test and mask were out-of-phase. Adaptation was at 3.8% contrast. Data is for J.C. at .5 c/d.

A lower adapting contrast (3.8%) was explored at .5 c/d for J.C. yielding no effect other than a deepening of the trough at the SOA of 33 msec (Fig. 17C). This effect is believed to be real since a similar trough deepening also occurred at 4 c/d (see below).

At 4 c/d adaptation to .96% contrast had no effect upon thresholds. At the higher adapting contrast, 2.6%, there was a small .1 log threshold elevation during the intermediate SOAs in the out-of- phase condition only (Fig. 18C). Furthermore, secondary peaks increased by .1 to .15 log. Finally, there was a marked .2 log increase in facilitation at the troughs in the in-phase condition (Fig. 18B) and a shift in the SOA of these troughs by 20-30 msec. (Fig. 18B-C).

Thus, after contralateral transient adaptation, some threshold changes were similar to those associated with the ipsilateral condition, for example, the shift of the secondary peaks to earlier asynchronies and an increase in primary and secondary peaks. Other changes were not, such as the failure of low contrast contralateral adaptation to have any affect, the failure of any contrast adaptation to reliably alter thresholds during the intermediate SOAs, and finally, the INCREASE in facilitation at some of the troughs after contralateral adaptation, as opposed to the virtual LOSS of facilitation in the ipsilateral condition.

These differences between ipsilateral and contralateral

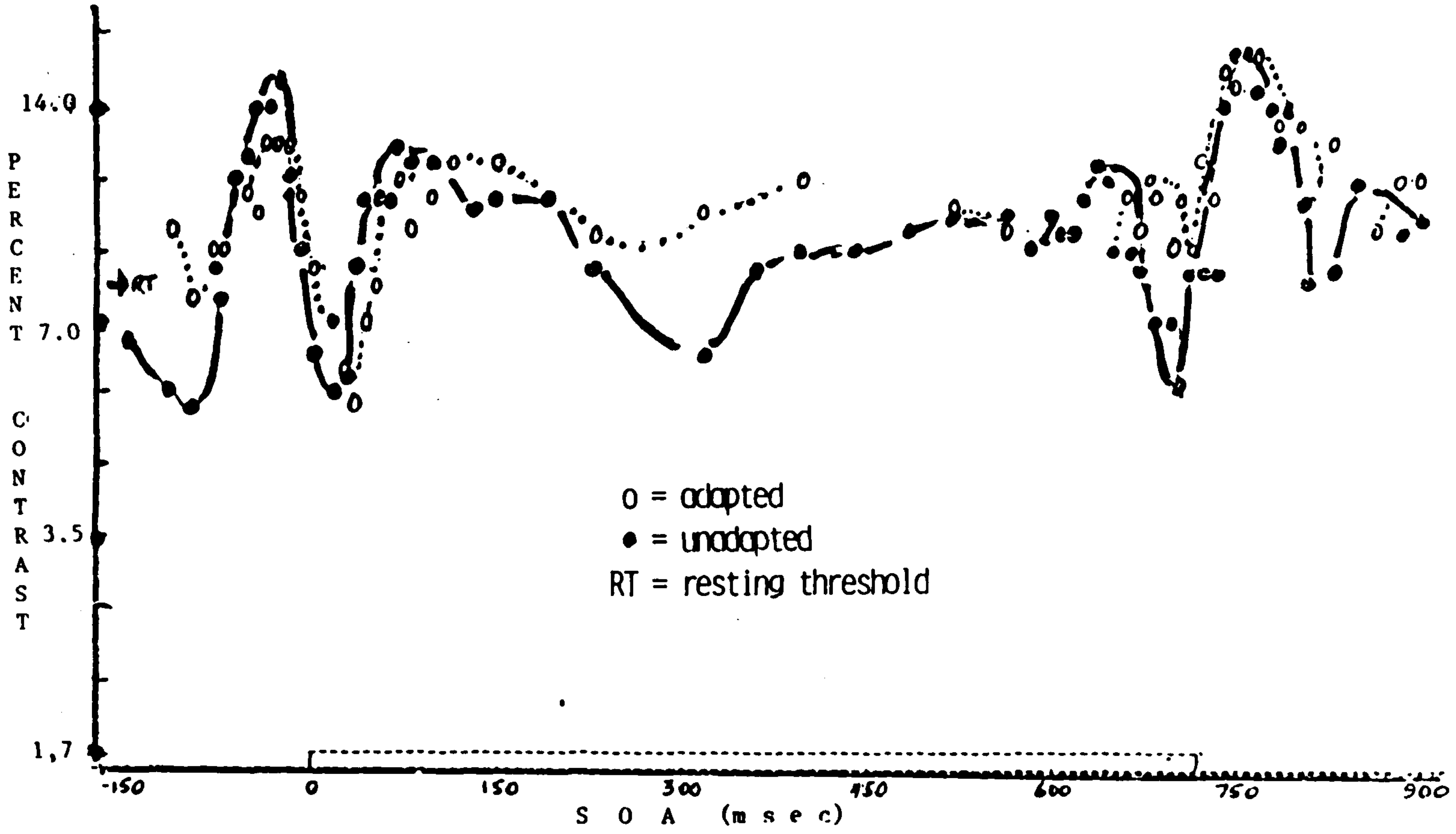


Fig 18A. Contralateral transient adaptation. The test and mask were in-phase. Adaptation was at .96% contrast. Data is for J.G. at 4 c/d.

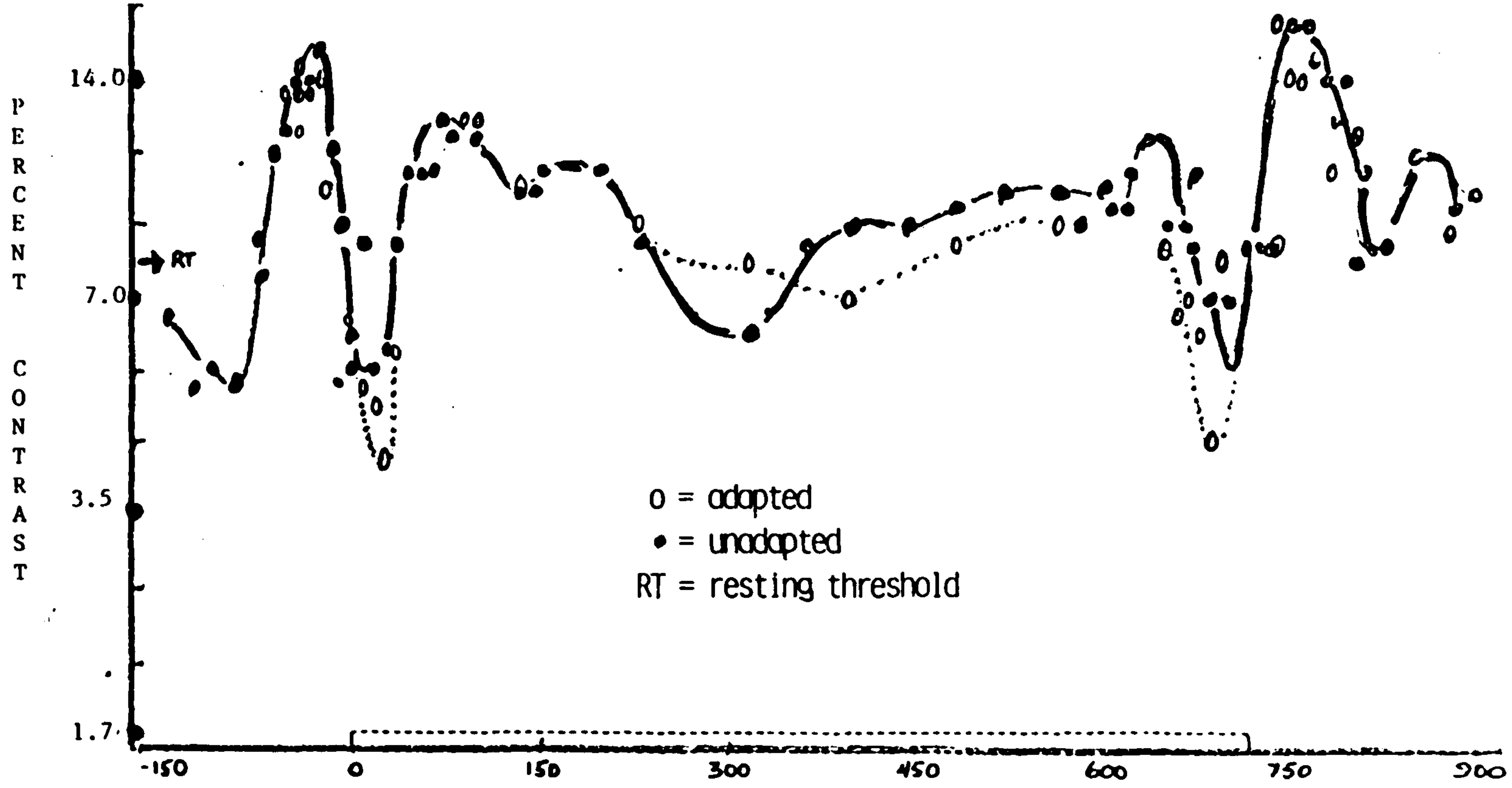


Fig 18B. Contralateral transient adaptation. The test and mask were in-phase. Adaptation was at 2.6% contrast. Data is for J.G. at 4 c/d.

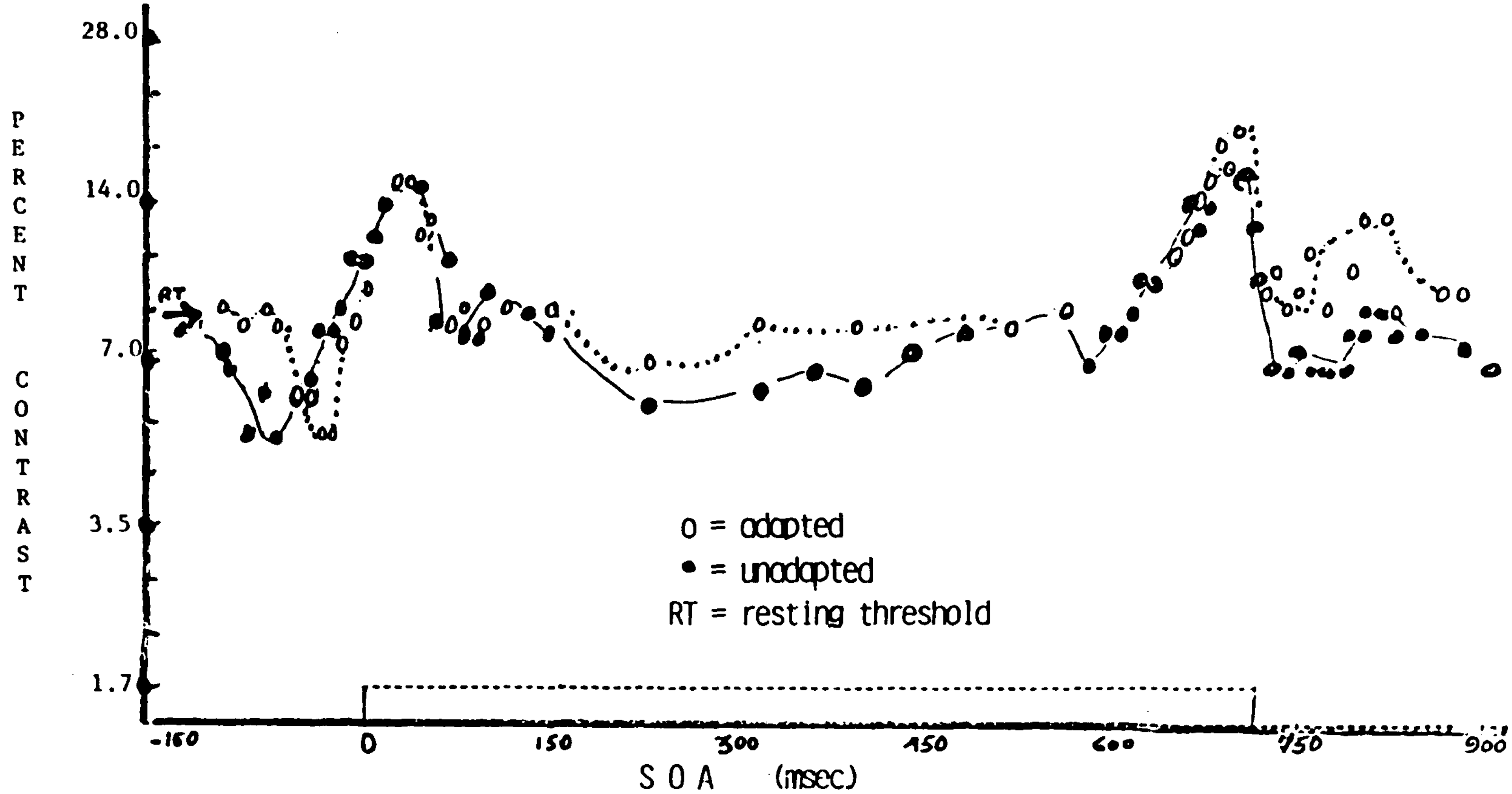


Fig. 18C. Contralateral transient adaptation. The test and mask were out-of-phase. Adaptation was at 2.6% contrast. Data is for J.G. at 4 c/d.

transient conditions suggest either that (1) the site of adaptation is neuroanatomically beyond the site of masking; or that (2) the transient system is monocular and cannot be adapted via the contralateral eye. The data do not allow the verification of either hypothesis. However, the latter argument will be supported and extended in the following section.

IV. Discussion: adaptation data

Although adaptation effects were small, ranging from .1 to .4 log units, certain trends were quite clear. Considering, first the IPSILATERAL data ONLY, the following findings were reported;

TRANSIENT but NOT STEADY adaptation elevated all thresholds, consistent with the interpretation that the detecting mechanism belongs to the transient system. This effect was similar to adding a single-contrast dependent constant to the entire function plus an ADDITIONAL, also contrast-dependent constant, at the temporal delays associated with secondary peaks and troughs. Furthermore, these adapted peaks shifted closer to the temporal edge. According to reasoning presented earlier, both of these findings suggest that S-T interactions occur at the secondary peaks and that T-T interactions occur at the primary peaks and troughs. These interpretations were supported by the findings that steady adaptation DECREASED and temporally shifted the secondary peaks (although this change was not always in the predicted direction). Additionally, steady adaptation decreased the primary peaks and deepened the troughs suggesting that sustained mechanisms also operate at these SOAs. The exaggeration of the troughs after steady adaptation is contrary to predictions made earlier, suggesting that the route of this effect is different than originally proposed. This will be discussed shortly.

An interpretation that two sources of inhibition (mask transient AND mask sustained) contribute to the primary peaks whereas ONLY mask sustained inhibition contributes to the secondary peaks is supported by the greater heights of the primary as opposed to the secondary peaks. Furthermore, at 6 c/d (when the contribution of the transient system is theoretically very small; Tolhurst, 1975b) primary and secondary peaks are the same height, suggesting that at this spatial frequency, T-T inhibition does not occur.

Please note that fatigue and boredom cannot be responsible for threshold elevations after transient adaptation, as an IMPROVEMENT in detection occurred after steady adpatation. Thus, experimental tedium was not the cause of the adaptation effects.

CHAPTER 5

GENERAL DISCUSSION

The current theory of masking presume that test sensitivity is reduced when the fast transient response to the mask temporally overlaps with, and inhibits the slow, sustained response to the test stimulus (Breitmeyer & Ganz, 1976; Weisstein, 1972). It was already mentioned that, although this explanation is theoretically adequate for explaining backwards masking, it does not predict forward masking in which the temporal sequence is such that the mask transient response must subside long before the test sustained response occurs (Kahneman, 1968). With respect to the present data, this theory also fails to explain why the same temporal delays associated with the inhibition of gratings in one spatial phase are also facilitory of the opposite spatial phase, why facilitation occurs at all or why a given spatial phase is forward masked at one side of the temporal edge, (e.g., onset) but backwards masked at the other. In fact, this theory does not predict masking at all since it concerns inhibition of the test SUSTAINED response and, as has already been discussed, the present data are consistent with TRANSIENT mediated detection of the test. Therefore, in order to understand the present findings, the Breitmeyer & Ganz model must be modified.

I. Explanatory model

A. Assumptions

If the following assumptions are made, a model can be constructed which closely predicts the present data.

ASSUMPTION 1: UNITS WITH THE RESPONSE PROPERTIES OF "X" AND "Y" CELLS EXIST IN THE HUMAN AS WELL AS THE PRIMATE VISUAL SYSTEM

It has long been a problem in vision research that human data, derived psychophysically, could not be directly compared with that of animals, derived electrophysiologically. However, recent contrast sensitivity studies in rhesus monkeys have shown functions which correspond so closely to human data (Harwerth, Boltz & Smith, 1980; Miller, Pasik & Pasik, 1980) that it is not unlikely for the underlying physiology to be similar in both species; that is, humans must have X and Y cells such as have been described in the monkey and cat visual systems (De Monasterio, 1978; Enroth-Cugell & Robson, 1966; Schiller, Finlay & Volman, 1976). Since the present model demands some approximation of human transient and sustained neural responses and since human electrophysiological data are lacking, it will be assumed that the response characteristics associated with cat and monkey X cells; long latency, preference for stationary high spatial frequency stimuli underlies the human sustained system, whereas Y characteristics; short latency, preference for brief low spatial frequency stimuli form the basis for the transient response.

If this subdivision is not valid, then attempts to predict the data should be unsuccessful. On the other hand, a close prediction would strengthen the hypothesis that X and Y type cells also exist in the human visual system.

ASSUMPTION 2: BOTH THE LONGER MASK AND THE BRIEF TEST STIMULI ELICIT RESPONSES FROM BOTH THE TRANSIENT AND SUSTAINED SYSTEMS.

It is well established that the OPTIMAL stimulus for a Y cell is brief e.g., the test pattern, whereas longer-lasting stimuli, such as the mask, are preferred by X cells. However, both types of cells also respond to non-preferred stimuli; that is, in the cat retina, Y cells respond to stimuli of long duration (specifically at onset and offset) (Enroth-Cugell & Robson, 1966) whereas X cells give clearcut responses to stimuli as brief as 2 msec (Cleland, Levick & Sanderson, 1973). Thus, it is not unreasonable to presume that both the test and the mask elicit a response from both systems.

ASSUMPTION 3: THE DURATION OF THE NEURAL RESPONSE TO A BRIEF STIMULUS IS LONGER THAN THE STIMULUS ITSELF.

Investigating the response of cat ganglion cells to brief flashes of light, Levick and Zachs (1970) observed that, regardless of stimulus brevity, e.g., 2 msec., there is a minimum response duration of 50-70 msec to a light flash.

Thus, even the 8 msec test grating of this study would be expected to display a relatively long lasting response train.

ASSUMPTION 4: ALL STIMULI USED IN THIS EXPERIMENT, EVEN THE 8 MSEC TEST GRATING, ELICIT NEURAL RESPONSES FROM BOTH THE TRANSIENT AND SUSTAINED SYSTEMS AT BOTH THEIR ONSETS AND OFFSETS.

This assumption relies upon a distinction between detection which is presumed to be mediated by the transient system, and a neural response which may occur within both systems.

The existence of "on" and "off" cells, that is, cells which respond with increased firing to either increases or decreases in luminance (Hartline, 1938; Jacobs, 1965) or contrast (Enroth-Cugell & Robson, 1966) have been identified electrophysiologically. Purely transient cells which respond to stimulus onset and/or offset have already been described as the Y subtype. X cells, although predominantly sustained, also show an exaggerated response at the temporal edges.

In a psychophysical study, Ikeda and Boynton (1965) measured the threshold of a brief 1.2 msec test probe as a function of onset delay with respect to a negative conditioning flash of varying durations. They found that, even when the conditioning flash was extremely brief (2.8 msec), the threshold function showed separate peaks at onset and offset. Thus we might conceive of the neural responses to each stimulus as (a) transient/sustained (T/S) to onset and (2) transient/ sustained (T/S) to offset.

ASSUMPTION 5: DIFFERENT CELL POPULATIONS RESPOND TO GRATING ONSET AND OFFSET

In the present study, offset masking occurred for a longer duration than onset. Psychophysical data show asymmetrical masking effects, with onset peaks being greater than those at offset (Battersby & Wagman, 1959; Crawford, 1947; Makous & Polous, 1980). In an electrophysiologcial study of the gold fish retina, differences were found in the variability of the neural responses to light onset and offset (Levine & Sheffner, 1977). On- and off-center cells can be distinguished electrophysiologically (cat; Enroth-Cugell & Robson, 1966) pharmocologically (Ikeda, 1982; Schiller, 1982) and morphologically (Wassle, 1982).

Thus, for the purpose of a model, we can postulate a cell population "1" to respond to onset and population "2" to offset. Therefore, a stimulus would elicit responses from one population of transient and sustained cells at onset (T1 and S1) and another population (T2 and S2) at offset. Fig. 19 shows the hypothetical neural responses of transient and sustained neurons to the test and mask stimuli. In the case of the long duration mask, all onset responses completely run their courses before the offset activity is initiated. However, when the stimulus is extremely brief, the onset response may commence before the offset response subsides

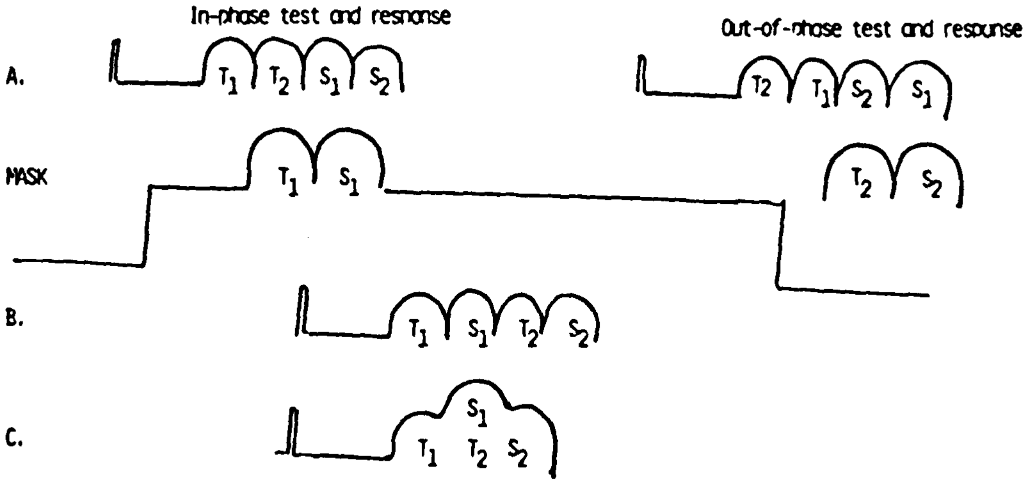


Fig 19. Hypothetical neural responses to the in- and out-of-phase test and mask stimuli. T represents the transient whereas S represents the sustained neural contributions. Different neural subpopulations are distinguished by the numbers 1 and 2 where the 1 population represents cells excited by the onset of an in-phase grating and the offset of one which is out-of-phase. Similarly, 2 indicates a different neural population which is excited by the onset of an out-of-phase grating but by the offset of one which is in phase.

Fig 19A. shows one possible temporal pattern of neural output; that is, when the onset and offset responses of the transient system terminate completly before the sustained response begins.

Fig 19B-C demonstrates other possible response patterns. The liklihood of any specific combination to occur would depend upon the test duration.

and the two will temporally overlap. The sequence of temporal overlap shown in Fig. 19 A represents the hypothesis used in subsequent figures, although several other response configurations (Fig. 19B-C) are possible and probably do occur as the duration of the test stimulus changes. All response distributions predict the same basic masking function.

Finally, all these schemes of interaction assume that, within a given system, onset and offset responses to the same stimulus (e.g., T1 and T2) are either temporally or effectively discrete, that is, any overlap between the trailing edge of the onset response is cancelled by the leading edge of the offset response so that only purely "on" or "off" portions need be represented here.

ASSUMPTION 6. GRATINGS WHICH ARE OPPOSITE IN PHASE EXCITE THE SAME ONSET AND OFFSET MECHANISMS BUT IN THE REVERSE ORDER; that is, both in- and out-of-phase gratings excite "T1 & S1" and "T2 & S2" cell populations. However, the in-phase pattern excites the "T1 & S1" population at ONSET and "T2 & S2" at offset, whereas the out-of-phase grating excites the "T2 & S2" cells at ONSET and "T1 & S1" at offset (Fig. 19 D). The psychophysical basis for this assumption is the common observation that the afterimage of a stimulus tends to be the negative of the image (the 180° phase reversal;De Valois, 1977a). Electophysiological support is derived from the work of Enroth-Cugell (1966) who studied the response of cat ganglion cells to the onsets and offsets of grating stimuli. All cells studied, regardless of whether they were X or Y subtypes, could be classified as being either on- or off-center. On-center cells respond maximally when the brightest portion of the test grating is presented to the center of their receptive fields and give little response (if a Y cell) or none at all (if an X cell) when the stimulus is turned off (Appendix ii). On the other hand, when the grating is shifted 180° so that the dark bar falls on the center of these receptive fields, the response patterns of these cells is reversed and they either respond weakly (if Y subtypes) or fail to respond (if X) to stimulus onset, but give a clear response to OFFSET.

Off-center cells show the reverse behavior. These cells are excited by the onset of a stimulus whose darkest part falls upon the center of their receptive fields or by the offset of the this same stimulus when it is shifted 180° so that the brightest portion illuminated their centers. Thus, the SAME cells which respond to the onset of an in-phase grating also respond to the offset of an out- of-phase grating. Similarly, those cells which respond to the offset of an in-phase grating respond to the onset of one which is out-of-phase. Similar findings have also been reported for higher levels of the visual system (Kratz, Webb & Sherman, 1978; So & Shapley, 1979). (Note: For my model, it is an important requirement that sustained, as well as transient, cells have phase specific responses. This requirement is in distinction to the previously mentioned postulation that phase detection in psychophysical studies seems to be a function of transient cells or low spatial frequency stimuli. However, it is well known that sustained cells are more phase specific than transient cells in that they will not respond at all to gratings shifted 90° from optimal placement. Such "null positions", do not exist for Y cells (Enroth-Cugell & Robson, 1966). Additionally, the adaptation effects found in this study, do not suggest that either system alone is responsible for phase encoding since it was shown that the phase dependent timing of the in- and out-of-phase functions could not be eliminated.

The hypothetical responses to in- and out-of-phase test stimuli are shown in Fig. 19 A. Notice that the magnitudes of these responses are the same for both phases in accordance with the finding that cells respond with equal vigor regardless of whether the stimulus is in-phase onset or out-of-phase offset (Enroth- Cugell & Robson, 1966, So & Shapley, 1979).

The above six assumptions deal with the descriptive aspects of the model; that is, they describe the types of cells which respond to the test and the mask as well as the temporal characteristics of these responses. All of these assumptions are implicit in Fig. 19 A-B. The time course of the neural responses in the present model were based on data by Enroth-Cugell & Robson (1966) and Cleland, Levick & Sanderson (1973) whose transient and sustained stimuli have similar temporal characteristics to the test and mask used in the present study. These figures suggest that the duration of the neural response to the longer lasting stimulus is about twice that of the shorter one. For this reason, BOTH the onset and offset responses to the test are shown to require the same time span as only the onset OR the offset response to the mask.

Finally, the neural responses of a transient cell are shown to terminate prior to the initiation of the sustained. The data of Cleland, Levick and Sanderson (1973) show this to be true as early as the retinal ganglion level in cats (Appendix iii). Since the shorter latency and rapid response characteristics of the transient system (Cleland, Dubin & Levick, 1971; Hoffman, Stone & Sherman, 1972; Laak & Thjssen, 1978) occurred at every level of the visual system from LGN to cortex (Ikeda & Wright, 1974) it would be expected that this delay between the transient and sustained systems be preserved if not also amplified at higher levels.

A further assumption of these schemes (Fig. 19) is that the gross responses to the test and mask closely resemble those of specific single units when, in actuality, the neural responses to the test and mask are diverse and are generated by cells, some of which are non-optimally tuned to the stimuli and therefore, have different response characteristics. For example, the degree to which a Y cell is either "on" or "off" (as opposed to "on-off") depends upon the placement of the stimulus in its receptive field (Enroth-Cugell & Robson, 1966). Optimal stimulus placement results in a vigorous response at EITHER onset or offset, whereas shifts from this position yield a weaker output characterized by peaks at BOTH onset and offset. Non-optimal responses, however, are not included in the model since, presumably, because they are always present in the CNS and probably act as "noise" (Green & Swets, 1966).

Finally, implicit in Figure 19 is the presumption that the predominant portion of both the transient and sustained responses occur at onset and offset despite the fact that sustained responses, by definition, are maintained thoughout stimulus presentation (Enroth-Cugell & Robson, 1966). This is justified by the finding that, all cells, regardless of whether they are transient or sustained, respond most vigorously at stimulus onset or offset and then taper off in output during the continued presentation (or after the termination) of the stimulus (Hochstein & Shaply, 1976; Kratz, Webb & Sherman, 1978, Cleland, Dubin & Levic, 1971; Enroth-Cugell & Robson, 1966). Furthermore, it is reported that responses of BOTH X and Y cells tend to become more transient as one goes from retina to cortex (Lennie, 1980) and also as light adaptation is increased (Enroth-Cugell & Shapley, 1973). In the present study, luminance levels were in the mesopic range, which means that sustained cells should show more transient-like behavior than they do under scotopic testing conditions. Finally, the data themselves show a great reduction (4 c/d) or absence of (.5 c/d) test-mask interaction at long durations (e.g., the intermediate SOAs) from the temporal edge.

B. The DYNAMIC aspects of the model concern the interactions between the test and the mask. Here further assumptions are made,

(1) If the neural response to the test stimulus is temporally discrete from that of the mask, there can be no interaction between the two and test thresholds will not change.

(2) However, when these responses temporally coincide, some type of interaction e.g., facilitation, inhibition or both, occurs. Finally,

(3) the nature of the interaction (whether excitatory or inhibitory) depends upon the types of cell populations involved;

1. When the response distributions of like cell populations (e.g., T1-T1, S1-S1, T2-T2 or S2-S2) overlap, the interactions are facilatory.This situation would be comparable to temporal summation within a common neural pool (Sherrington, 1906).

2. If the cells are unlike but from the same system

(e.g., T1-T2, T2-T1, S1-S2, S2-S1), their interactions are inhibitory. This situation would be comparable to reciprocal inhibition between on- and off-center cells and has been reported by Singer & Creutzfield (1970) and would be suggested psychophyscially by the perception of 180° phase reversed after-images following the prolonged viewing of a given spatial phase (De Valois, 1977a).

Since only transient activity can be monitored by the test stimulus, the effects of S-S interactions will not be revealed in the present study.

3. Interaction also occurs ACROSS systems, as has been suggested by both psychophysical (Bodis-Wollner & Hendley, 1979) and electrophysiological data (Singer & Bedworth, 1962). Based upon the time time course of masking obtained in the onset in-phase data, it was hypothesized that the following interactions are inhibitory; S1-T1 and S2-T2, whereas the remaining possibilities, S1-T2 and S2-T1, are facilatory. These proposed interactions were then used to predict the out-of-phase onset functions and the offset data for both spatial phases.

To simplify this explanation, let us, for the moment, ignore the interactions with the sustained system and consider masking as if only the transient system was involved. Fig. 20 depicts the transient response to the test and mask in the temporal relationships which would result in peaks or troughs. Notice the differing SOAs associated with the in-

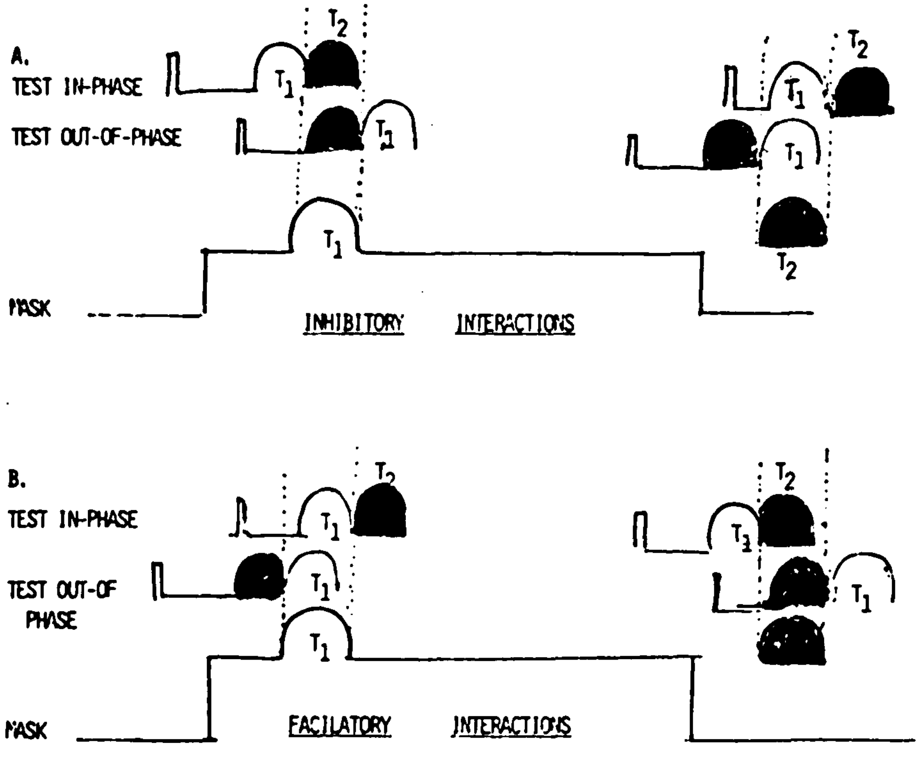


Fig 20. Hypothetical neural interactions and SOAs predicted to result in (A) inhibition or (B) facilitation of the in- and out-of-phase test stimuli. T_1 neural responses are white whereas T_2 neural responses are black. The time course of the neural response to mask onset and offset is bordered on each side by dotted lines. When the neural response to the test falls within the time domain of these dotted lines, it will interact with that of the mask. Unlike-colors (T_1,T_2) interact inhibitorally whereas like-colors (T_1-T_1 ,T_2-T_2) will be facilitory. Notice that the in- and out-of-phase test stimuli must commence at different asynchronies in order to have the same type of interactions. These predicted SOAs correspond to the empirical peaks and troughs.

and out-of-phase interactions. These correspond to the empirically obtained SOAs as well as those deduced to occur based upon the results of transient adaptation.

Additionally, notice that this model predicts the same magnitude of neural interaction regardless of whether the test is presented in conjunction with mask onset or offset.

Fig. 21 shows the predicted interactions when BOTH the transient and sustained systems are considered. Notice that T-S interactions are predicted to occur at the primary peaks and troughs as well as the secondary. This conclusion was also drawn from the adaptation data. (S-S interactions also occur at these SOAs, although, again, these effects are presumably not measurable).

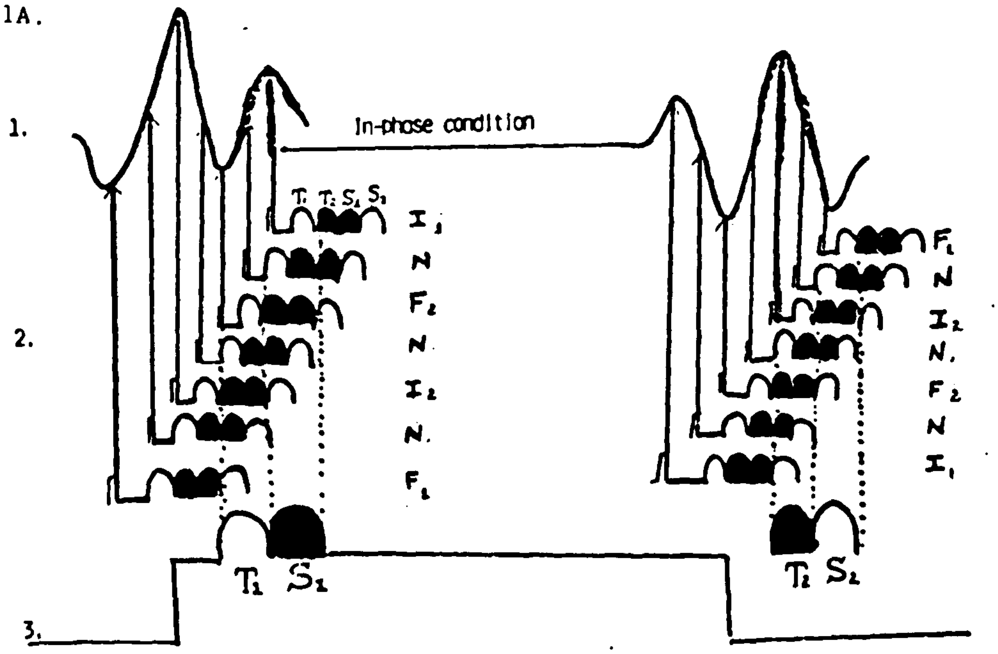
Consistent with the adaptation data, the model predicts that transient and sustained interactions occur at the secondary peaks and troughs. Secondary trough SOAs, unfortunately, were not sufficiently sampled to substantiate this prediction.

Notice that the model predicts a threshold change when a transient response there is interaction with a transient response regardless of whether it is elicited by the test or the mask; a logical expectation since these stimuli are identical. As the resemblance between the test and mask decreases, the characteristics of the test are probably the more important determinants of threshold. When test and mask configurations differ, the magnitude of masking

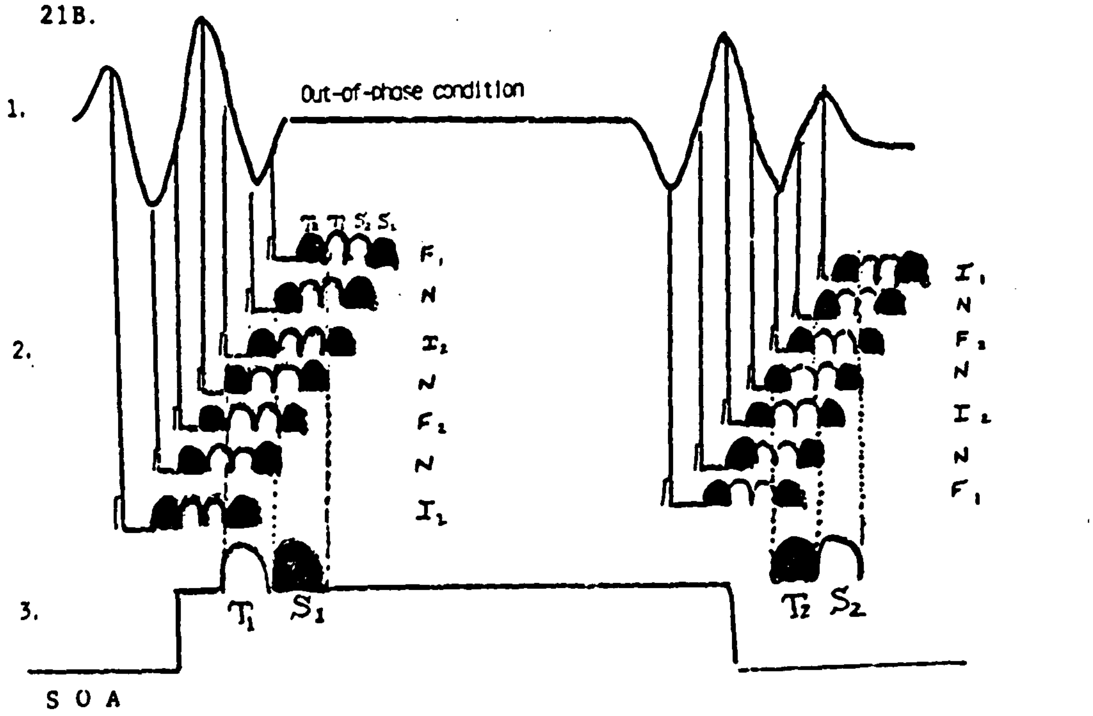
Fig 21. Predicted threshold changes when both transient and sustained neural responses are considered. T_1 and S_2 responses are white; T_2 and S_1 responses are black. The portion of the figure labled (2) demonstrates the neural response to the test as it is temporally shifted with respect to that of the mask (3). Test-mask interactions occur between responses which fall within the dotted lines. The interactions of like-colors (T_1-T_1; T_2-T_2; T_1-S_2; T_2-S_1) are facilatory (F) whereas the interactions of unlike-colors (T_1-T_2; T_1-S_1; T_2-S_2) are inhibitory (I). The simultaneous combination of like-like and like-unlike responses are neutral (N). The subscripts to the right of the letters I, F and N indicate the number of nerual interactions involved in the prediction; for example, I_1 indicates S-T interactions whereas I_2 indicates BOTH S-T and T-T interactions. The solid lines extending upward from the test signal to (1) show the SOAs at which these threshold changes are expected.

Fig 21A predicts the in-phase threshold function.

21A.


1.
In-phase condition
T1 T2 S2 S1
I1
N
F2
N
I2
N
F1
2.
T1 S1
F1
N
I2
N
F2
N
I1
T2 S2
3.

21B.

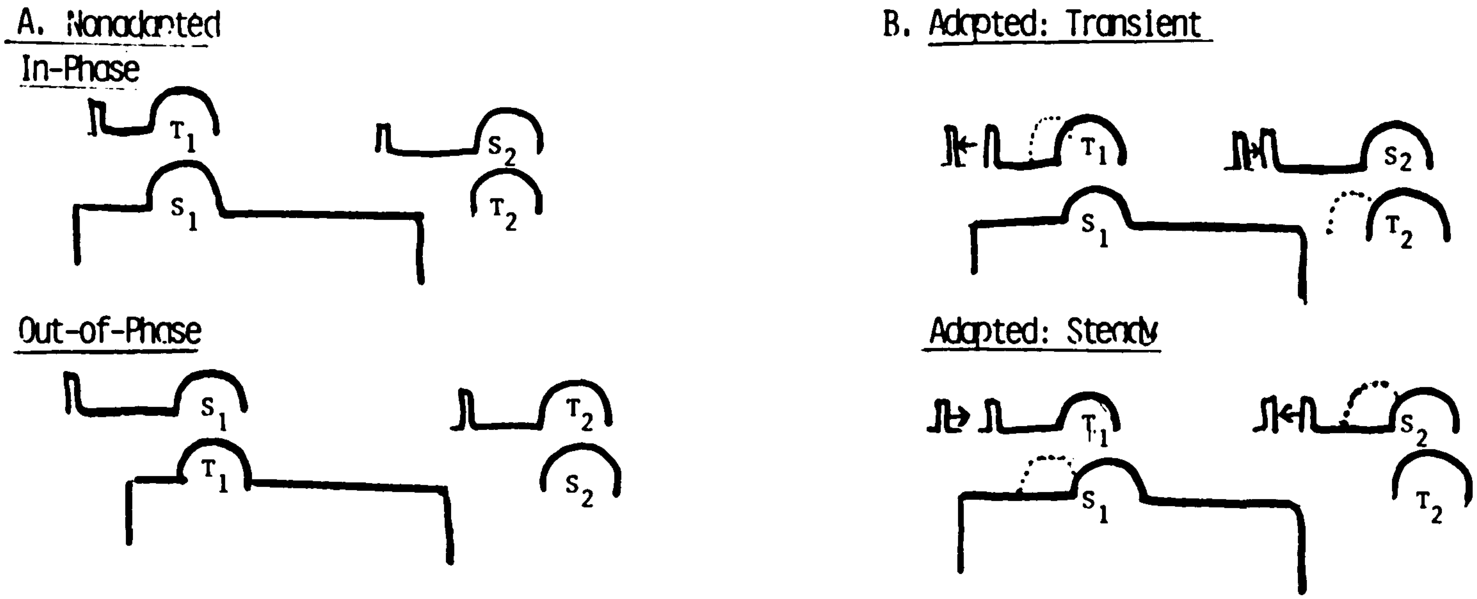

1.
Out-of-phase condition
T2 T1 S2 S1
F1
N
I2
N
F2
N
I1
2.
T1 S1
I1
N
F2
N
I2
N
F1
T2 S2
3.
S O A

decreases (Battersby & Wagman, 1962; Watson & Nachmias, 1980).

Looking at the predicted (S-T) interactions for the secondary peaks, it apparent that in some situations, the transient neural response is elicited by the TEST stimulus, whereas in others, it is elicited by the MASK. Therefore, the latency shifts within the masking funtion following adaptation are sometimes due to the response of the test mechanism and at other times, to that of the mask. Fig. 22 shows how selective adaptation should change the SOAs of the secondary peaks. Notice that the model predicts a shift CLOSER to the temporal edge after transient adaptation and a shift AWAY following steady adaptation. Predictions for transient adapation were substantiated by the data. However, the shift in steady adapted peaks was not always in the expected direction; (prediction errors involved the out-of-phase secondary peaks).

Finally, the model predicts facilitation when either T1 & S2 or T2 & S1 responses overlap. However, to account for the decrease in threshold after the so-called REMOVAL of facilitation, it must that S-T facilitation is not true summation, but rather the RELEASE from inhibition. One possible conceptualization of the events at the S-T troughs is that S1, for example, normally inhibits T1 (see below).

S1.------.T1.------.T2


A. Nonadapted

In-Phase

Out-of-Phase

B. Adapted: Transient

Adapted: Steady

Fig 22A. Hypothetical neural response overlap which would account for the secondary peaks in the nonadapted condition (Taken from Fig 21).

Fig. 22B. Presumes that adaptation selectively increases the latency of the adapted system and illustrates the changes in timings predicted for the in-phase peaks. Similar reasoning can be applied to the out-of-phase situation. Note that transient adaptation predicts a shift CLOSER whereas steady adaptation predicts a shift FURTHER from the temporal edge. Dotted lines indicate the temporal positions of the unadapted neural responses in comparison with those of the delayed adapted positions. Arrows indicate the shift in the SOA at which the test and mask interact.

where the symbol ".----." represents an inhibitory connection. However, T1 (in the same figure) is inhibitory of T2. Stimulation of S1, therefore, releases T2 and consequently facilitates T2 detection which is occurring at that time. Similarly when S2 is activated (similar figure not shown) , T2 is inhibited and T1 is released. This hypothesis could be tested using a RT design. According to Tolhurst (1975a), when transient mechanisms are responsible for detection, latency histograms show two reponse peaks, one associated with onset (e.g., T1) and the other with offset (e.g., T2). If, during S1 facilitation, T2 is released from inhibition, then the RT response distribution should show more detections at the onset of an in-phase and the offset of an out-of-phase test stimulus, whereas the reverse would be true of S2 facilitated SOAs. Furthermore, it would be predicted that steady adaptation, which reduces all S-T inhibition, would restore the RT function to a bimodal distribution.

The major features of the present model agree with the psychophysical literature. For example, it is known that as spatial frequency increases, the contribution of the sustained system increases, whereas that of the transient system becomes less important. One would therefore expect secondary (S-T) peaks to be more pronounced at higher spatial frequencies, whereas primary peaks should decrease (lose the T-T inhibition) as spatial frequency increases. Since both primary and secondary peaks are characterized by S-T inhibition, they should begin to resemble each other in height as spatial frequency increases and T-T interactions began to drop out. These expectations were met and have already been discussed.

Secondly, psychophysical studies have shown that the response latency of the sustained system increases with spatial frequency (Breitmeyer, 1975). One would therefore expect the latency of S-T interactions to increase accordingly. This expectation was also met by these studies.

Finally, such a model predicts the onset-onset law of masking (Kahneman, 1967) since fixing the luminance of the test stimulus also fixes the latency of its neural response to onset. Thus, test mask interaction should occur at the same SOA regardless of test duration.

II. Evaluating the model

A. Predicting results of studies using similar paradigms.

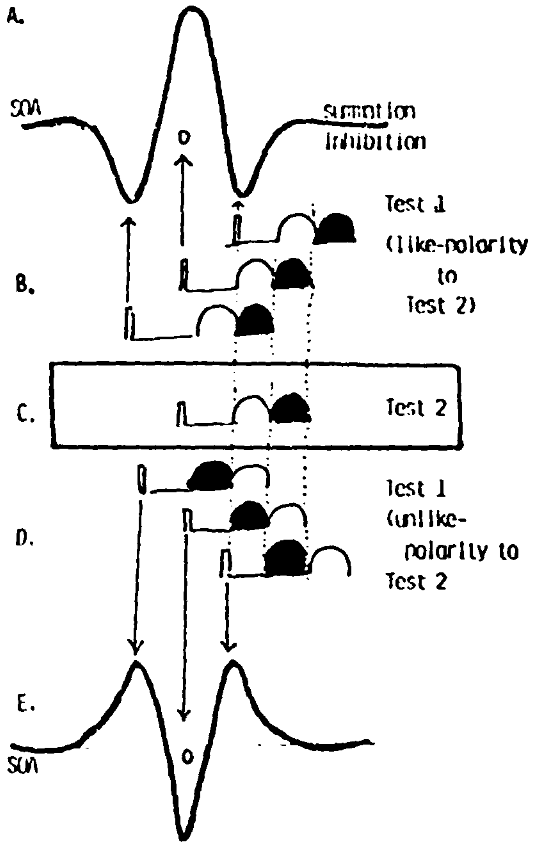
Tolhurst's (1975b) data shows spatial phase dependent peaks which are similar to those reported here, and in this sense, the present model is consistent with his data. However, there are two other studies in the literature (those of Ikeda, 1965 and Watson & Nachmais, 1977) whose stimulus paramters and resulting functions are different enough to constitute new data but whose designs are similar enough to be evaluated within the context of the present model. In both of these investigations the interactions between brief, equal duration stimulus pairs were explored as a function of

SOA. In the former case, the stimuli were circular pulses of the same or opposite polarity, whereas, in the latter, they were sinusoidal in- or out- of-phase gratings. Fig. 23 shows the hypothetical neural response to stimulus pairs, the interactions presumed to occur as SOA is varied, the predicted threshold changes as a consequence of these interactions and the empirical findings of these investigations. It can be seen that the model completely predicts Ikeda's (1965) data. Similarly, it explains the early facilitative effects reported by Sperling (1965) as well as the data of Watson & Nachmias (1977 Fig. 24A-B), although, in the latter study, the authors did not extend their temporal sampling to a broad enough range to demonstrate secondary (S-T) facilitation.

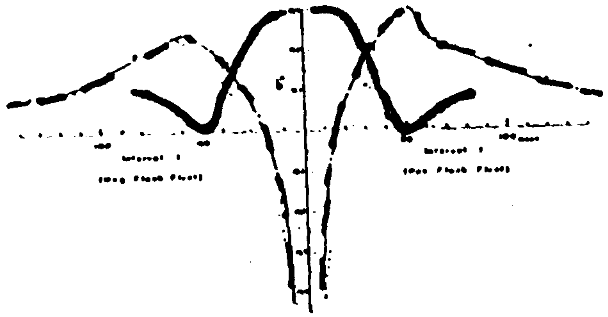
B. Predicting the results of masking and metacontrast studies. As a final test of the model, we might ask how well it predicts the findings of masking and metacontrast studies. A good starting point might be to treat masking as the outcome of predominantly in-phase interactions (since in both situations the test and mask stimulate the same retinal loci) whereas metacontrast could be likened to the out-of-phase condition since in both cases, the contrast of the test and mask are reversed. Additionally, because the traditional test and mask tend not to be identical in size and shape, (and are therefore easier to distinguish from each other than sinusoidal gratings) we might assume that in the traditional studies, task judgments are based upon the visi-

Fig 23. Predicted neural interactions between test stimuli of like- (B & C) and unlike-polarity (C & D) flashes as the SOA of Test 1 is changed with respect to Test 2. The slender rectangles represent the onset of the test stimuli . Transient responses to these stimuli are shown to the right of these rectangles. The T1 response is white and the T2 response is black. All neural responses to Test 1 which fall within the time domain indicated by the dotted lines extending upwards and downwards from the response to Test 2 will interact. White-White or Black-Black interactions are predicted to be facilatory whereas Black-White interactions are predicted to be inhibitory. The functions determined by these predictions are represented at (A) and (E). Arrows extending upwards from the test stimuli to these functions indicate the SOAs at which these interactions should occur, Notice that the model predicts more summation for like-polarities as opposed to unlike-polarities since two interactions occur in the former case, as opposed to only one in the latter.

Fig 23F. shows the empirical data of Ikeda (1965) JOSA 55 1527-1534. The solid and interrupted lines show the interactions of like- and unlike-polarity stimulus pairs, respectively, Notice that these data are the same as predicted by the model.


A.
SOA
summation
inhibition
0
Test 1
(like-polarity
to
Test 2)
B.
C.
Test 2
Test 1
(unlike-
polarity to
Test 2
D.
E.
SOA
0

F.



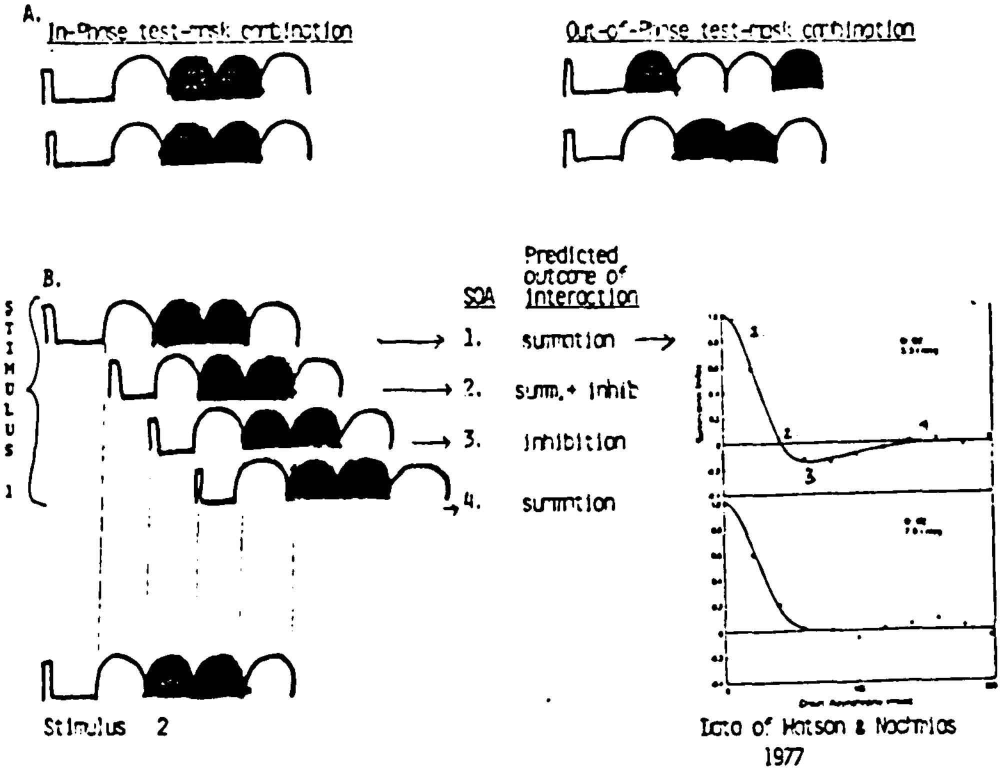


Fig 24. The data of Watson & Nachmias can be predicted by presuming the neural responses to the test and mask gratings to be identical. The rectangles in Fig 24A represent the test stimuli. White domes represent the neural responses of T_1 and S_2 cell populations black domes represent the neural responses of T_2 and S_1 cell populations.

Fig 24B. shows the differing test mask interactions between in-phase gratings as the SOA is changed. Interactions between out-of-phase gratings are not shown but are the opposite of those shown for in-phase gratings. Like-colors summate, unlike-colors interact inhibitorally. Notice that at the SOA of 0, all temporally overlapping responses summate. The reverse would be true for the out-of-phase gratings at this SOA. In the Watson & Nachmias data, the summation index in this situation is designated as +1. At the SOA labled 3, notice that inhibition is predicted between in-phase gratings, whereas out-of-phase gratings would summate. The summation index in this situation was given a negative sign by Watson & Nachmias. Notice that SOA 3 involves interactions between three neural populations whereas SOA 1 involved four. Therefore, the summation index should be smaller at SOA 3 than at SOA 1. Empirical data of Watson and Nachmias are shown in the lower right hand corner. Notice that summation indices go from +1 to -1 as SOA increases. The model also predicts a return to a slightly positive summation index at very late SOA's. Data reprinted from Vis. Res. 1977 893-902.

bility of the TEST stimulus only. This differs in experiments using gratings in which masking occurs when EITHER TEST OR MASK transient activity is interrupted). Fig. 25 shows the predicted and empirical results. It can be seen that, whereas the model predicts a metacontrast peak at SOA = 0, (a Type A function), the most usual finding is the backwards Type B effect. Similarly, expectations of masking are unfulfilled, with the obtained peak at SOA = 0 or forward, as as opposed to the predicted backward effect. Finally, as mask contrast is raised (thus, decreasing the latency of its neural response) more backwards masking is predicted. However, empirical results show the reverse; that is, a progression towards FORWARD Type A functions. It is therefore obvious that one of the following conclusions must be appropriate;

Either (1) the test and mask stimuli in the two types of paradigms are so different that they invoke different neural mechanisms

(2) there are differences in the methodology and data analysis between the traditional and present studies

(3) Task performance in a metacontrast study is not mediated by the transient system.

1. Differences between the two paradigms

Stimulus Characteristics.

a. Spatial configuration. Metacontrast stimuli are ostensibly non-overlapping in space, whereas sinusoidal

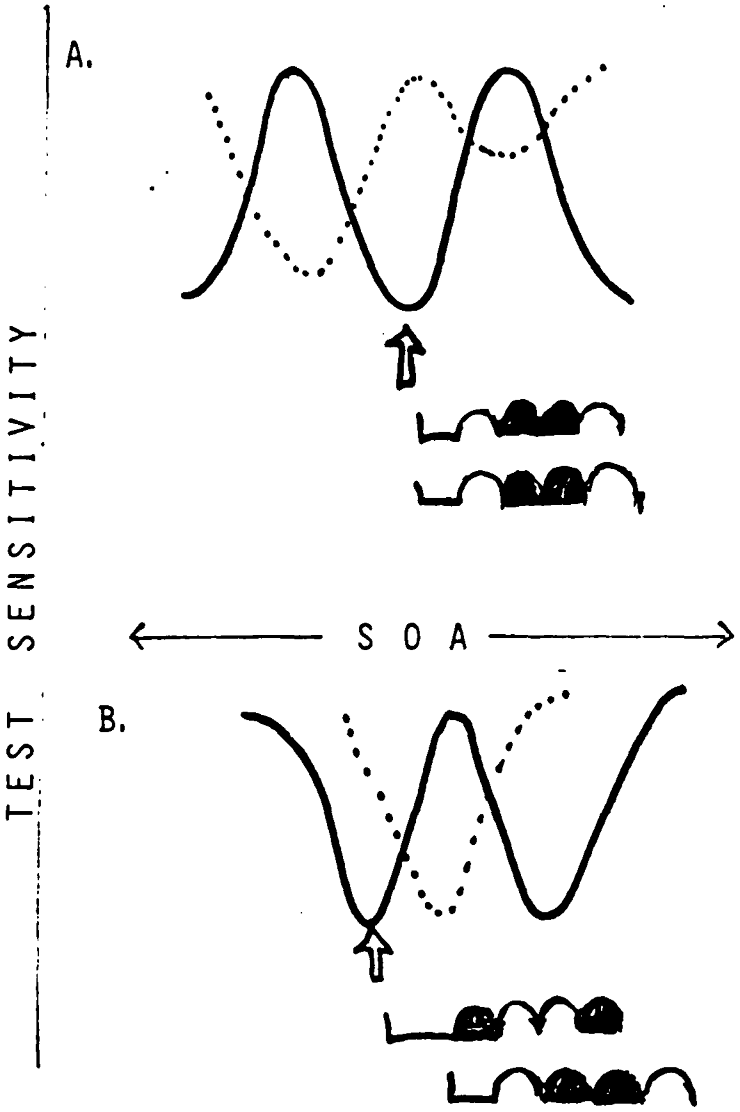


Fig 25. Predicted (solid line) and typical empirical (dotted line) functions for metacontrast (Fig 25A) and masking (Fig 25B) Below each function is the temporal arrangement of the test and mask anticipated to result in maximal masking. Symbols as in Fig 21

gratings occupy the same field. This argument presumes the annular center to be void whereas in reality, it is a circular luminance patch which falls on the same retinal area as the test stimulus. Recently, in fact, Green & Shor (1981) found that metacontrast effects are greater when the mask (of grating flanks) covers the whole stimulus field instead of bordering the outside of the test stimulus.

b. Outer border. The annular mask of metacontrast studies has an outer border, whereas, except for the shifts in spatial phase, grating stimuli are identical. Border diameter DOES in fact affect both the magnitude (Battersby & Wagman, 1962; Battersby, Ostereich & Sturr, 1964; Growney & Weisstein, 1972; Markoff & Sturr, 1971; Matteson, 1969) and timing (Battersby & Wagman, 1962) of masking. Furthermore, the addition of extra annuli may abort masking altogether (Breitmeyer, 1978a, Sturr & Teller, 1973).

Following Westheimer's (1967) studies some investigators have suggested that the falloff in masking with very large annuli occurs when the limits of an inhibitory retinal area are reached, although other possible explanations exist, such as changes in the dominant spatial frequency of the mask or the phase relationship between the test and mask.

c. Spatial frequency differences. As spatial frequency increases, masking effects decrease in magnitude (Tolhurst, 1975b, Watson & Nachmias, 1977) and delay (Rogowitz, 1977). However, these changes are not pronounced enough to explain the the dramatic timing differences between grating and metacontrast masking. In the present study, the change in timing of the secondary peaks with spatial frequency was always on the same side of the temporal edge.

d. Phase. The masking peak occurs either before or after the temporal edge depending upon the phase relationship between the grating stimuli. However, when the mask is a homogeneous field and therefore has no specific phase characteristics, the peak effect occurs at the SOA of zero (Green, 1980). Despite the importance of phase in determining temporal characteristics of masking it was already pointed out that in- and out-of-phase predictions are the reverse of those obtained empirically in masking and metacontrast studies.

2. Methodological differences

a. Temporal sampling rates. Threshold sampling in metacontrast studies is more extensive for backward rather than forward SOAs, (e.g., Weisstein, 1972; Kahneman, 1967; Petry, 1968a, 1968b) a strategy which, in the present study, would have aborted the discovery of the secondary peaks.

b. Differences in test and mask energy. Metacontrast models for backward interactions assume that when the test and mask are equal in energy, the latencies of the resulting neural responses are also equal so that the simultaneous presentation of the two stimuli should result in simultaneous outputs from the responding cell populations. If, however, spatial frequency is an important feature in masking, as an earlier discussion suggests it is, and if the spatial frequency contents of the test and mask are different (as certainly must be true in most metacontrast studies in which the test and mask differ in configuration) then there is no reason to believe that the equalization of the total stimulus energy necessarily distributes this energy equally among the different spatial frequency components, both because of the inherent neural latency differences as a function of spatial frequency (Breitmeyer, 1975) as well as the fact that the Fourier component amplitudes of two stimuli may differ even when their contrasts are the same. For example, the fundamental of a square wave grating has 4/3 greater amplitude than an equal contrast sinusoidal grating of the same spatial frequency.

c. Differences in Criteria. The traditional explanation of masking describes it as an interruption of the test SUSTAINED but not transient response and predicts a Type B function. As already discussed, there is evidence that inhibition of the test sustained response does occur (Breitmeyer & Ganz, 1976) and that in this situation, the test transient response measured by RT is unaffected (Fehrer & Raab, 1962).

However, the present model emphasizes an interaction with the TRANSIENT response to the test. The sustained response *to the test, although it exists, was not measured.*

If the different masking functions of the traditional and present paradigms occur because the former involves sustained and the latter transient criteria, an obvious question is how this selectivity can be accomplished; that is, how can an observer manage to detect transient activity in some masking studies but not others?

The answer probably lies in the energy level of the test stimulus. Since it has been established that low spatial frequency targets have two thresholds (a low threshold for the transient system and a relatively higher one for sustained detectors; Kulikowski & Tolhurst, 1966) a target energy can be chosen which is enough above the transient threshold to avert transient masking, but not sufficiently above the sustained threshold to resist the inhibition of this component. Thus, in such a situation, masking at S-T SOAs, but not at T-T SOAs, would be predicted; that is, masking backward and forward delays, but not at SOA = 0 (see Fig. 26).

As the test energy is reduced (above the transient threshold but below the sustained), the neural response it elicits will be relatively longer in latency than that related to the mask and (1) backward peaks should become even more backward (2) forward peaks should move closer to the SOA = 0 and (3) the susceptability of transient as well as sustained mechanisms to masking should increase; that is,

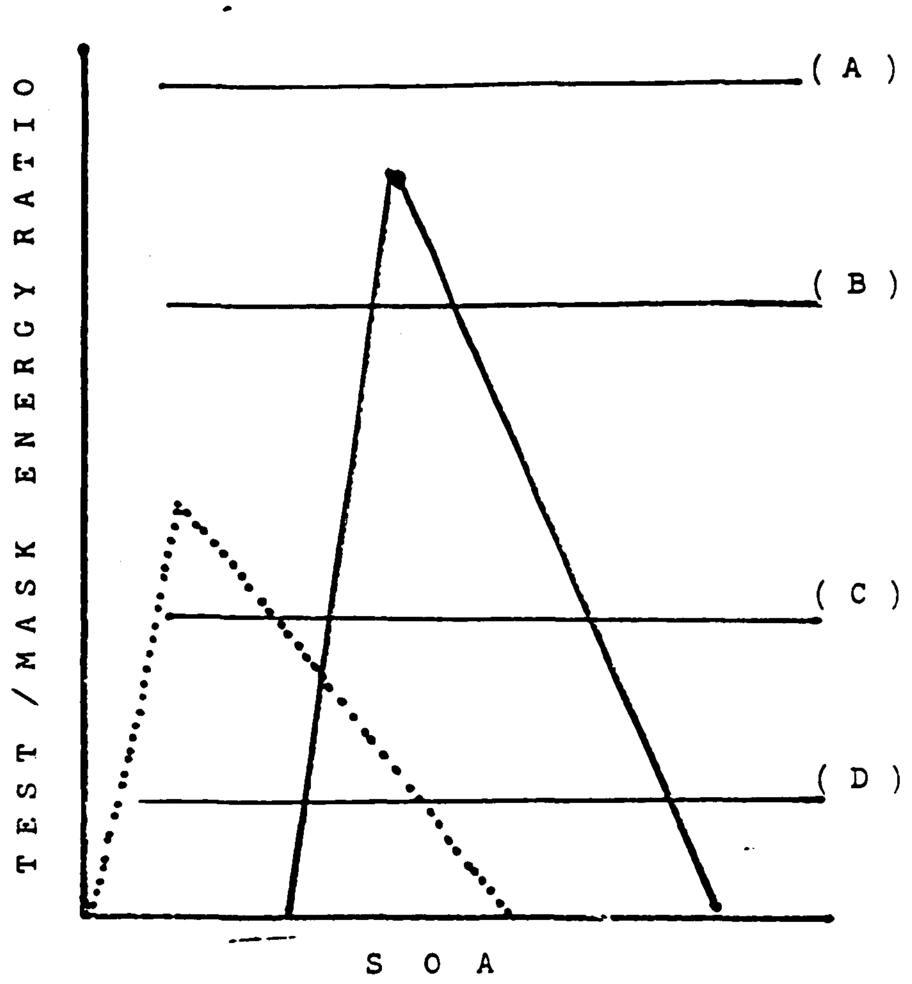


FIG 26. Hypothetical decision scheme for detection of a test stimulus using transient (dotted line) and sustained (solid line) criteria as the Test/Mask energy ratio decreases. At the horizontal line (A), test energy is sufficiently high so that no masking occurs. (B) predicts a backward function based upon sustained masking only. (C) predicts a W-shaped function in which BOTH the transient and sustained responses to the test are subthreshold. (D) predicts a Type A function.

masking should occur at the SOA of 0 as well as forward and backward peaks. These are precisely the trends reported by Weisstein (1972) (Fig. 1) and described earlier. Recall that when the Mask/Test (M/T) energy ratio was < 5, the masking function was characterized by a single backward peak. However, at M/T = 5, a new forward peak occurred at small positive SOAs. As the M/T ratio increased, this peak increased in magnitude but decreased in SOA so that by M/T = 16, it was so large as to completely obscure the backward fuction. Thus, it would seem likely that the large new peak represents T-T interactions whereas the smaller reflects that of S-T. Thus, backward Type B masking may represent T-S interactions whereas Type A masking demonstrates BOTH S-T and T-T inhibition. Recall also, that whether or not masking results in an A or B function frequently depend upon the criteria of the subject and that reaction time measures (transient mediated detection) yield a Type A function (Kahneman, 1968) whereas verbal reports frequently give Type B function. Stated again, the difference between Types A and B functions may be attributable to criteria, where Type A functions result only when the presence or absence of the test is reported (its transient characteristics, detectable at low M/T energy ratios) and Type B functions, when the form of the test must be identified (its sustained characterics which are detectable at high M/T ratios).

III. Ipsilateral vs contralateral adaptation effects

Lastly, let us consider theP#ifferences between the ipsilateral and contralateral adaptaton data. Recall that steady adaptation of EITHER eye yielded the same results, the interpretation being that the threshold-determining neurons within the sustained system are binocular. However, the effects of transient adaptation depended upon which eye was adapted. The ipsilateral effect was an elevation of the entire masking function by a constant and of the secondary peaks by yet another constant. Contralateral transient adaptation, on the other hand, elevated only the peaks. Additionally, whereas ipsilateral transient adaptation nearly eliminated the troughs, this reverse occurred after contralateral adaptation and thresholds greatly decreased (by as much as .4 log). To interpret these findings, we must first remember that (1) thresholds are determined by the transient mechanism and that (2) contralateral adaptation must either affect this mechanism or it does not. If it directly affects this mechanism, then EVERY threshold must be raised regardless of SOA. Since contralateral adaptation altered only SOME thresholds but not others, then contralateral transient adaptation does not directly impinge upon transient detectors in the test eye. On the other hand, it has already been concluded that the sustained system is binocular and that S-T interactions do occur ONLY at the those same SOAs affected by contralateral transient adaptation. Therefore, these effects are probably mediated through the sustained system. The question now, is how transient adaptation of one eye can enhance sustained inhibition in the contralateral eye?

1. To answer this, let us immediatly rule out cross-adaptation of the sustained system as a possible cause since inadvertant sustained adaptation would DECREASE the excitability of this system as well as its associated inhibition.

2. Therefore, in order for transient adaptation of one eye to potentiate the sustained system, a resting antagonism between the two systems must normally exist.

Consider the following hypothesis; The sustained system is binocular which means that the same cells can be activated by the stimulation of either eye. In addition, these neurons are antagonistically linked to transient cells which are monocular (Fig. 27). Thus, stimulation of sustained cells via either eye results in the inhibition of transient cells in BOTH eyes and conversely, steady adaptation of either eye disinhibits transient cells binocularly and improves detection.The identical results of ipsi- and contralateral steady adaptation support this interpretation.

Also relevant to this argument are Lipkin's (1962) findings that monocular CFF can be decreased by the presentation of a steady bright light to the contralateral eye, regardless of the luminance of the flickering light over a wide range (6 log units). In other words, steady (sustained) stimulation of one eye interferes with the detection of

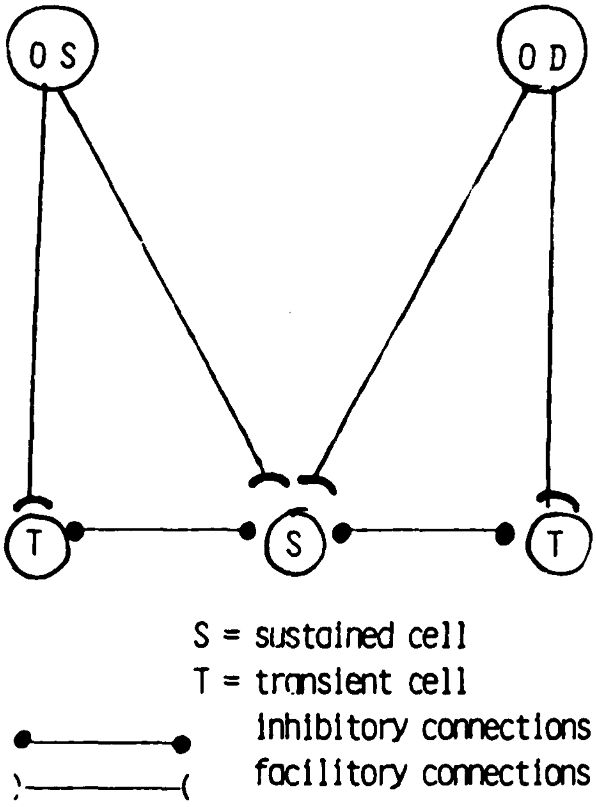


Fig 27 Hypothetical interconnections between transient and sustained neurons in cortex. Note that transient neurons are monocular whereas sustained neurons are binocular.

transient stimulation in the other.

On the other hand, since transient cells are monocular, excitation through one eye can not directly combine with that of the other. Hence, binocular summation of low contrast low spatial frequency gratings does not occur (Levi et al., 1979) and observers can distinguish the occular origin of low but not high spatial frequency stimuli (Blake & Cormack, 1974, Martens, Sloane & Blake, 1980).

Although direct binocular facilitation is hypothesized not to occur between transient neurons, they can interact indirectly; that is, stimulation of monocular transient cells can inhibit the binocular sustained neurons to which they are connected. As a consequence of this inhibition, the normal sustained antagonism of transient cells in BOTH eyes whould be weakened and transient facilitation should occur.

The concept of transient facilitation as the release from sustained inhibition gives rise to several expectations:

a. Since transient excitation is relatively brief in duration (e.g., onset burst of approximately 300 msec; Enroth-Cugell & Robsom, 1966), its supressive effect upon the sustained system should also be short lived. Thus, interocular facilitation between low spatial frequency gratings should be unimpressive when the stimuli are relatively long in duration but quite pronounced when they are inter-

mittent. This expectation was supported by Rose (1977) who found that binocular summation of low spatial frequency counterphase gratings was superior to that of steady stimuli. Additionally, Blake & Rush (1980) report that a visual mechanism which is sensitive to temporal frequency shows binocular summation for a very limited time period whereas a second mechanism, which is relatively insensitive to temporal modulation, summates binocularly over a long time span.

b. Furthermore, since transient cells must first be excited before they can in turn, inhibit sustained cells, T-S facilitation would would be predicted, not when two stimuli are simultaneous, but rather at some small interstimulus delay. In the present experiment, T-S facilitation ocurred only at non-zero delays(approximately 25 msec).

c. Thirdly, if interocular transient summation depends upon the escape from sustained inhibition, then it should only occur when the contrasts of the test stimuli are low and selectively excite transient mechanisms in each eye. If they are high in contrast, they will also activate the sustained system, even though they are temporally modulated (Tolhurst, 1973) or of relatively high spatial frequency (Bodis-Wollner, 1979). Excitement of the sustained system will in turn inhibit transient activity in BOTH eyes and interfere with summation. In accordance with this expectation, Levi et al., (1979) found that binocular summation occurred between low contrast gratings whereas inhibition occurred when the contrasts were high.

d. Finally, if the interruption of tonic sustained inhibition is the cause of S-T facilitation, then obviously steady adaptation (which atte/ates sustained inhibition), should enhance transient facilitation regardless of whether the S-T interaction had been inhibitory or facilitory; that is, at SOAs representing S-T inhibition, steady adaptation should reduce sustained inhibition and lower transient thresholds. At SOAs at which facilitation results from a reduction in the tonic sustained inhibition, then sustained adaptation should further reduce this inhibition. This explanation accounts for the earlier mentioned paradox that steady adaptation results in GREATER rather than lesser facilitation.

The outcome of transient ADAPTATION, on the other hand, depends upon which eye is being tested. According to the present interpretation, unilateral transient adaptation should not only raise transient thresholds in the adapted eye, but should also disinhibit binocular sustained cells thereby releasing and potentiating the sustained inhibitory influence upon BOTH eyes. Thus, following transient adaptation, there should be (1) a general rise in the entire fuction (similar to a D.C. shift) in the adapted eye only plus (2) a SELECTIVE increase in transient thresholds at all SOAs where S-T inhibition is operative (a binocular effect representing the inhibitory advantage of the sustained system gained by transient adaptation). Thus, the ipsilateral and contralateral functions should be identical except for the D.C. shift and the difference in facilitation. The adaptation data of Experiment II conform to this prediction and support the theory of a monocular transient but a binocular sustained system linked by mutual antagonism. Similar conclusions can be drawn from other studies;

IV. Data supporting the theory that the sustained system binocularly inhibits transient activity

A. A large flickering windmill type stimulus will simultaneouly mask a 375 msec concentric stimulus only when the two are presented to the same eye; that is, transient masking is monocular (Johnson & Enoch, 1976). When the windmill is presented to the contralateral eye, it has the same small effect whether it is moving or stationary. Presumably, this is because dichoptic presentation ultimately stimulates the same (sustained) neurons regardless of the temporal parameters of the stimulus.

B. Dichoptic adaptation has been reported to occur only at spatial frequencies below 2 c/d (Breitmeyer et al., 1977). Since low contrast/low spatial frequency adaptation selectively adapts transient cells in the exposed eye, then the subsequently disinhibited binocular sustained cells will exert stronger inhibition upon the transient cells in the contralateral eye and dichoptic adaptation will be reported.

At higher spatial frequencies, transient adaptation of one eye should affect, not only the transient cells, but ALSO the binocular sustained cells. Obviously, adaptation of these sustained cells minimizes their inhibitory influence upon transient cells of the contralateral eye so that dichoptic transient adaptation does not occur.

C. Finally, in both amblyopia and stereoblindness an interruption of binocular connections results in inferior HIGH spatial frequency performance in the affected eye (Hess, Howell & Kitchen, 1978; Levi & Harwerth, 1977) but NORMAL (Von Noorden & Leffler, 1976) or IMPROVED (Apkarian, 197;) Hess & Howell, 1977; Hess, 1978) LOW spatial frequency detection. These clinical data are consistent with the notion of a binocular high spatial freqency system which tonically inhibits a monocular low spatial frequency system.

V. Morphological and electrophysiological evidence of a binocular-sustained and monocular-transient system.

Investigating the properties of cortical macaque cells, Schiller et al., (1976 a,b) reported that the majority of cells with transient type properties tended to be monocular whereas those which had sustained outputs were most often binocular. When the eyelids of kittens are monocularly sutured, the preponderance of neuronal loss in the LGN is of Y cells (Garey & Blakemore, 1977; Lehmkule, Kratz, Mangel & Sherman, 1978) presumably because their primary source of input has been interrupted.

IV. Evidence of antagonism between the transient and sustained systems.

Transient inhibition of sustained cells has been demonstrated electrophysiologically (Singer & Bedworth, 1962) and suggested by psychophysical data (Breitmeyer & Ganz, 1976; Weisstein, 1972). On the other hand, sustained inhibition of transient activity was suggested by other investigators (Breitmeyer, 1978a; Bodis-Wollner, Hendley & Kulikowski, 1972, Von Grunau, 1978).

The notion of a resting antagonism of sustained cells upon transients has not previously been suggested although there is evidence that resting antagonism can occur in the CNS. For example, on a cellular level, the amblyopia of a monocularly deprived kitten can be temporarily reversed by the cortical administration of biccucilline (Duffy & Campbell, 1976; Sillito, Kemp & Blakemore, 1981).

VII. Some predictions inherent in the model

A. A small extension of this model (Fig. 28) would explain the earlier confusion regarding the binocular transfer of the MAE (motion after effect). Consider that motion information enters parallel visual channels, exciting the transient system monocularly and the sustained system binocularly via a common cortical unit.The sustained system, once activated, binocularly inhibits the transient cells specific for the same direction of motion. The amount of

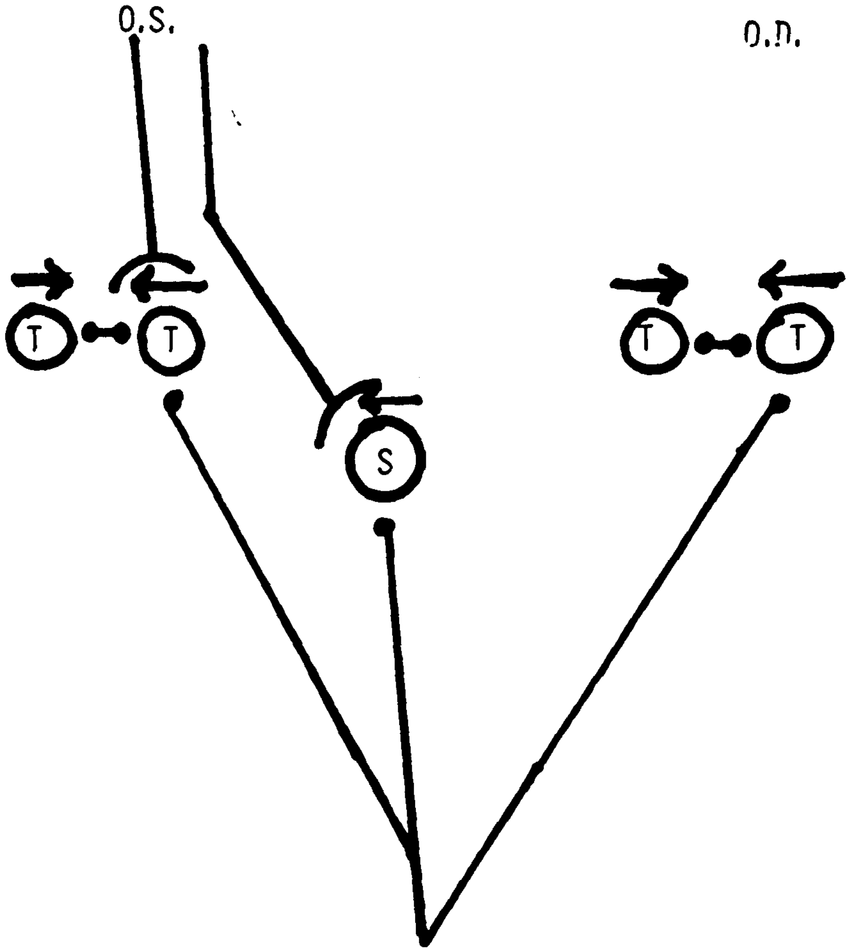


Fig. 28. Hypothetical neural arrangement responsible for the motion after-effect which follows monocular stimulation. T and S represent transient and sustained cells, respectively. Axonal connections ending with dots are inhibitory whereas semicircular connections are excitatory. Arrows indicate the directional preferences of the cells involved. The sustained cells can be excited via either eye whereas transient excitation is monocular.

inhibition upon the transient system would vary according to the contrast and duration of the stimulus as well as the degree of binocularity of the sustained cell, being greatest when the adapting stimulus enters through the dominant eye. Upon the termination of the adapting stimulus, while the previously excited transient cells of the two eyes recover from this inhibition, the MAE, or the perception of movement in the opposite direction, arises from the temporary disinhibition of movement opponent cells.

Such a model would explain the puzzling absence of the MAE in many amblyopes and steroblinds (Lehmkule & Fox, 1975, Mitchell, Reardon & Muir, 1975, Wade, 1976) who have normal low spatial frequency detection. If binocular SUSTAINED neurons are responsible for the MAE and these are nonfunctional in stereoblindness, then the lack of MAE is predictable. Additionally, in those subjects who do show adaptation aftereffects, these effects are always maximal when the dominant eye (which retains its suppressive influence upon the amblyopic eye <Duffy & Campbell, 1976, Silletto, et al, 1981) is stimulated (Wade, 1976).

B. Another finding which the present model can explain is that monocular masking occurs in both backward and forward conditions whereas dichoptic masking is only backward (Kietzman, Boyle & Lindsely, (1971).

Using a test stimulus of a sectored disc and a luminous flash as a mask, Kietzman et al (1971) reported that the monocular presentation of two stimuli resulted in both backward and forward masking whereas dichoptic presentation led to backward masking only (Fig. 29) According to the proposed model;

1. The response to the test can be represented as a transient (T1, T2) followed by a sustained (S1, S2) response. The transient response should register only in the eye of presentation whereas the sustained response should be binocular.

2. The mask response, however, is TRANSIENT ONLY since the stimulus is a blank field and unlikely to elicit a significant response from the sustained population. Also, since the stimulus contains Fourier components in many spatial phases T1 and T2 would discharge simultaneously. Finally, this response should register only in the stimulated eye.

3. In the monocular condition, the mask transient response interacts with BOTH the test transient and sustained responses. Fig. 29 shows the predicted outcome of these interactions which is essentially a Type A function characterized by backward and forward masking as well as at SOA = 0.

d. When the test and mask are presented to separate eyes, the only possible interaction is between the monocular mask transient and the binocular test sustained. This is a backward effect and hence, only backward masking would be pre-

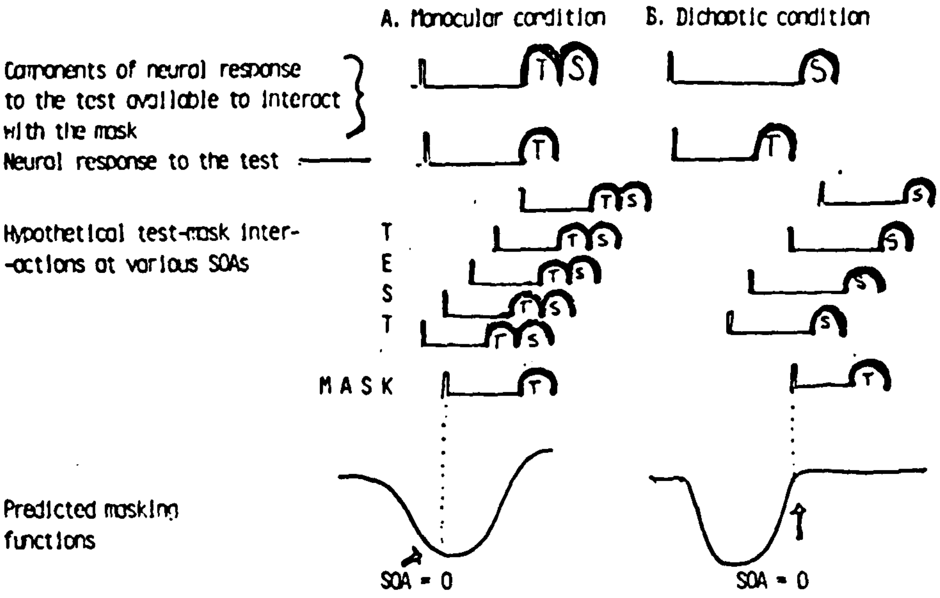


Fig 29. Illustrates predicted differences between monocular and dichoptic flash masking in a monocular-transient/dichoptic-sustained system.

Fig 29A. The neural response to a patternless flash is hypothesized to be transient. This response can interact with the transient test response ONLY when the two occur in the same eye. The earliest predicted component of monocular masking is T xS (where T and S are transient and sustained, respectively); followed by T x T masking. This predicts a U-shaped (Type A) function with the minimum sensitivity level at SOA = 0.

Fig 29B. When the test is presented to the contralateral eye (dichoptic masking), only the binocular sustained component of the test response can interact with the transient response to the mask. This interaction occurs only at backward SOAs and yields a Type B function.

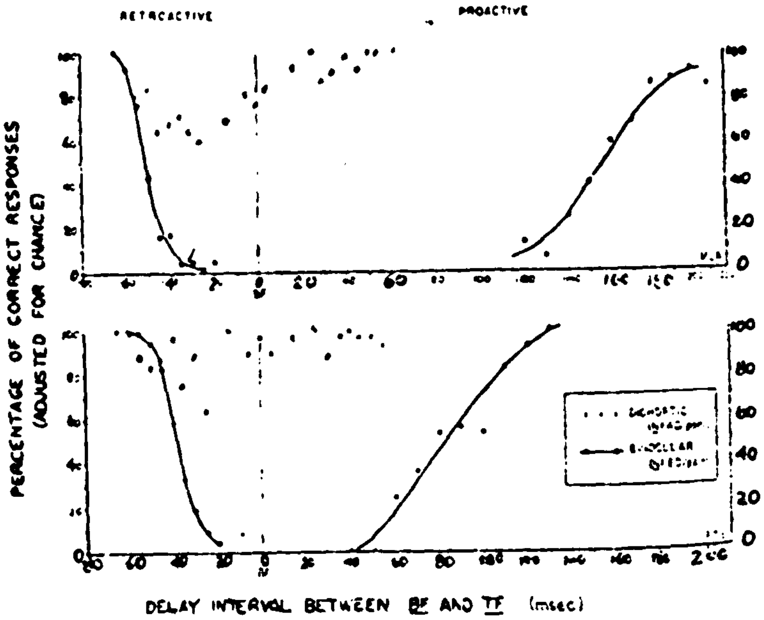


Fig 29C. Data of Kietzman, Boyle & Lindsley, 1971 demonstrating the difference between binocular and dichoptic flash masking. A model predicting these findings is presented in Fig 29. Data reproduced from Perception & Psychophysics 1971 9 350-351.

dicted. In addition, the magnitude of this effect should be much smaller than the monocular since at low spatial frequencies, T-S interactions are much weaker than those confined to the transient system (T-T).

C. Finally, this model predicts dichoptic masking to be smaller in magnitude than monocular (Battersby & Wagman, 1959; Weisstein 1971).

If monocular masking is characterized by both a large T-T and a small T-S component whereas dichoptic involves only the latter, smaller of the two, then the reduced masking which occurs dichoptically would be expected. Furthermore, since sustained neural responses are longer lasting than transients (Enroth-Cugell & Robson, 1966) one might expect the central component of masking to be relatively long lasting (as was described by Wagman & Battersby, 1959).

SUMMARY AND CONCLUSIONS

When a brief test grating was presented at varying asynchronies with respect to a longer duration sinusoidal mask of the same spatial frequency, the following contrast threshold changes were observed;

1. At all SOAs, .5 c/d thresholds were always lower than 4 c/d suggesting that test detection was mediated by a system more sensitive at lower spatial frequencies. It was presumed that this mechanism belongs to the transient visual system.

2. At different SOAs, interactions with this test stimulus were either inhibitory or facilitory, causing peaks and troughs in the threshold function.

3. These peaks and troughs occurred with mirror-like symmetry in magnitude and timing about the onset and offset of the mask but NOT during the intermediate SOAs. The similarity in the magnitude of the onset and offset peaks is generally not observed in studies using unpatterned test and mask stimuli.

4.Two types of peaks, referred to as "primary" and "secondary", were distinguished.

a. Primary Peaks;

(1) always occurred about 25 msec from the temporal edge and were at least least 8 msec in duration -

(2) decreased in magnitude as spatial frequency increased.

(3) were the same height, for a given spatial frequency, regardless of spatial phase.

(4) Transient adaptation raised, whereas steady adaptation lowered the primary peaks. These findings were interpreted to mean that the neural response to the test stimulus was inhibited by BOTH the transient and sustained responses to the mask at these asynchronies.

b. Secondary peaks;

(1) occurred at longer delays from the temporal edges (approximately 40-100 msec) and on opposide "sides" of the temporal edge as the primary peak. For example, if the primary peak preceded the mask onset, the secondary peak followed it.

(2) As spatial frequency increased, the temporal separation of the primary and secondary peaks increased.

(3) Additionally, the heights of the secondary peaks increased with spatial frequency and at 6 c/d were approximately as great as the primary peaks.

(4) After transient adaptation, secondary peaks were markedly raised and shifted closer to the temporal edge. Sustained adaptation frequently had the reverse effect, reducing secondary peaks and frequently shifting them away from the temporal edge. These findings were interpreted to mean that, at this SOA, the sustained neural response to the mask ordinarily interferes with the transient neural response to the test.

5. Primary and secondary TROUGHS.

(1) Primary troughs occurred about 17-25 msec from the temporal edges. Secondary troughs occurred at longer (approx 50- 100 msec away from and on the opposite side of the temporal edge as the primary troughs).

(2) With increasing spatial frequency, troughs diminished at a faster rate than the primary peaks indicating minimal facilitation at high spatial frequencies.

(3) the duration of facilitation was less than 8 msec.

D. Spatial Phase

The latency, but not the heights of all peaks and troughs depended upon the relative spatial phases of the test and mask, indicating that spatial position is temporally encoded in the CNS. Primary IN-PHASE peaks preceded mask onset and followed offset whereas OUT-OF-PHASE peaks followed onset and preceded offset. Facilitation of one spatial phase (primary troughs) corresponds closely in timing with inhibition of the opposite spatial phase (primary peaks).

6. Transient adaptation of the ipsilateral eye dramatically reduced troughs, whereas steady adaptation deepened them. These findings were interpreted to mean that both transient and sustained facilitation occur at the primary troughs. Transient facilitation was concieved as an excitatory interaction between the mechanisms detecting the test and the mask. Sustained facilitation was conceived as release from inhibition.

7. Ipsilateral and contralateral adaptation had the same effect after steady adaptation ONLY, suggesting that the sustained system is binocular whereas transient influences are predominantly monocular. Threshold changes which did occur after contralateral transient adapation can be explained if a constant antagonism is presumed between the transient and sustained systems.

8. The present findings can be predicted by a model which presumes that;

a. The test and mask elicit responses from BOTH the transient and sustained systems at both onset and offset.

b. Different cell populations respond to onset and offset.

c. The same cells that respond to the onset of gratings of one spatial phase respond to the offset of the opposite phase.

d. Inhibition or facilitation occurs when the neural responses from specific subpopulations temporally overalp.

The model, which is elaborated in the discussion section, is in agreement with the present data and also predicts the findings of earlier investigations involving sinusoidal gratings (e.g., Watson & Nachmias, 1977). Based upon the present data, an attempt was made to account for the two types of masking functions reported in the traditional literature.

GLOSSARY

ADAPTATION- prolonged exposure to a specified stimulus. In the present study, the transient adapting stimulus was a grating which reversed its phase at the rate of 7.6 Hz. The steady adapting stimulus was a grating which was continuously presented during the adaptation period.

DICHOPTIC- presentation of the stimuli to each eye independently

FACILITATION - a decrease in threshold

INHIBITION - an increase in threshold

INTERMEDIATE SOAS- portion of the Crawford function at which thresholds are relatively stable

MASK- a stimulus whose presentation is presumed to alter test sensitivity

MASKING- the interaction between stimuli which are presented closely in time. Frequently, the term also implies an increase in threshold.

METACONTRAST- the situation in which the test and mask are spatially adjacent rather than overlapping.

ONSET/OFFSET MASKING- threshold changes which occur when the test is presented in close temporal association with the onset or offset of the mask

PRIMARY PEAKS- large increases in threshold which occur approximatly 17-25 msec from the temporal edges.

RESTING THRESHOLD- contrast threshold of the test stimulus presented alone (that is, in the absence of the mask).

SECONDARY PEAKS- smaller threshold increases which occur *at longer delays from the temporal edges.*

S-T INTERACTIONS- interactions between the sustained neural response to the mask and the transient neural reponse to the test.

SENSITIVITY- the inverse of threshold

TEMPORAL EDGE - the SOAs associated with either onset or offset of the mask

TYPE A MASKING- see page 5

TYPE B MASKING - see page 5

TEST- brief (8.3 msec) stimulus used to tap threshold changes.

T-T INTERACTIONS- interactions between the transient response to the test and the transient response to the mask.

TROUGH- decrease in threshold

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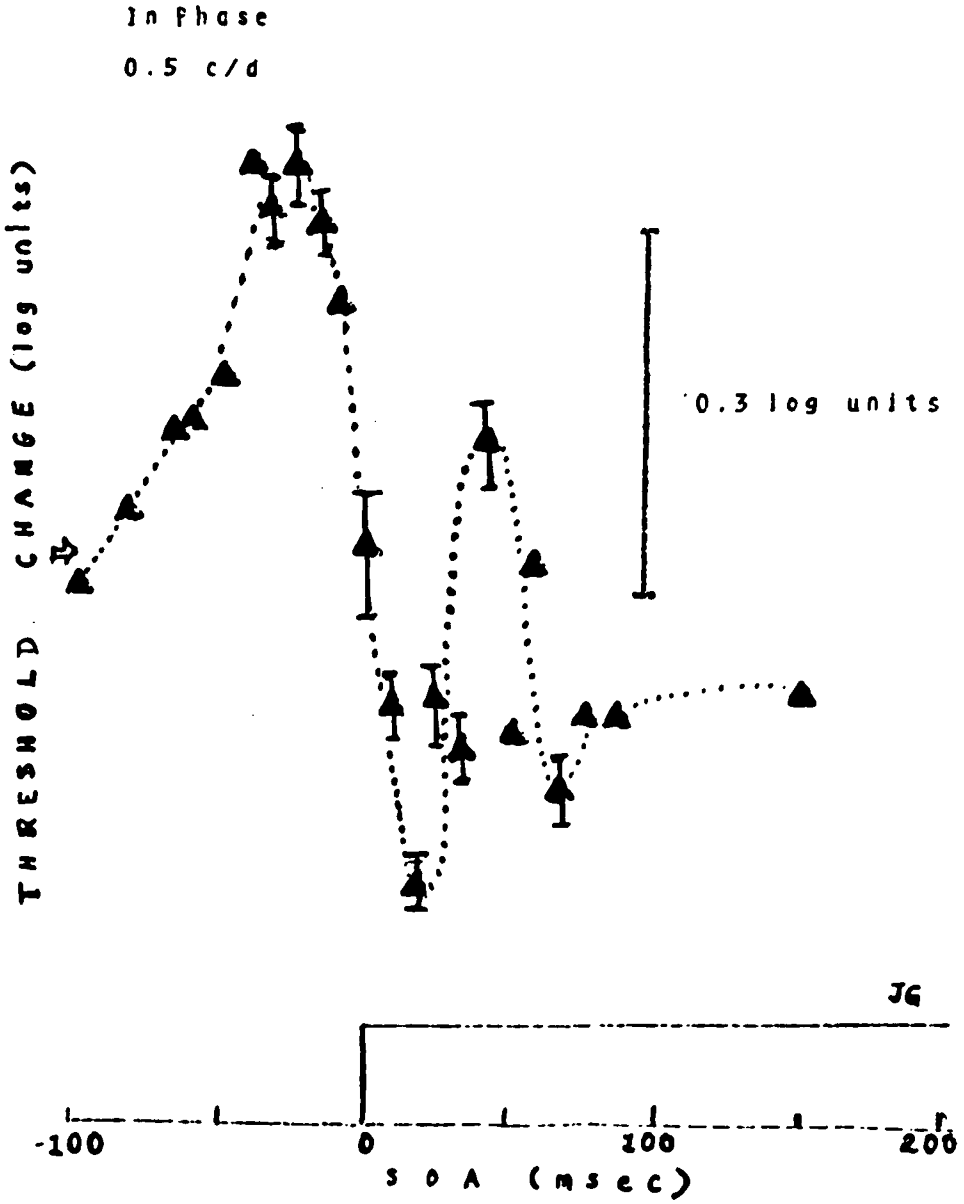
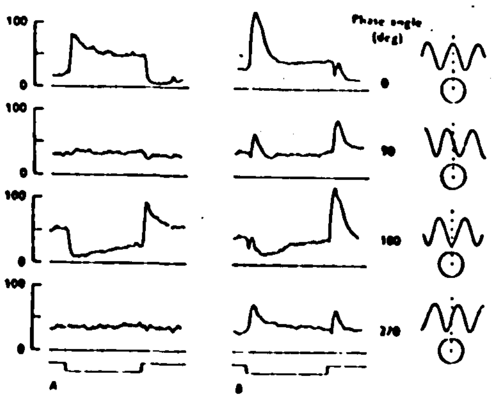
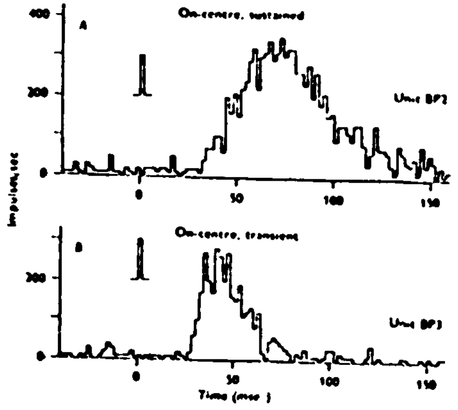


Appendix 1. MEAN THRESHOLDS AND STANDARD ERRORS FOR ALL SOAs AT WHICH THRESHOLDS WERE DETERMINED MORE THAN THREE TIMES ABOVE IS THE IN-PHASE DATA FOR J.G. AT .5 C/D. THESE STANDARD ERRORS ARE TYPICAL FOR BOTH SUBJECTS AT BOTH SPATIAL FREQUENCIES.



Appendix II. Electrophysiological recordings from cat retinal ganglion cells. Response histograms of off-center sustained (left column) and off-center transient (right column) cells to a .13 c/d grating as spatial position is shifted. Stimulus duration was 1.1 sec. Notice that cells which respond to the onset of the 0° phase respond to the offset of the 180° phase position. Data reprinted from Enroth-Cugell & Robson, 1966. J. Physiol. 187 512-552.



Appendix III. Electrophysiological recordings from cat retinal ganglion cells showing the different time courses of responses from transient and sustained cells. Stimuli were diffuse 2 msec light flashes. Notice the latency differences between the to response distributions. Reprinted from Cleland, Levick & Sanderson 1973 J. Physiol. 228 649-680.