

An Investigation of Sustained and Transient
Mechanisms in the Human Visual System
Using the Reaction Time and
Metacontrast Paradigms

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The present set of experiments investigated the proposed sustained and transient mechanisms in the human visual system. Experiments 1 and 2 assessed Reaction Times (RTs) to different spatial-frequency sinusoidal gratings as a function of contrast. For moderate spatial frequencies, biphasic RTs were produced as a function of contrast. The results were interpreted as providing evidence that sustained and transient mechanisms may differentially mediate RT, depending on the duration, contrast and location of the grating. It was hypothesized that if the same mechanisms mediating RT are also involved in producing metacontrast, then by using the same foveal and peripheral grating stimuli as employed in Experiments 1 and 2, metacontrast could be investigated while differentially manipulating the involvement of the sustained and transient systems. Type B metacontrast functions were not produced in Experiment 3. Experiments 4 and 5 investigated various parameters in the metacontrast paradigm in an attempt to produce U-shaped metacontrast functions. The low contrast

and luminance levels of the gratings may have accounted for the absence of type B functions. Using a higher-energy mask in Experiment 6, type A monotonic functions were produced. Maximum metaccontrast occurred when the target and mask shared the same spatial frequency. This was interpreted as giving evidence for either sustained-sustained or transient-transient intrachannel inhibition.

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TABLE OF CONTENTS

	Page
GENERAL INTRODUCTION	
Multiple Channel Models of Visual Processing	1
Single and Multiple Channels	3
Grating Stimuli	6
Fourier Theory	8
Psychophysical Evidence for Multiple Channels	13
Neurophysiological Evidence for Sustained and Transient Processing Systems	17
Evidence for Sustained and Transient Neurones in the Human Visual System	
Contrast Thresholds	22
Subthreshold Summation	29
Reaction Time Experiments	29
Metacontrast	
Independent and Dependent Variables	33
Theories of Metacontrast	39
STATEMENT OF THE PROBLEM	53
EXPERIMENT 1	55
Method	55
Results	63
Discussion	74
EXPERIMENT 2	84
Method	86
Results	88
Discussion	88
EXPERIMENT 3	99

Method	107
Results and Discussion	110
EXPERIMENT 4	120
Results and Discussion	120
EXPERIMENT 5	129
Method	129
Results and Discussion	131
EXPERIMENT 6	141
Results	143
Discussion	147
GENERAL DISCUSSION	149
REFERENCES	160
APPENDICES	171

GENERAL INTRODUCTION

Multiple Channel Models of Visual Processing

One of the ultimate goals of scientists studying human visual processes is to determine how information is encoded from the initial stimulation of the photoreceptors, to at least the visual areas of the brain. In this pursuit, theorists have studied many aspects of perception and proposed various models in the hope of specifying the nature of visual processing. In recent years, the manner in which the form and size of a visual stimulus (i.e., spatial vision) is processed, has been studied in the context of specifying whether spatial information is processed via a single channel or along multiple "independent" channels, each responding to a different aspect of the visual stimulus.

The discussions below will describe how most of the results of recently reported psychophysical and physiological studies support the view that spatial information is processed by multiple channels rather than in a single channel. Before this discussion begins, however, it is first necessary to present some basic neurophysiological findings, as well as define some of the concepts that will be used throughout this discussion.

Receptive Fields

Kuffler (1953) conducted one of the most important investigations on the spatial characteristics of the retina. By implanting a microelectrode into the cat's optic nerve fibres, he was able to record the action potentials of cells in the cat's retina. When projecting a small spot of light onto the cat's eye, Kuffler found that each retinal ganglion cell would maximally respond when the spot of light was projected onto an area in close proximity to it. However, he also reported that the ganglion cell would respond when light was projected within a circular area around the optimum position. This region was labeled as the "receptive field" of the ganglion cell being studied. Kuffler reported that the response of the cells were of two kinds. If the probe was projected onto the center of the receptive field of one type of cell, its spontaneous firing rate would increase. However, if a light projecting onto the center of the receptive field of another type of cell was turned off after having being on for some time, the spontaneous firing rate of that cell would only then increase. From this study, Kuffler suggested that there were at least two types of ganglion cells: on-center and off-center cells. Furthermore, Kuffler found that when the peripheral area (surround) concentric to the receptive fields of these cells were stimulated, the response of each ganglion cell was in opposition to the way in which it responded to a stimulus presented in the middle of its receptive field. Thus, an

on-center cell would give an off response when its receptive field surround was stimulated, while an off-center cell would give an on response when it was stimulated in the periphery.

Single and Multiple Channels

The mechanisms outlined above, may help define in the following discussion, the concept of a visual processing channel. The definition of a "channel" can vary from one theorist to another. For instance, a channel can be defined as that which elicits a single neuronal output, or viewed as a collection of cells with identical receptive fields (such as in their size or response property) except with respect to retinal location. It seems that the most useful definition would be flexible in its application to the various models of visual perception. The following definition taken from Graham (1980), seems to have this characteristic: "A channel can be viewed as a single neuron (receptive field) or set of neurons (receptive fields) responding to a particular aspect of the visual stimulus, which may or may not produce a distinctive perceptual effect".

The single channel view assumes that processing involves an array of cells which have receptive fields that are identical in shape and size. These receptive fields

4

overlap and cover different portions of the visual field. When a stimulus is presented to the eye, this array responds by transforming the spatial information in the optical array into neural activity, which is transmitted via pathways to the cortex. The magnitude of the response at any point in the single channel's response profile (i.e., the response characteristics of a channel to visual stimulation), can be specified by a weighting function, which indicates to what extent light falling on different parts of the retina, adds or subtracts to form the final output of this channel. (Graham, 1980).

In order to best understand the nature of the multiple channel view of visual processing, it may be helpful to review how other theorists have envisioned multiple channels mediating the processing of other aspects of vision, such as colour perception or feature detection. The Young & Helmholtz theory of colour vision for instance, proposed that there are three types of cones in the retina; "red", "green" and "blue", corresponding to the physical colour primaries. Each type of cone is aroused by all wavelengths but is maximally excited by only one wavelength. The theory went on to describe a non-primary colour being processed by all three sets of colour cones which would each be differentially sensitive to that colour. The different stimulation combinations of the primary colour cones could account for perception of the spectrum of colours.

(Helmholtz, 1909).

The work of Hubel & Weisel (1959, 1962) alluded to multiple channel processing of spatial information. They found for instance, that neural cells in the cat and monkey cortex responded differentially to bar widths, orientation and direction of movement. These results seemed to provide the first neurophysiological evidence for the existence of independent detecting mechanisms (i.e., multiple channels) processing visual information.

In the attempt to describe whether visual information is processed along single or multiple channels in humans, theorists have designed models of visual processing that have taken into account both the data from animal neurophysiological studies, as well as the results of psychophysical investigations. One model proposed by Campbell & Robson (1968), has gained much attention in the past decade. The authors extrapolated from the work of a mathematician, J.B. Fourier, in their model of a multiple-channel visual-processing system. This theory not only attempts to describe how visual information is processed but it also describes how a visual stimulus may be physically decomposed into its basic sinusoidal components. Although this theory has been criticised in its application to human visual processing, it has been useful in its concise mathematical description of the visual stimulus.

Because of its impact, the Fourier theory of visual processing will be presented below. Before describing this Fourier view, however, it is first necessary to introduce the concepts of spatial frequency, sinusoidal and square-wave gratings.

Grating Stimuli

Figure 1a displays a spatially periodic stimulus (i.e., grating) with a square-wave luminance profile. It consists of a repetitive pattern of light and dark bars. Bar width is usually defined in terms of spatial frequency, which is the number of cycles in a grating per degree of visual angle (c.p.d.). Unless otherwise specified, the luminance of the light and dark bars modulate around a constant mean luminance level. The degree of modulation is defined as the contrast of the grating, which is expressed as a function of the luminance at the peak and trough of the display. Conventionally, this is termed the Michelson Contrast Ratio (MCR) and is defined by the following formula:

$$\text{Contrast} = \frac{\text{Lum}(\text{max.}) - \text{Lum}(\text{min.})}{\text{Lum}(\text{max.}) + \text{Lum}(\text{min.})} \quad (1)$$

where Lum(max.) = the luminance at the peak of the grating,
and Lum(min.) = the luminance at the trough of the grating.

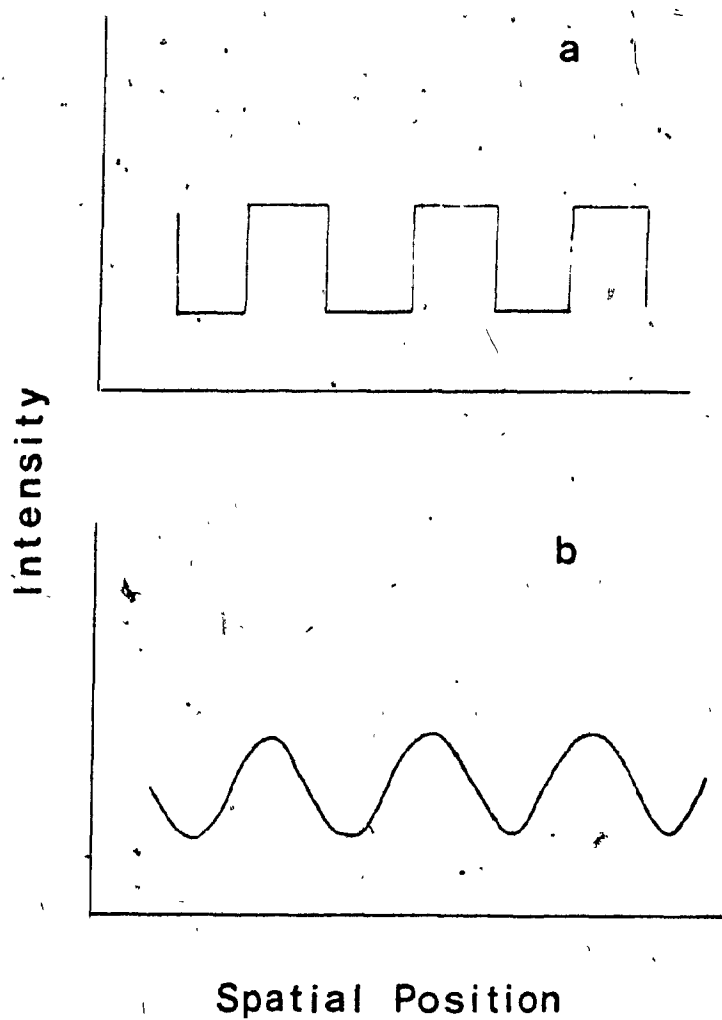


Figure 1. Luminance profiles of typical square-wave (a) and sinusoidal-wave (b) grating stimuli as a function of spatial position.

While the change from a light to a dark region is abrupt in a square-wave grating, it is more gradual in the sinusoidal grating. As can be seen in Figure 1b, the luminance of this grating varies sinusoidally across space. The image appears to consist of alternating, blurry, light and dark bars.

Fourier Theory

Fourier demonstrated that any periodic waveform can be analysed into a series of sinusoids made up of the fundamental frequency and of integer multiples (harmonics) of that frequency, each harmonic having a particular amplitude and phase. For example, consider the simple square-wave depicted in Figure 1a. Fourier theory suggests that there are an infinite number of odd harmonics (sinusoids) that may be combined to synthesize it. As an example, if one combines only the first, third, fifth and seventh harmonics of this square wave, it results in the formation of an approximated square wave (Figure 2, from Kaufman, 1974). As more harmonics are added, the synthesized wave becomes more defined. The process of analysing a particular waveform into its sinusoidal frequency components is called power spectrum analysis.

Incorporating Fourier's theory into a model of visual processing, Campbell & Robson (1968) proposed that the

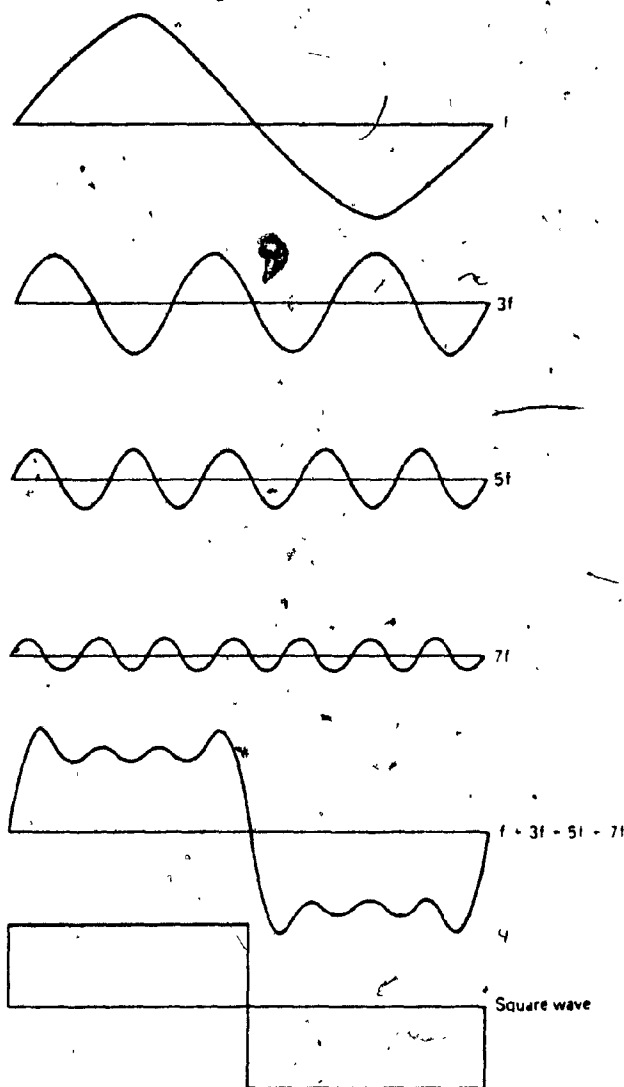


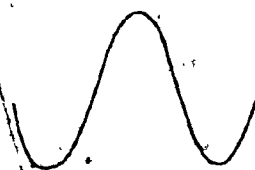
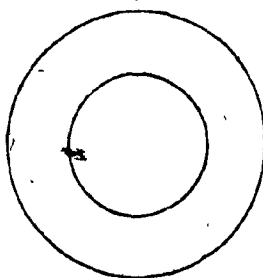
Figure 2. This illustrates how a square-wave may be approximated by summing a finite number of simple sinusoids (taken from Kaufman, 1974, pp. 105).

visual system performs a power spectrum analysis on visual information. The visual system was depicted as containing cells which are differentially sensitive to spatial frequency. They proposed that a visual stimulus is decomposed into its fourier components due to the differential stimulation of separate neural units.

Since Campbell & Robson's proposal of a multiple channel Fourier-analysing visual system, sinusoidal gratings have been more frequently used as stimuli in neurophysiological and psychophysical studies. Within the context of a "Fourier description" of visual processing, these types of stimuli are ideal, for any spatial distribution of luminance across the retina can be expressed as a sum of its sinusoidal components. Since, according to Fourier's theorem, a sinusoidal grating consists only of one frequency - the fundamental, it is a useful stimulus in assessing the spatial frequency sensitivities of neural cells. Even if one does not subscribe to the Fourier view, sinusoidal gratings have proven to be valuable stimuli in mapping out the size of receptive fields in neurophysiological studies. For instance, Figure 3 shows how a neural cell might maximally respond to a grating if the peak stimulates the center of its receptive field, while the trough overlaps with the inhibitory surround. Using gratings with different spatial frequencies, the neurophysiologist can differentially stimulate neural cells.

on-center, off surround

receptive field



grating luminance
profile

Figure 3. A sinusoidal grating may maximally stimulate a receptive field if its peak overlaps with the on-center and the troughs with the surround.

As well, these stimuli may be used to aid the psychophysical theorist in modeling human visual processing.

There have been a number of criticisms of the Fourier model. For example, one of the major criticisms is this model's inherent assumption of a linear visual system. A linear system would envision that the response of a ganglion cell for instance, would be directly related to its input (e.g., luminance). However, not all ganglion cells have been shown to behave in this linear fashion. As will be reviewed below, Enroth-Cugell & Robson (1966), as well as Maffei & Fiorentini (1977), reported that one type of ganglion cell (Y or transient cells) does not behave linearly.

Whether or not the Fourier model is a valid description of visual processing, the results of many psychophysical and neurophysiological studies strongly support the view that the visual system contains many separate channels tuned to discrete frequencies, which may or may not be independent and linear. The results of many recent studies have also demonstrated that channels may be divided into two processing systems, sustained and transient, which process different aspects of visual stimulation. The discussions below review how theorists have arrived at these conceptualizations.

Psychophysical Evidence for Multiple Channels

Psychophysical evidence for the existence of multiple channels initially came from a number of grating "adaptation studies". Gilinsky (1968) and Blakemore & Campbell (1969a), for instance, found that prior observation (adaptation) of a high contrast grating attenuated the perception of a subsequently presented grating of the same spatial frequency. Test gratings which differed in orientation from the adapting grating, however, were not affected by prior adaptation. The authors suggested that this aftereffect could have been due to the selective adaptation or fatiguing of a particular population of orientation sensitive neurons, responding to the adapting grating. Once these cells were fatigued, their subsequent stimulation by the test grating would result in reduced stimulation and hence, degraded perception. If this interpretation is correct, then the visual system would consist of at least, separate independent channels which are sensitive to orientation.

Pantle & Sekuler (1968) and Blakemore & Campbell (1969b), however, presented data which suggested that there may also exist cells, which are frequency selective. They found for instance, that adaptation to a suprathreshold square-wave (Pantle & Sekuler) or sinusoidal grating (Blakemore & Campbell) of a particular spatial frequency, resulted in an elevation of the contrast threshold for

detecting a subsequently presented grating of the same spatial frequency. This threshold elevation occurred for test gratings with spatial frequencies within approximately one and a half octaves of the adapting frequency. These data seemed to give evidence for the selective fatiguing of neural cells responding to the spatial frequency of the adapting stimulus.

These adaptation experiments supported the idea of cells independently responding to different qualitative aspects of a visual stimulus. Studies using other paradigms have further supported this multiple-channel view of visual processing. Graham & Nachmias (1971), for instance, used a novel approach in an attempt to answer this question. In their study, they compared the contrast thresholds of simple versus complex gratings. The latter were formed by superimposing two simple sinusoidal gratings (one grating had a low spatial frequency, while that of the other was three times higher), such that their peaks overlapped ("peaks add" condition). The authors argued that since a single channel is generally viewed to be linear, one would expect that a single channel's response to the compound grating would merely be the sum of the responses to the simple gratings which make it up. That is, one might have predicted that the compound grating should have been more visible than either of the simple gratings presented alone. The data however, showed that the compound grating was not

more visible than the simple ones, suggesting that a single channel model of the visual system is not sufficient in explaining these data. A multiple channel model however, seems to have less difficulty in accounting for the data.

According to the multiple channel view, the high and low spatial frequency channels would have both been responding when the compound grating was presented to the observers. The contrast threshold of the compound grating would have been reached when either of the channels began firing. This should not have differed from the case when either of the simple gratings were presented alone. That is, the contrast threshold for the complex grating should not have differed from the minimum contrast threshold of either of the simple gratings presented alone, a prediction which was supported by the data.

Campbell and Robson's (1968) notion of a multiple channel model of the human visual system was based on a contrast sensitivity study. In their experiment, they assessed the "contrast threshold" (i.e., the minimum light-dark contrast necessary to detect the presence of a grating) for various sinusoidal, square-wave and saw-toothed spatial frequency gratings. They found that thresholds for sinusoidal gratings varied as a function of spatial frequency, producing what is now known as the "contrast sensitivity function" (sensitivity being defined as the

reciprocal of threshold). They also found that observers could discriminate a square-wave grating from a sine wave grating only when the third harmonic (of the square wave) exceeded its own detection threshold. This they claimed, gave evidence for independent multiple channels of processing. They maintained that "... a model of this kind could account for (the finding) that the contrast at which a square wave grating can be distinguished from sine-wave gratings is that at which the higher harmonics reach their own threshold, since the mechanisms detecting the fundamental and the harmonics are assumed to operate more or less independently". They envisioned that the "visual system behaves not as a single detector mechanism... but as a number of independent detector mechanisms each... 'tuned' to a different frequency."

In summary, the results of the psychophysical experiments reviewed above, suggested that visual information may be processed along multiple channels consisting of cells which differentially respond to visual stimulation. Many neurophysiological studies have been conducted in an attempt to find out whether cells independently responding to visual stimulation, exist in mammalian visual systems. The following reviews studies which have found evidence for the existence of two types of neurons which respond differentially to stimulation.

Neurophysiological Evidence for Sustained and Transient Processing Systems

Kuffler's techniques of mapping out the receptive fields of the cat retina have been useful in these investigations. Using similar procedures, Enr  th-Cugell & Robson (1966) investigated the receptive field properties of retinal ganglion cells. They found that the receptive fields of both on-center and off-center varieties, possessed different spatial-summation properties. Using grating stimuli, they found that one type of cell (X cells) "responds to the sum of a number of signals from different parts of (its) receptive fields, each proportional to the local retinal illumination. That is, in the initial processes of photoreception, signal transmission and signal summation are linear". However, the behavior of another type of cell (Y cells) was described as non-linear, in that these cells would respond to any change in the light distribution over its receptive field without regard to the overall stimulation. Cleland, Dubin & Levick (1971) further characterized these two classes of cells. Their results showed that X cells, characteristically responded to the continuous presence of a stimulus (see Figure 4a), while Y cells, responded with a burst of firing to the onset of a stimulus and then minimally responded to its offset (see Figure 4b). In view of these characteristic firing responses, these cells have been referred to by many investigators as "sustained" and "transient", respectively.

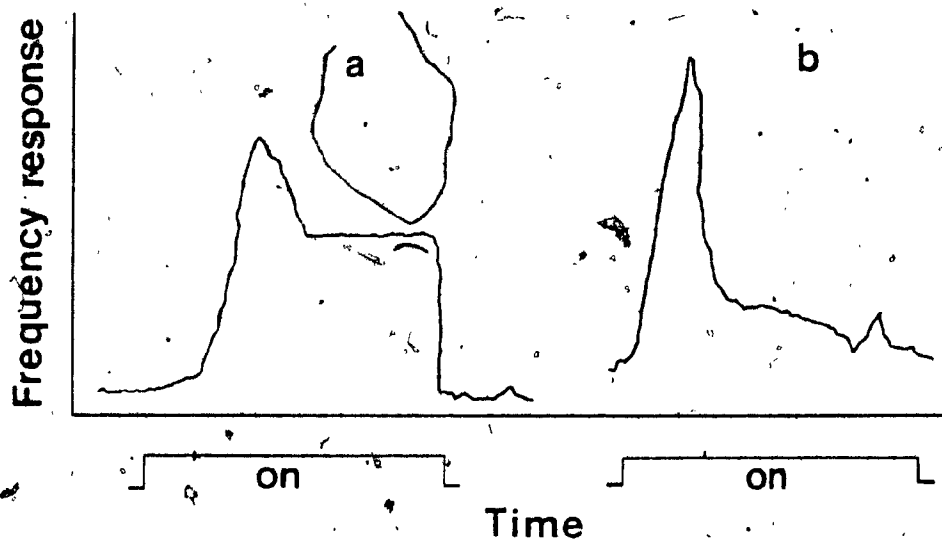


Figure 4. This is the typical response profile of oncenter, sustained (a) and transient (b) cells. Sustained cells have a longer latency to respond to stimulation than transients. They also maintain responding until the stimulus is turned off, as opposed to the transients which respond mainly to the onset and offset of a stimulus.

Since this study was published, other investigators have found these two types of cells not only in the retina (Ikeda & Wright, 1972, for example), but also in the Lateral Geniculate Nucleus (L.G.N.) (Cleland, Dubin & Levick, 1971), as well as in the visual mammalian cortex (Dow, 1974; Ikeda & Wright, 1974). Furthermore, it has been shown that sustained retinal ganglion cells project onto sustained L.G.N. neurons which in turn project onto sustained striate (cortical) neurons (Hoffman & Stone, 1971; Hoffman, Stone & Sherman, 1972). As well, transient channels originating at the retina and projecting to the L.G.N. and onto the cortex have also been reported. The results of these experiments suggested that at least two neural channels exist in the mammalian visual system.

Other physiological studies have been conducted in an attempt to elucidate the different characteristics of these two classes of cells. For instance, Dow (1974) reported that X type cells responded in a sustained manner to stationary stimuli, while Y type cells responded only to the onset and offset of stimuli and were most sensitive to rapid motion. Both types of cells showed orientation and motion direction selectively in the cortex, but they differed in transmission time. For instance, a number of studies have reported that in cats, transient cells have faster transmission rates (50 msec) than sustained cells (100 msec) (Fukuda, 1973; Dow, 1974; Ikeda & Wright, 1975).

These two groups of cells have been further delineated. Hoffman et al. (1972) and Fukuda & Stone (1974), for instance, found that the receptive fields of transient cells are larger than those of sustained cells, however the sizes of both types of receptive fields increase in the periphery. Fukuda & Stone (1974) also showed that the concentration of sustained cells is maximal in the fovea and drops off when measuring out into the periphery, while the number of transient cells is sparse in the fovea and progressively increases in the periphery.

In other neurophysiological studies, cells selectively responding to spatial frequency have been found in the retina, L.G.N., as well as in the cortex of cats. Enroth-Cugell & Robson (1966) as well as Maffei & Fiorentini (1973; 1977) for instance, used sinusoidal gratings in a neurophysiological study. In the attempt to examine the neural properties in area 17 of cats, Maffei & Fiorentini (1973) presented to the cat eye, a sinusoidal grating which could be varied in spatial frequency as well as orientation. They found that cells which had the same preferred orientation were maximally sensitive to different spatial frequency gratings.

The Maffei & Fiorentini study showed that sustained cells are more responsive to higher spatial frequencies than

transient cells. This finding has not only been supported by other studies of the cat's visual system (e.g., Cleland, Dubin & Levick, 1971; Ikeda & Wright, 1975; Hochstein & Shapley, 1976), but also with monkeys (e.g., Campbell, Cooper, Robson & Sachs, 1969; De Valois, Morgan & Snodderly, 1974; Fukuda & Rodieck, 1976).

In summary, a number of psychophysical studies have reported data supporting the proposal that visual information is processed along more than one channel. Many physiological investigations have isolated two types of cells which differ in many aspects, such as their response profiles, sensitivities, transmission times, etc. It is proposed that there may exist two broad channels in the visual system, sustained and transient and within each, there are independent channels processing different attributes of the stimulus such as spatial frequency. A number of psychophysical studies reviewed below, have provided evidence for the existence of these sustained and transient channels in the human visual system.

Evidence for Sustained and Transient Neurons in the Human Visual System

1. Contrast Thresholds

Psychophysical evidence for the existence of sustained and transient channels was first reported by Kulikowski (1971). In that study, grating stimuli were presented to observers at various spatial and temporal frequencies as well as different contrast levels. For spatial frequencies above 4 c.p.d., the perception of flicker or movement of the temporally modulated stimulus was only apparent when the contrast of the grating was elevated much above its detection threshold. However, for lower spatial frequency gratings (below 4 c.p.d.), the perception of flicker or movement, occurred consistently at the detection threshold of the grating. This seemed to imply that there may exist two mechanisms, each sensitive to different aspects of the visual stimulus. Specifically, these results suggested the existence of two types of channels, one processing spatial information and the other processing information about flicker. The mechanisms responding to flicker were also sensitive to low spatial frequency gratings, while those responding to spatial information per se, were most sensitive to higher spatial frequency gratings.

Subsequent studies have supported these findings. Keesey (1972) and Kulikowski & Tolhurst (1973) for example,

measured contrast-sensitivity functions for two separate criteria. At threshold, observers in the Kulikowski & Tolhurst experiment were asked whether or not they considered the temporally modulating stimulus to be flickering. If it did not, they were required to increase the contrast until the flicker was just apparent ("flicker threshold"). A "pattern recognition threshold" was assessed for flickering and stationary gratings by increasing the contrast of the grating until the "individual bars were evident". Kulikowski & Tolhurst reported that the results of this experiment seem to indicate that there are two distinct detection thresholds for a temporally modulated spatial frequency grating. These two thresholds vary independently with changes in temporal or spatial frequency. They went on to suggest that: "The simplest explanation is that the two thresholds are mediated by two independent sets of neurons with different spatial and temporal properties".

These investigators named these two sets of neurons as "movement analysers" and "form analysers". The movement analysers were optimally responsive to gratings of about 2 c.p.d., while the highest spatial frequency to which they would respond was about 30 c.p.d. Form analysers, however, were optimally sensitive to spatial frequencies of about 3.5 c.p.d. and may have still responded to spatial frequencies of about 50 c.p.d. The movement analysers were also

optimally responsive to stimuli temporally modulating at 5 - 6 Hz., while the form analysers, "preferred" stationary gratings. Although Kulikowski & Tolhurst admitted that there are similarities between their "analysers" and the sustained and transient cells found in the neurophysiological literature, they were hesitant to say that their data could have been readily explained by the sustained-transient models proposed by the neurophysiologists. One reason, they claimed, was that, "At present, the human form-analysers seem to be too sustained to be completely consistent with the neurophysiology".

The Kulikowski & Tolhurst study has recently come under some criticism. Burbeck (1981) for instance, suggested that the method of adjustment employed by Kulikowski & Tolhurst, may have produced methodological problems. In their procedure, the subject set his own criteria for flicker detection and pattern recognition. Burbeck claimed that in using this procedure, the data become dependent on the observers' conception of what constitutes pattern recognition and flicker detection. She also maintained that a subject in a method-of-adjustment study is required to detect flicker and recognize pattern. It may be argued that since detection of flicker is a simpler task than the recognition of a particular pattern, it may require less information to perform the task and might therefore have resulted in the lower flicker thresholds reported in the

Kulikowski & Tolhurst experiment. In the pursuit of obtaining a less subjective dependent measurement, Burbeck assessed two "independent" thresholds. A "pattern" threshold was defined as the lowest contrast at which a flickering grating could be reliably distinguished from any flickering spatially uniform stimulus. The "flicker" threshold on the other hand, was assessed by asking an observer to differentiate a flickering grating from a non-flickering one. Burbeck claimed that these two dependent measures were "criterion free" since the subject's task was to merely discriminate between pattern and spatial uniformity and between flicker and temporal uniformity. Using these dependent measures, Burbeck produced results in some disagreement with those of Kulikowski & Tolhurst. For instance, she showed that pattern sensitivity was always greater than or equal to flicker sensitivity for all temporal frequencies, whereas Kulikowski & Tolhurst showed that flicker sensitivity was always greater than pattern sensitivity. That notwithstanding, Burbeck could not disagree with Kulikowski & Tolhurst's contention that flicker and pattern may be detected by different physiological mechanisms.

Derrington & Henning (1981), however, argued against the idea of two independent processes mediating flicker and pattern perception. They found for instance, that the contrast at which subjects were able to discriminate between

horizontal and vertical gratings, showed the same dependency on spatial and temporal frequency as did detection alone.

The Derrington & Henning study has, however, has been criticised on methodological grounds. Burbeck (1981) pointed out that subjects in that study had to discriminate vertical gratings from horizontal ones, in a two-alternative forced-choice procedure. These data were compared with detection data obtained in a two-alternative forced-choice procedure in which a test stimulus had to be discriminated from a blank field. Derrington & Henning found that the discrimination and detection threshold curves had the same shape, and concluded from this that pattern sensitivity must be responsible for detection thresholds (i.e., they are mediated by the same mechanisms). Burbeck argued that in this study, two separate measurements were made. In the discrimination experiment, the observers had to make decisions regarding orientation, while in the detection task, they had to detect the presence of any spatial variation. Burbeck viewed these two measurements as being incomparable, since they were measuring two separate mechanisms. According to Burbeck, the comparison of the shapes of the threshold curves for these measurements therefore was not valid. Burbeck further argued that the methodology employed may have resulted in the artifactual lowering of discrimination thresholds. In the discrimination experiment, a test stimulus varying in

orientation was presented in two separate intervals.

Determining the orientation of one of the test stimuli was sufficient to reach the criterion. Thus, the subject had two chances to make that decision. In the detection task, however, a test was presented in one interval, while a blank field was presented in the other. The observer, in this task had only one opportunity in two to detect the presence of the test stimulus. Therefore, it was suggested that having two opportunities in the discrimination task, as opposed to one in detection, would have biased the data producing artifactually lower pattern discrimination thresholds. This controversy may continue, but that notwithstanding, many other studies seem to have implicated sustained and transient-like multiple processing mechanisms in the human visual system.

Derrington & Henning and Burbeck were testing the idea that separate spatial and temporal channels exist in the human visual system. This may or may not be associated with sustained or transient pathways. The following studies, however, asked whether there are sustained and transient pathways in the human visual system, without placing much emphasis on their functions.

Breitmeyer & Julesz (1975) investigated contrast sensitivities to sinusoidal gratings of variable spatial frequencies, when their onsets and offsets were either

abrupt or gradual. It was found that stimuli which were presented with abrupt on- and offsets as opposed to gradual ones, increased the contrast sensitivity for low spatial frequency gratings (.5 - 5 c.p.d.). This mode of presentation, however, did not alter the contrast sensitivity of the higher (5 - 15 c.p.d.) spatial frequency gratings, further supporting the idea that low spatial frequency channels are particularly sensitive to detecting temporal transients.

The results of this study were further supported by Arend (1976) and more recently by Breitmeyer & Ganz (1977), who presented sinusoidal gratings to their observers at various exposure durations. The data from these experiments suggested that contrast sensitivity for moderate to high spatial frequency gratings benefits more from increases in exposure duration than it does for low spatial frequency gratings. These results were consistent with the view that low spatial frequency stimuli are processed by channels that are sensitive to short lasting presentations, while higher spatial frequency stimuli seem to be mediated by channels most sensitive to long durations. To further elucidate these differences a number of studies have used other approaches to this problem.

2. Subthreshold Summation

Tolhurst (1975b) employing a contrast sensitivity paradigm, superimposed a subthreshold 4 msec grating (target) upon another subthreshold 800 msec grating. He found that for low spatial frequency gratings (approximately 2 c.p.d. or lower) the detectability of the target was only affected for 100 msec following the onset or offset of the longer background grating. That is, the sensitivity to the mixture of gratings seemed to have a transient profile. However, when a target with a spatial frequency of 7.6 c.p.d. was presented, the background grating (of the same spatial frequency) seemed to have a deleterious effect on target threshold for its entire 800 msec. This suggested the action of a sustained-like mechanism that could be sensitive to stimuli for the length of their exposure. From these results, Tolhurst suggested that 2 c.p.d. gratings seem to involve channels that have transient responses while gratings with spatial frequencies of 7.6 c.p.d. seem to be mediated by other mechanisms that have sustained responses. In an accompanying paper, Tolhurst (1975a) used another paradigm which has since become popular in the investigation of sustained and transient mechanisms in the human visual system.

3. Reaction Time Experiments

The use of reaction time (RT) to measure the extent to

which a visual stimulus affects visual processing has its roots in experiments conducted by Berger (1886) and Cattell (1886), both of which showed that RT is inversely related to the intensity of the visual stimulus. More recently, a number of investigators (e.g., Tolhurst, 1975a; Breitmeyer, 1975; Lupp Hauske & Wolfe, 1976; Vassilev & Mitov, 1976; Harwerth & Levi, 1978; Harwerth Boltz & Smith, 1980) have used RT in an attempt to differentiate between sustained and transient activity in human and animal visual systems.

Breitmeyer (1975), Lupp et. al. (1976) and Vassilev & Mitov (1976) for instance, all found that RT increases as a function of spatial frequency. This was interpreted as suggesting that lower spatial frequency gratings may be processed by "quick" transient cells while higher spatial frequency gratings might be processed by "slower" sustained cells.

Tolhurst (1975a), however, presented data which showed that both sustained and transient mechanisms may respond to the same spatial frequency grating. He measured reaction times to low contrast (near threshold) sinusoidal gratings, presented for long durations (500 - 2000 msec). The results of his experiment suggested that the 2 c.p.d stimuli could, under the "right conditions" (in this case, long durations) be processed by sustained mechanisms. This led the author (Tolhurst, 1975b) to later suggest that there are probably

sustained and transient channels which both respond to gratings at moderate spatial frequencies. However, he continued, "gratings of .25 c.p.d are detected solely by transient channels at all flash durations, while gratings of 10 c.p.d are detected solely by sustained channels at all durations".

Harwerth & Levi (1978) also maintained that both sustained and transient mechanisms may both respond to a single spatial frequency. For each of their suprathreshold spatial frequency gratings, they assessed RT as a function of contrast. They discovered a complex relationship between spatial frequency, contrast and reaction time. Figure 5 depicts a sample of their findings. For low and high spatial frequencies (.5 & 12 c.p.d.), a monophasic relationship between RT and contrast was evident. However, for middle spatial frequency gratings, a biphasic relationship between RT and contrast existed. For instance, for a 4 c.p.d grating presented at 50 msec, RT decreased monotonically as contrast was increased from threshold until approximately a contrast of .10. A further increase in contrast, however, resulted in a relative drop in RT, producing a break in the smooth monophasic curve. According to the authors, this "break in the curve" is consistent with the hypothesis that sustained and transient channels were operating within different contrast ranges. More specifically, the biphasic relationship between RT and

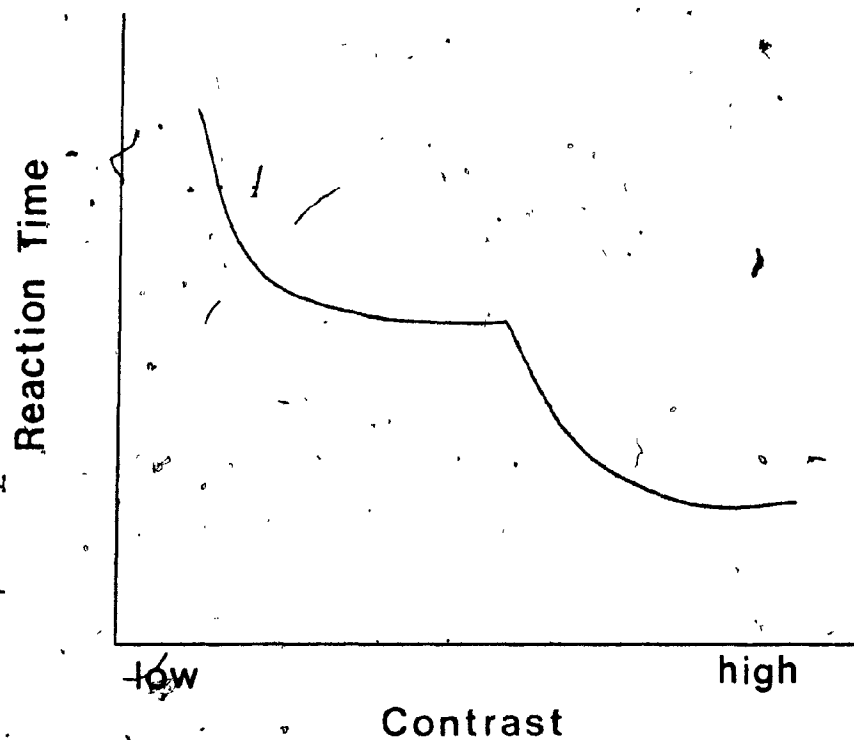


Figure 5. This is an idealized biphasic RT curve depicting the results of Harwerth & Levi (1978). It was proposed that the top portion of the curve represented the involvement of sustained cells, while the bottom portion of the curve reflected the operation of transients.

contrast suggested that "... at high contrast levels the transient channels, which have a shorter response latency than the sustained channels, are the most sensitive channels ... at lower contrast levels, the sustained channels become more effective". Further manipulations of target duration and field size were consistent with predictions that were made in the context of a sustained-transient model of the human visual system. In summary, similar to Tolhurst's (1975a) contention, Harwerth & Levi maintained that "even high spatial frequency stimuli may be detected by the transient channels", under the right stimulus conditions, and conversely low spatial frequency stimuli may be detected by the sustained channels. These results were replicated by Harwerth et al. (1980) using a combination of behavioural and psychophysical procedures with rhesus monkeys.

Both Harwerth & Levi (1978) and Harwerth et al. (1980) did not offer a description of a neural model that might account for the differential sensitivities of sustained and transient mechanisms to varying levels of stimulus contrast. Since the procedures used by these studies are of critical importance to this thesis, a model incorporating their findings will be presented in the discussion section of the first experiment.

One of the major points that was brought out in the Harwerth & Levi (1978) study, was the claim that RT is a

very sensitive measure of the processing of suprathreshold gratings, which "allows one to independently observe the function of sustained and transient channels of the visual system". If that contention is indeed correct, then RT studies offer an ideal vehicle for investigating other psychophysical phenomena which seem to implicate these two classes of cells.

Metacontrast

1. Independent and Dependent Variables

Under certain conditions, the perception of a briefly presented stimulus (target) may be degraded or occluded by another stimulus (mask), which shortly follows it in time. This effect is generally known as masking. However, with spatially non-overlapping stimuli, it is conventionally referred to as metacontrast. Metacontrast stimuli have consisted of letters (Schiller & Smith, 1965), geometric forms (Alpern, 1952), flashes of light, (Alpern, 1965) as well as square-wave (White and Lorber, 1976) and sinusoidal (Gronney, 1978) gratings.

In a typical metacontrast experiment, some measure of the effective visual impact of the target, such as brightness, contrast clarity, or detection threshold may be assessed as a function of such variables as the temporal, spatial or energy relationship between the target and mask. Changes in the dependent measure, which reflects variations in the perceptual effectiveness of the target, can be used as an index of the amount of metacontrast.

In all masking conditions, the temporal relationship between the target and mask is often used as an independent variable. The interstimulus interval (ISI) refers to the

temporal interval, usually expressed in milliseconds (msec), between the presentation offset of the first stimulus and onset of the second, while the stimulus onset asynchrony (SOA) refers to the interval separating the onsets of the two stimuli. The ISI would generally be used if the concurrent presentation of the two stimuli produces a physical contrast reduction in the target. Masking would not be an interesting phenomenon if it were merely described by a physical reduction in the contrast of the target. In fact, masking studies are invariably interested in target suppression in the absence of concurrently presented overlapping stimuli. Since physical superposition is not a problem in metacontrast, this paradigm usually involves the use of SOA as an independent variable, while other non-metacontrast masking experiments, usually employ the ISI.

The temporal order in which the target and mask are presented have been semantically distinguished in the literature. When the presentation of the target precedes that of the mask, the paradigm has been conventionally defined as metacontrast, however, when it follows the presentation of the mask, it has been referred to as paracontrast. Various metacontrast studies have assigned positive and negative values of SOA to distinguish metacontrast from paracontrast. For instance, Raab (1963) used negative values of SOA to represent metacontrast, while

Weisstein, Jurkens & Onderisin (1970) employed negative SOAs to refer to paracontrast and positive SOAs to denote metacontrast. In being consistent with Weisstein et al., positive and negative values of SOA will be used throughout this thesis to refer to metacontrast and paracontrast conditions, respectively.

Two general types of metacontrast functions have been documented in the literature. Kolars (1962) has referred to these as type A and type B functions. Type A functions (Figure 6a) usually depict maximum masking as occurring at an SOA of 0 msec. Paracontrast as well as metacontrast is evident and the masking effect tapers off as the SOA departs (either positively or negatively) from 0. Type B functions (Figure 6b) usually reflect little or no paracontrast, while peak masking occurs at some SOA (positive) greater than 0, usually between 30 - 100 msec. Type A functions have been referred to as being monotonic, while type B functions are known as non-monotonic or U-shaped. The salient parameter which seems to be related to the shape of the metacontrast function is the energy relationship (energy being defined as the product of luminance and duration) between the target and mask. It has been shown repeatedly that when the target to mask energy ratio approaches 1, the metacontrast function becomes U-shaped (Alpern, 1953; Matteson, 1969), and when the energy of the mask is greater than that of the target; that is, as the energy ratio approaches 0, monotonic

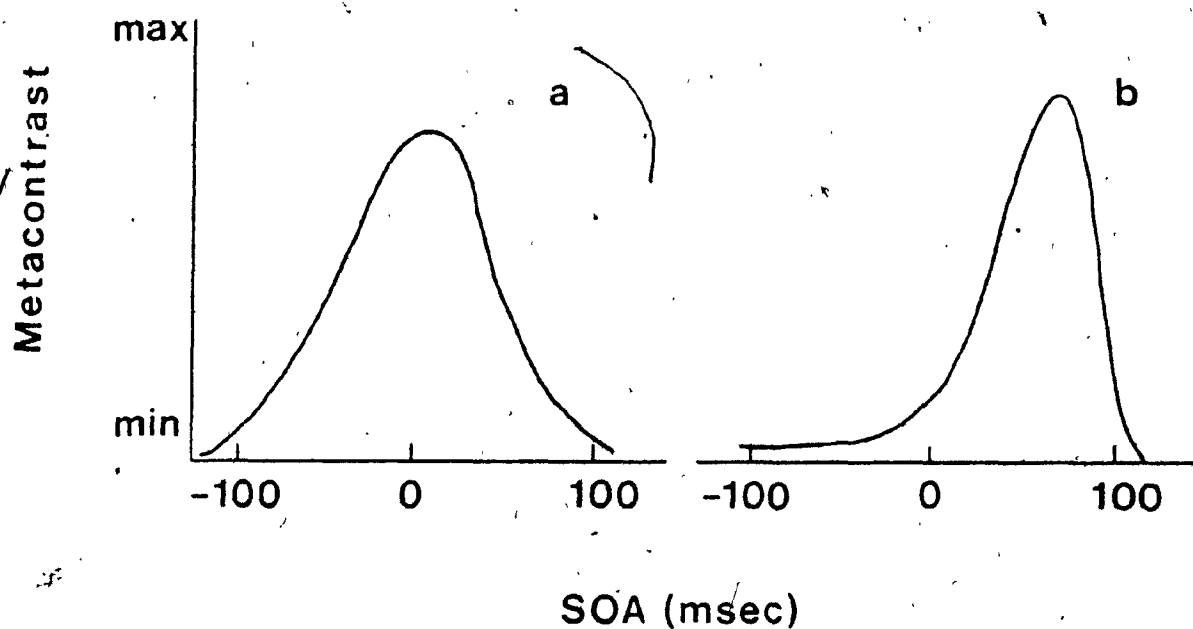


Figure 6. Function (a) depicts the typical type A or monotonic function found in metacontrast. The masking effect is maximum at an SOA of 0 and tapers off with a departure from 0. Function (b) illustrates the typical type B or non-monotonic function where little or no paracontrast is evident and maximum masking occurs at some SOA greater than 0.

functions are usually produced (Fehrer & Smith, 1962; Kolers, 1962).

2. Theories of Metacontrast

Throughout the years, many theorists have attempted to describe the perceptual, cognitive or neurophysiological mechanisms that might be responsible for this retroactive effect. Kahneman (1967) for instance, believed that metacontrast was the result of the visual system suppressing a form of "impossible motion" that was being created by the stimuli. Averbach & Coriell (1961), Lindsley (1961) and Sperling (1960) all argued that the mask, which is presented after the target, somehow interferes with any ongoing processing of the target, so that its perceptual representation is degraded. This "interference" approach developed more credence with the introduction of other more recent theories (Purcell, Stewart & Dember, 1968; Stewart & Purcell, 1974; Weisstein, 1968; Weisstein, Ozog & Szoc, 1975; Matin, 1975; Breitmeyer & Ganz, 1976) which have incorporated some of the neural mechanisms that have been recently reported in the neurophysiological literature. The theories that have received the most attention and are in addition, crucial to this discussion are those proposed by Weisstein (1968), Weisstein, Ozog & Szoc (1975) and Breitmeyer & Ganz (1976). The following reviews these theories.

a.) The Weisstein Models.

While investigating the compound eye of the Horseshoe Crab (*Limulus*), Hartline, Wagner & Ratliff (1956) reported that there are conditions in which the firing rate of cells is attenuated due to the activity of neighboring ones. They termed this suppression effect, "lateral inhibition". Since metacontrast is a perceptual phenomenon which is the result of one visual stimulus degrading a neighboring one, Weisstein (1968) proposed a single channel model of metacontrast which was based on the principles of lateral inhibition.

Her theory depicted a model of five neurons which interact in a manner producing metacontrast. The description of these neurons are based on the Rashevsky (1948) two-factor neuron which is a "responding element that combines both excitatory and inhibitory processes" having the following characteristics: If the sum of the inhibitory and excitatory influences to a neuron is above zero, it will respond in proportion to its excitation. However, if the degree of inhibition exceeds excitation, the neuron will not fire.

Two of these neurons are identical "peripheral neurons" which transmit information about the stimuli: one conveys

messages about the target, while the other processes information about the mask. The three other "centrally located" neurons are responsible for the interaction between the target and mask. One neuron is a second-order neuron which continues processing excitatory messages about the target, while the other is an inhibitory collateral coming from the peripheral neuron excited by the mask. The excitatory and inhibitory influences from the stimuli converge upon the fifth or "decision neuron".

One assumption of this model is that maximum metacontrast occurs when there is a large overlap in time between the inhibitory response of the mask and excitatory response of the target, which both converge on the "decision neuron". Another important assumption is that with equal energy stimuli, inhibition and excitation develop at different rates. With these assumptions, a U-shaped metacontrast function can be explained.

With equal-energy stimuli, the model assumes that the rate constant for the build-up of excitation for the target is slower than the rate constant for the build-up of inhibition from the mask. Therefore, at an SOA of 0, there would be a quick build-up of inhibition coming from the mask, and some time after the onset, the excitation from the target would begin to grow. Figure 7a illustrates this temporal relationship. It shows that there is minimal

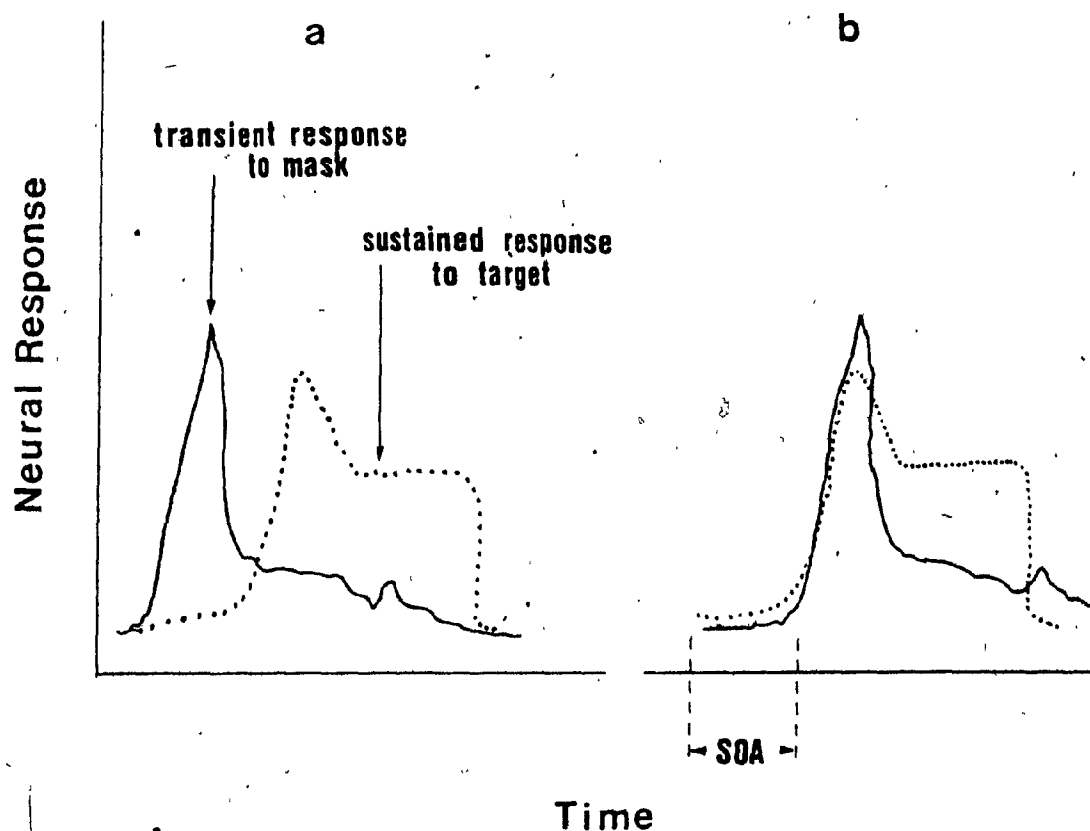


Figure 7. Weisstein's (1968) model depicts (a) the transient cells responding quicker than the sustained cells. In order to produce metacontrast the transient response to the mask must temporally overlap with the sustained response to the target. In order to accomplish this, the mask must be delayed in time (b) with the introduction of a positive SOA.

overlap of these two neural response functions, which according to the theory, would result in an absence of masking. However, if the mask was delayed in time, by introducing a longer SOA (Figure 7b) then it is possible to obtain maximum overlapping of inhibition and excitation at the "decision" neuron, resulting in maximum metacontrast. As the SOA is further increased, the excitation response to the target might build-up and terminate before the onset of the mask, resulting in little or no masking. Weisstein, Ozog & Szoc updated this model in 1975 in response to criticisms by Bridgeman (1971).

According to the authors, this revised theory seems to be able to describe metacontrast, paracontrast as well as predict when to expect U-shaped and monotonic metacontrast functions. As opposed to the earlier single-channel model of metacontrast, this modified model assumes multiple spatial and temporal channels. In addition, this model was one of the first to address the possibility that metacontrast was the result of the interaction between sustained and transient cells. The authors maintained that: "A high spatial frequency response may be thought of as a response to edges, and a low spatial frequency response may be thought of as a response to non-edges-blobs, or large, blurred shapes...". They continued to say that "... both an edge response and a non-edge response may be tied to the accumulating evidence for the presence in the visual system

of channels that respond to transient, low spatial frequency stimuli and channels which respond to sustained, high spatial frequency stimuli." It was suggested that metacontrast consisted of the "blob" (transient) response of the mask inhibiting the edge (sustained) response of the target.

The Weisstein, Ozog & Szoc model also addressed type A metacontrast functions. They maintained that as one increases the energy of a stimulus, there is a resultant spreading out in time, or "smearing" of the neural response to that stimulus. That is, with high energy masks, the response of the inhibitory neuron would be so great (in response time and firing rate see Figure 8) that "one will not have to delay presentation of the mask as much, as its energy increases, in order to have it interfere with the target, and thus the metacontrast functions will shift their minima toward the origin".

To account for paracontrast, this version describes an inhibitory collateral coming from the target and excitatory component emanating from the mask. That is, the model proposed that the sustained response from the mask inhibits the transient response from the target, which produces minimal (because of the limited role transients play in mediating form perception) paracontrast functions. This function would normally be U-shaped, because the target

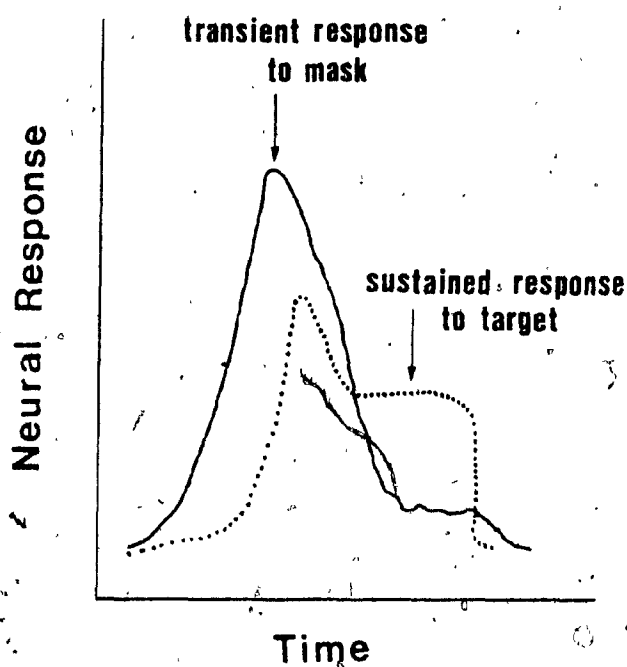


Figure 8. Weisstein et al. (1975) suggested that with higher energy masks, the transient cells respond with a greater magnitude and "smeared" out over time. That is, in order to produce metacontrast, the mask does not have to be delayed in time for its transient response to overlap with the sustained response to the target.

would have to be delayed in time in order to maximize the neural overlap between the excitatory and inhibitory influences at the "decision" neuron. The sustained-transient view of metacontrast has gained further support from a model proposed by Breitmeyer & Ganz (1976).

b.) The Breitmeyer & Ganz (1976) Model.

Breitmeyer & Ganz (1976) described inhibitory interactions between sustained and transient classes of cells in a similar manner to Weisstein, Ozog & Szoc (1975). Their theory differs, however, in their description of the neural mechanisms mediating paracontrast, and type A metacontrast functions. In describing metacontrast, Breitmeyer & Ganz do not basically differ from that of Weisstein et al. They portray the mechanism of interchannel inhibition producing metacontrast. This consists of the transient cells responding to the mask inhibiting the sustained cells responding to the target. Similar to the Weisstein model, the authors also maintained that inhibition is the result of the temporal overlap of the responses of the sustained and transient channels. When a stimulus is presented, the transient response immediately results with a burst of activity. The sustained response to that stimulation occurs sometime between 50 - 100 msec later (as a result of the different response latencies of the two channels). When two stimuli are presented in rapid,

succession (with a 50 - 100 msec delay), the delayed faster transient activity produced by the mask presentation overlapping between the two channels, results in the production of metacontrast at some SOA greater than 0.

Weisstein et al. (1975) proposed that paracontrast is the result of the inhibition of transient channels by sustained channels. Breitmeyer & Ganz however, cite Fiorentini & Maffei's (1970) study which showed that strong paracontrast existed between a disk and annulus which were both modulated at low temporal frequencies, where transient channels are usually not operating. This suggested to Breitmeyer & Ganz, that paracontrast may be mediated by intrachannel inhibition rather than interchannel inhibition as proposed by Weisstein et al. More specifically, the authors suggested that paracontrast arises in the antagonistic center-surround organization of sustained-type visual receptive fields. This suppression, in the form of lateral inhibition is exerted by the antagonistic surround on the excitatory center of the receptive field. Since it is known that the response of the receptive field's antagonistic surround of the cat retinal ganglion cells is slower than that of the center, (Maffei, Cervetto, & Fiorentini, 1970), the model proposes that in order to generate maximum inhibition (paracontrast), the center excitatory stimulus (target) must be delayed in time after the onset of the inhibitory surround (mask). This

interaction would predict U-shaped paracontrast functions.

The model also differs from that of Weisstein et al's in the conceptualization of type A metacontrast functions. Rather than envisioning a "smearing out" of the higher energy transient response of the mask, Breitmeyer & Ganz suggested that as the energy of a stimulus is increased, the sensitive transient neurons would saturate sooner than the sustained neurons. This implies that as the mask energy is raised relative to that of the target, the mask sustained cells would produce a relatively greater response, while the mask transient neurons would show little if no increase in response rate. If the transient neurons saturate, then as the energy of the mask is increased, the activity of the sustained cells would be greater than that of the transient cells. It was proposed that because of this greater activity level, more inhibition develops if the sustained neural responses of the target and mask summate rather than if the transient and sustained responses combine. As the authors suggest, this would result in "larger intrachannel inhibition prevailing" while the model predicts "a shift of the peak metacontrast effect toward lower SOAs, as the target-mask energy ratio increases".

In summary then, Weisstein et al. (1975) and Breitmeyer & Ganz (1976) have proposed that the visual system contains multiple channels which have different temporal and spatial

characteristics. These channels process visual information in a manner that results, under certain conditions, in the production of meta² and paracontrast. Critical to these theories is the interaction of sustained and transient cells. If it was possible to differentially manipulate the activity of these two groups of cells in a metacontrast paradigm, then one might not only be able to test the validity of these theories, but it would be possible to examine how these two groups of cells interact.

3. Recent Experimental Approaches

One method of varying the activity level of sustained or transient cells was discussed earlier. That is, there is evidence that low spatial frequencies maximally stimulate transient cells, whereas higher spatial frequencies mostly stimulate sustained cells.

A number of studies have used sinusoidal and square-wave gratings as metacontrast stimuli. White & Lorber (1976) for instance, using high contrast square-wave gratings in a metacontrast paradigm, investigated how metacontrast varied as function of target and mask spatial frequency. Using targets of 6 and 12 c.p.d. and masks of 1.5, 3, 4, 6, 12 and 24 c.p.d. they found maximal metacontrast when the spatial frequencies of the target and mask were approximately equal, while masking decreased as

the spatial frequency of the stimuli diverged. The results led White & Lorber to speculate that the magnitude of the metacontrast effect depends on the spatial frequency similarity of the target and mask. This proposal is in contradiction with predictions that the Weisstein et al. or Breitmeyer & Ganz theories would have made. These theories would have predicted that if metacontrast is mediated by transient cells responding to the mask, inhibiting sustained cells reacting to the target, one would predict that maximum metacontrast would be produced by low spatial frequency masks (involving mostly transient cells) inhibiting higher spatial frequency targets (which involve mainly sustained cell activity).

Although the results of this experiment do not support the sustained-transient models proposed above, the paradigm may not have truly been a test of these theories, for two reasons. Firstly, the authors employed square wave gratings which can be analysed into a fundamental frequency and many other higher sinusoidal spatial frequency components (harmonics). Thus, the extent to which sustained and transient cells were responding to the different spatial frequency gratings, is not clear. Secondly, the authors employed high contrast stimuli (.78). According to the results of Harwerth & Levi (1978) these high contrast stimuli may have primarily stimulated the transient system, such that transient rather than sustained cells mediated the

processing of the target and mask. This would have precluding any sustained-transient interactions.

Growney (1978) avoided one of these problems by conducting a metacontrast experiment using sinusoidal gratings as the stimuli. In this study, metacontrast effects were assessed on a blank field (gate target) and a 5 c.p.d. spatial frequency grating (5 c.p.d. target) as a function of mask modulation frequency, ISI, and spatial separation between the target and mask. The results of this study were similar to those obtained with nonmodulated stimuli. That is, the metacontrast effect was shown to vary as a nonmonotonic function of ISI and was maximal when the target and mask were spatially adjacent. The effect of mask modulation, however, was not as clear. The perceived contrast of the 5 c.p.d. target was maximally attenuated by masks having spatial frequencies of 3 - 5 c.p.d., a finding in support of the "similarity" hypothesis proposed by White and Lorber. However, the perceived brightness of the "gate target" was highly degraded by most of the masks. For one observer it was best masked by a 5 c.p.d. stimulus, while for the other observer, a blank field mask (gate mask) was most effective. The sustained-transient description of metacontrast found support in the result that the ISI at which maximum masking occurred, was longer for the 5 c.p.d. target than that of the gate target. Presumably, the 5 c.p.d. target would have stimulated more sustained cells

than the gate (low spatial frequency) target. Since sustained cells have a longer latency, the onset of their excitation would have to be delayed in order to produce maximum overlapping of the sustained and transient responses.

In summary, then, the Growney experiment was not successful in elucidating the interaction of sustained and transient neurons. The failure of this experiment to do so, may be found by looking at the stimulus contrasts levels used. All of the stimuli used by Growney had a Michelson contrast ratio of .64. Harwerth & Levi (1978) presented data which implied that sinusoidal gratings presented at this contrast level are processed solely by transient cells. This would imply that if metacontrast involves the interaction of sustained and transient neurons, then Growney eliminated the possibility of this occurrence by using high contrast stimuli. It must be pointed out however, that the Harwerth & Levi investigation involved reaction times to suprathreshold gratings, while the Growney experiment consisted of brightness and clarity magnitude estimates of sinusoidal gratings in a metacontrast study. It is possible that these two paradigms are mediated by separate neural mechanisms that have little or no common properties. However, before entertaining this possibility, it is first necessary to study these two methods of investigating sustained and transient mechanisms and attempt to evaluate

their relationship, if any.

Statement of the Problem

The main impetus of this thesis is to attempt to elucidate the characteristics of sustained and transient channels in the human visual system. The approach is to first replicate Harwerth & Levi's experiment with two types of stimuli. In Experiment 1, the RT to a foveally presented 16-msec stimulus is assessed for various spatial frequency gratings. In Experiment 2, RT is measured to a 16-msec stimulus also varying in spatial frequency, presented in the periphery. Using an interpretation similar to Harwerth & Levi, sustained and transient channel activity is inferred for the different spatial frequency stimuli as a function of contrast. Using these inferences concerning the conditions under which sustained and transient activity are observed, a metacontrast experiment is conducted in Experiment 3. Using the same foveal and peripheral stimuli as used in Experiments 1 and 2, metacontrast functions are obtained under different contrast conditions of the target and mask. Based on the Weisstein et al. (1975) and Breitmeyer & Ganz (1976) models of metacontrast, various predictions about the shape of the metacontrast function are made as a function of the spatial frequency and contrast of the target and mask.

The physical characteristics of the stimuli in this

experiment (and that of Experiments 1 and 2) were similar to those employed by Growney (1978) (in both studies the stimuli were presented for 16 msec and were of similar size). The rationale of using these stimuli was an attempt to replicate Growney's metacontrast results within a condition of Experiment 3. That is, if the data from the Growney experiment were produced as a function of the high contrast stimuli, then these same stimulus conditions should generate similar metacontrast functions as those reported by Growney.

Experiment 1

Harwerth & Levi (1978) found that RT to a sinusoidal grating varied as a function of spatial frequency as well as contrast level. As was discussed earlier, this relationship was complex. For targets presented at 50 msec., the biphasic relationship between RT and contrast was evident for spatial frequencies of 1 - 12 c.p.d., and was monophasic for a .5 c.p.d. stimulus. In this study a shorter 16 msec target was used. It was hypothesized that if RT to a stimulus presented at this shorter duration is more likely to be mediated by transient cells (since these cells have been found to be involved in the processing of brief stimuli), then these cells may be involved in the processing of higher spatial frequencies. Thus, it was predicted that for Experiment 1, a monophasic RT function would occur for higher spatial frequency gratings than that found by Harwerth & Levi.

Method

Subjects. Three observers, all with normal or corrected-to-normal vision (Keystone School Vision Screening Test) participated in Experiment 1.

Apparatus. Sinusoidal gratings were produced using a method similar to that employed by Campbell & Green (1965). The stimuli were presented on the face of a Techtronix 5403

oscilloscope having a P-31 blue-green phosphor. A Tektronix FG 501 waveform generator fed a 100 kHz. triangle wave to the vertical amplifier (Y-axis), which resulted in the screen being entirely filled with a uniform luminance (10 cd/m^2). The grating pattern was created by modulating this raster with a sinusoidally-varying voltage input (synchronized to the X-sweep of the oscilloscope) to the intensity input (Z-axis) of the oscilloscope. A sine-wave generator specially designed for this study (Mundl, 1982) provided this voltage input to the Z-axis.

The face of the oscilloscope was masked by a piece of black paper. A rectangular hole was cut out, producing a stimulus of three degrees in width, by one and a half degrees in height (viewed from a distance of one metre). The Z-axis was modulated in such a way as to produce sinusoidal waveform patterns containing two abrupt transitions in frequency and amplitude. The two transitions divided the stimulus into three horizontally adjacent sections of equal area (see Figure 9). The centre section contained the target stimulus. Its onset, offset, contrast and spatial frequency were independently adjusted. The adjacent areas to the target consisted of the "peripheral" stimulus. As well, its onset, offset, contrast and spatial frequency were independently controlled.

The target and "peripheral" stimulus signals were fed

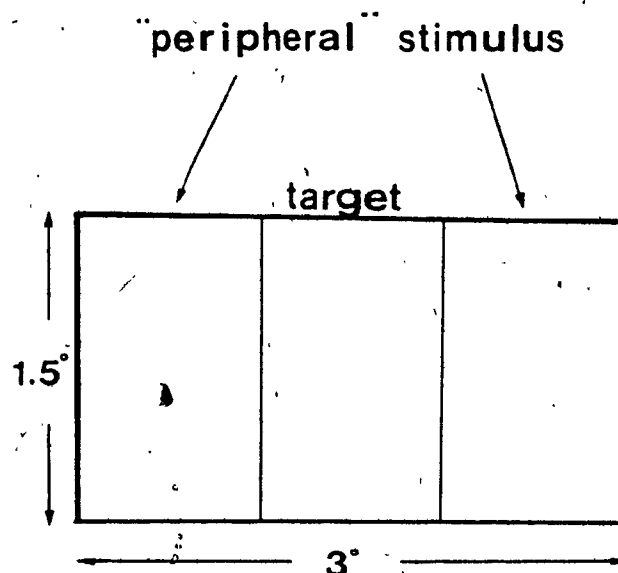


Figure 9. The stimuli used in these experiments are illustrated. The central area measures $1^\circ \times 1.5^\circ$ and consists of the target stimulus. The peripheral stimuli measure $1^\circ \times 1.5^\circ$ each. The lines dividing the sections corresponded to the "chart tape" which physically divided the screen in the experiment.

into "analog gates" which could each be independently "gated" by signals from a Coulbourn logic system. The output from these analog gates then converged onto a summing amplifier which produced the final output to the Z-axis.

One of the artifacts produced by the wave-form generator, were two narrow bright lines which occurred at the transition points between the stimuli. These lines varied in intensity as a function of contrast, spatial frequency and phase of the stimuli. In order to eliminate the possibility that these varying artifactual lines would influence the results of the experiments, two thin lengths of "chart-tape", which each had widths of less than one min. of visual angle, were affixed to the oscilloscope such that they superposed the bright lines. As a result, the display was physically divided into three perceptible sections.

As mentioned earlier, the contrast of a grating is measured as a function of the luminance at the peak and trough. Since the absolute peak or trough of a grating is merely one point on the display, it is impossible to take photometric readings with a conventional photometer. Thus, in order to measure the luminance at these points, a full screen of uniform luminance was created by driving the Z-axis with a steady voltage set to that of the peak or trough of the sinusoidal waveform. In this manner, for different Z-axis voltages, the luminance level at the peak

and trough of the sinusoid was adjusted and measured using a Spectra Spotmeter Photometer (Photo Research; model UBD -1/2). Using these peak and trough luminance values, the MCRs were assessed as a function of the Z-axis voltage level.

This procedure revealed, that as the contrast of the grating was increased beyond a critical amount, the mean luminance (i.e. the luminance at the peak plus the luminance at the trough divided by 2) of the display tended to increase. Pilot work revealed that two alternating blank fields differing in luminance level by more than 3 percent resulted in perceptual differences. Therefore, an apriori decision was made, limiting the use of stimuli which had mean luminance increases of not more than 3 percent. This precluded the use of gratings having MCRs more than approximately .41.

A Coulbourn logic system was used to control the experimental parameters. Reaction time was measured with a Lafayette Instruments (1 msec resolution) timer.

Procedure. In order to avoid difficulties arising with binocular fusion, all the observers monocularly viewed the stimuli. A timing schematic for the experimental procedure is illustrated in Figure 10. Prior to the beginning of the experiment, the observers dark adapted for 5 minutes. They

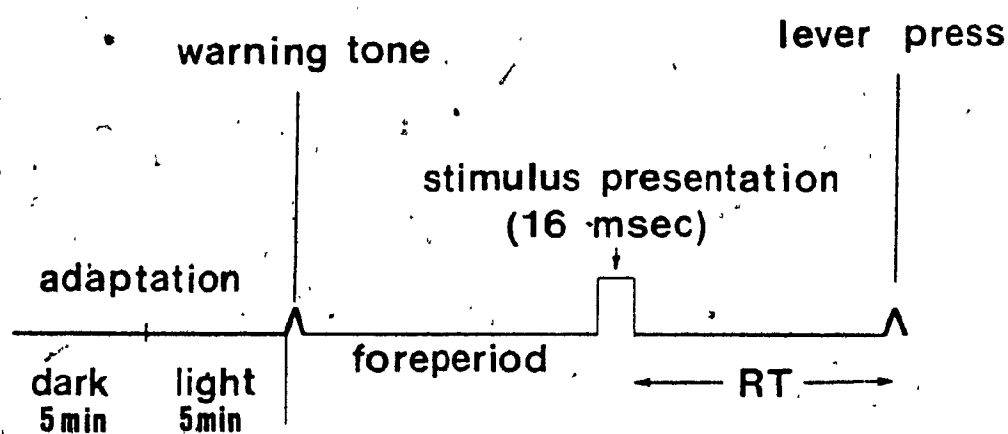


Figure 10. The timing schematic for the procedure of Experiment 1 is illustrated.

then, freely viewed the three adjacent 10 cd/m^2 blank fields (light adapted) for another 5 minutes.

The beginning of each trial was signaled to the observer with a warning tone that preceded a variable duration foreperiod to the onset of the central target. At the warning tone, the observers were instructed to fixate in the middle of the central target area. The duration of the foreperiod varied between 500 - 2000 msec in 100 msec steps. During this time, the target could occur with a .0625 probability at the end of any 100 msec period. The end of the foreperiod triggered both the presentation of the 16-msec. target, as well as the reaction time clock. Reaction time was measured from the onset of this clock to its offset, which was initiated with a lever press by the observer. If the observer did not press the lever within 1 second from the onset of the stimulus, then data from this trial was eliminated because it was assumed that he did not see the stimulus. Following each target presentation, there was a 10 second interval, at which time the observer freely viewed the lit fields. When the target was presented, the luminance level in the adjacent peripheral areas did not vary from the mean adapting luminance level.

Five (2, 4, 6, 8, & 10 c.p.d.) centrally located spatial frequency targets were used. For each target, 20 reaction times were taken at each contrast level in blocks

of ten trials. Contrast varied in approximate .05 log unit intervals, between the individually determined thresholds and a contrast of approximately .41. On a given session, a target spatial frequency was randomly selected. For each randomly selected contrast level, 10 RTs were taken, each preceded by a randomly determined foreperiod. This required 10 experimental sessions of one hour duration for each observer.

The observers practiced at this task for at least five sessions prior to collecting the data. The contrast threshold for each grating was determined at this time. It was defined as the level, at which approximately twenty trials were required to obtain ten reaction time measurements of less than 1 second (Harwerth & Levi, 1978). Data was collected on three observers, two of whom were naive with respect to the purpose of the experiment.

Results

The figures presented in this section each represent one block of replications (10) for each spatial frequency grating, instead of the collapsed average over both replications. The rationale for doing this, is demonstrated by referring to Figure 11. Figure 11a shows a RT curve plotted as a function of grating contrast. The idealized discontinuity (or break) in the curve reflects some of the typical data revealed in this study. Figure 11b shows how this break may occur at different contrasts, for two replications. As will be discussed below, this occurrence was not unusual in the data. That is, these breaks would occur at different contrasts for the same spatial frequency grating in both replications. Figure 11c displays what happens to the break in the curve if two functions with discontinuities occurring at different contrasts are collapsed; the break "washes out". Possible explanations of these replication differences is outlined in the following discussion section. In order to eliminate the possibility of "washing out" the effect being looked at, the data is presented in blocks of 10 replications each.

For all subjects, mean reaction time was plotted as a function of contrast level. The curve fitting procedure that was used, was first described by Mansfield (1973). Best fitting power functions were computed to maximize the

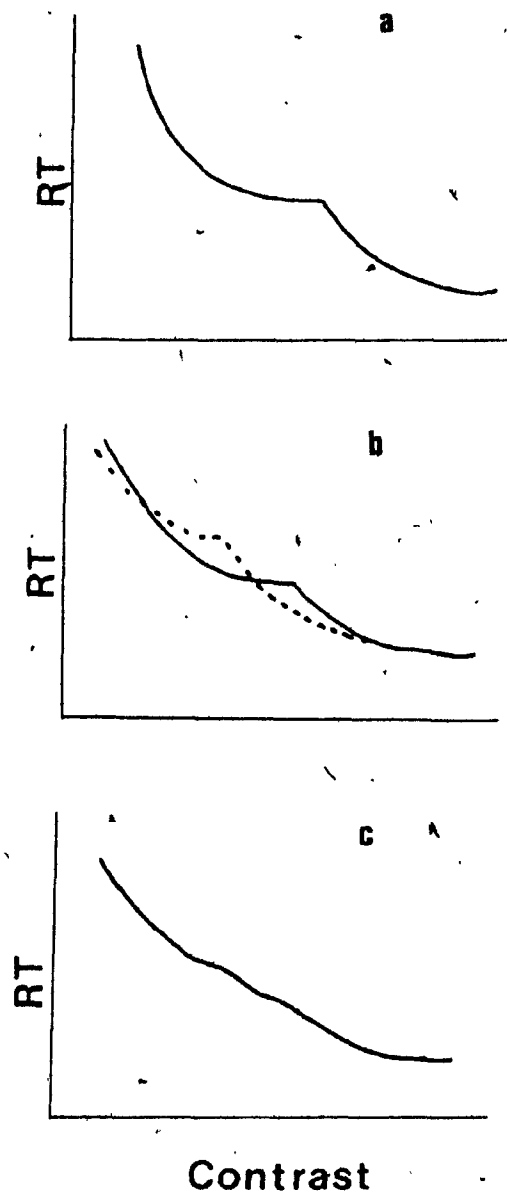


Figure 11. This illustrates how the discontinuity in the RT function (a) occurred at different contrasts for 2 replications (b). If the curves in (b) are collapsed, the resulting RT curve (c) "washes-out" the discontinuity.

resulting correlation coefficients between the predicted and obtained data. As an example, consider the RT points above the discontinuity. Through successive iterations, power functions were assessed (beginning with the values assessed at the lowest contrast level), each taking into account another data point. Correlation coefficients between .95 - .98 were commonly found prior to the discontinuity. However, at the "break-point" in the curve, the correlation coefficients would drop indicating the need for assessing another power function to describe the data beyond the break.

Figures 12a and 12b each displays subject BK's mean reaction times for the 5 target spatial frequencies, for one block of 10 replications each. For each spatial frequency, the longest RT was to a grating, approximately .05 log units above the contrast threshold. For all of the spatial frequencies, RT decreased as a function of contrast. The standard errors for the points near threshold were greater than those at the higher contrast levels, reflecting a more difficult task near threshold. The standard errors, which are displayed in BK's data, did not exceed 25 msec for any of the observers. BK's data typifies those of the other observers. RT seemed to increase as a function of spatial frequency, for gratings having a frequency of less than 8 c.p.d. For both BK and PB, standard errors revealed that RTs did not differ in magnitude for the 8 and 10 c.p.d.

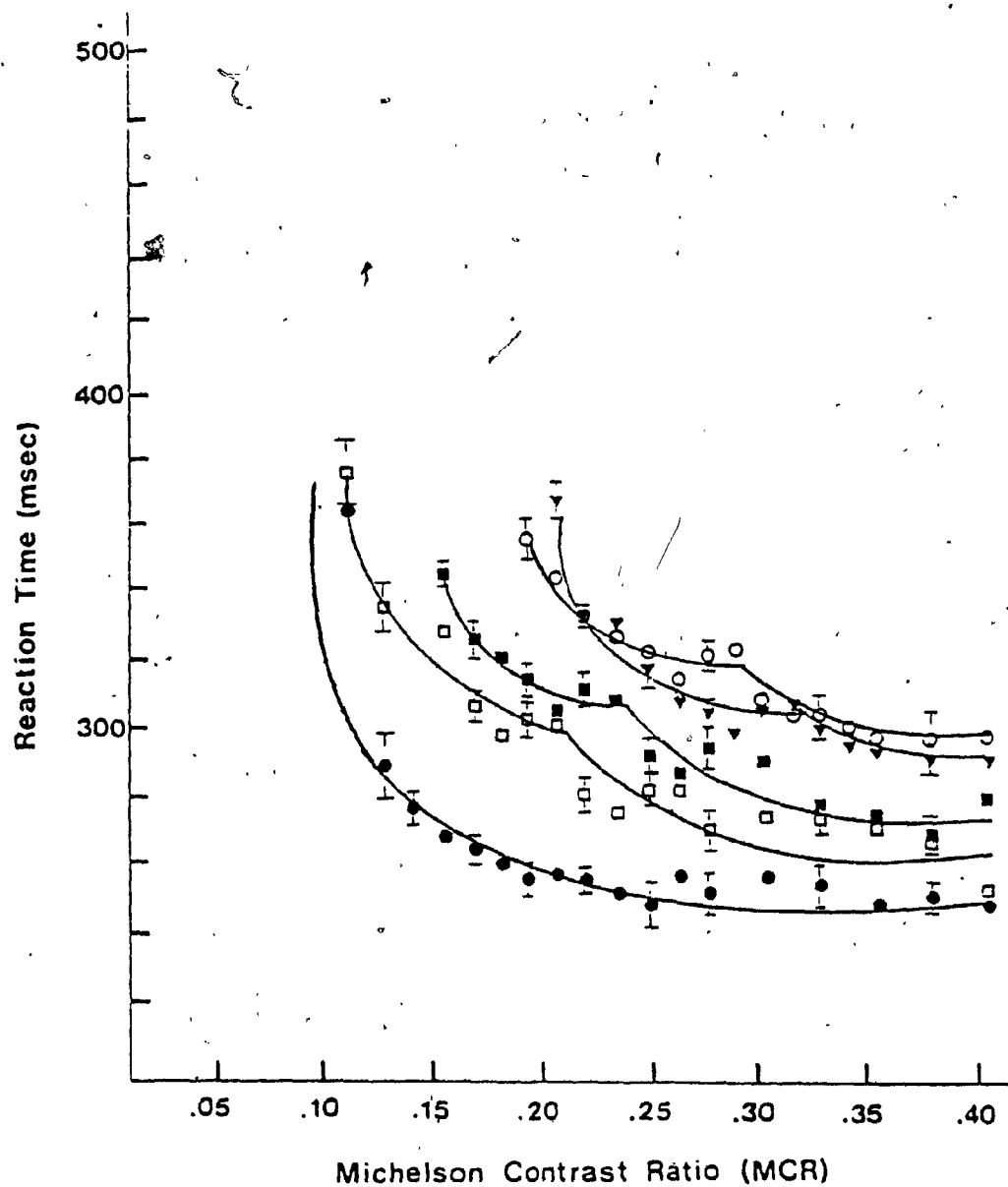


Figure 12a. Reaction Time as a function of target contrast for observer BK (Replication 1). Target frequency: ● 2; □ 4; ■ 6; ○ 8; ▼ 10.

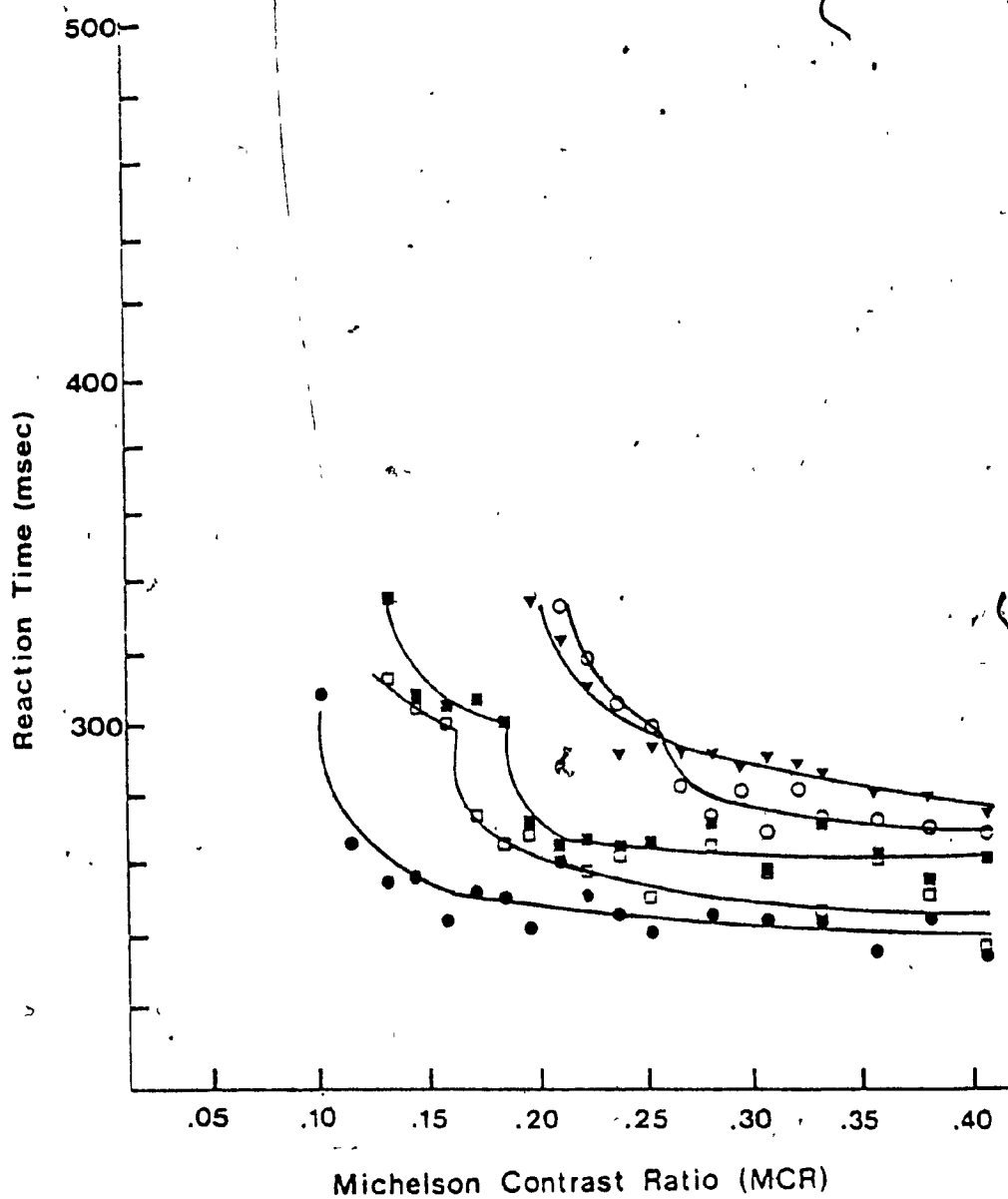


Figure 12b. Reaction Time as a function of target contrast for Observer BK (Replication 2). Target frequency: ● 2; □ 4; ■ 6; ○ 8; ▼ 10.

grating in both replications. However for SS, standard errors revealed longer RTs for the 10 c.p.d. grating than for the 8 c.p.d. stimulus.

Discontinuities were evident in the data. In Figure 12a, breaks occurred for all gratings with spatial frequencies greater than 2 c.p.d. With increasing frequency, the location of the break varied as a function of contrast. These discontinuities occurred at contrasts of .20, .24, .29 and .32 for spatial frequencies of 4, 6, 8, and 10 c.p.d., respectively. For the 2 c.p.d. grating, RT varied monotonically with contrast. That is, a break in the RT curve did not occur. Figure 12b also demonstrates that the discontinuity occurred at different contrasts for another replication of the same stimulus conditions. For these data, the breaks occurred at contrasts of .15, .18 and .26 for spatial frequencies of 4, 6 and 8 c.p.d., respectively. An absence of the discontinuity was also evident at 10 c.p.d., in this replication.

Similar results can be seen in Figures 13 and 14 which reflect the data of subjects PB and SS respectively. For both subjects, RT varied as a function of both spatial frequency and contrast. That is, RT seemed to increase with spatial frequency and decreased with contrast. Similar discontinuous curves were evident for all of the targets except the 2 c.p.d. stimulus where a monotonic curve was

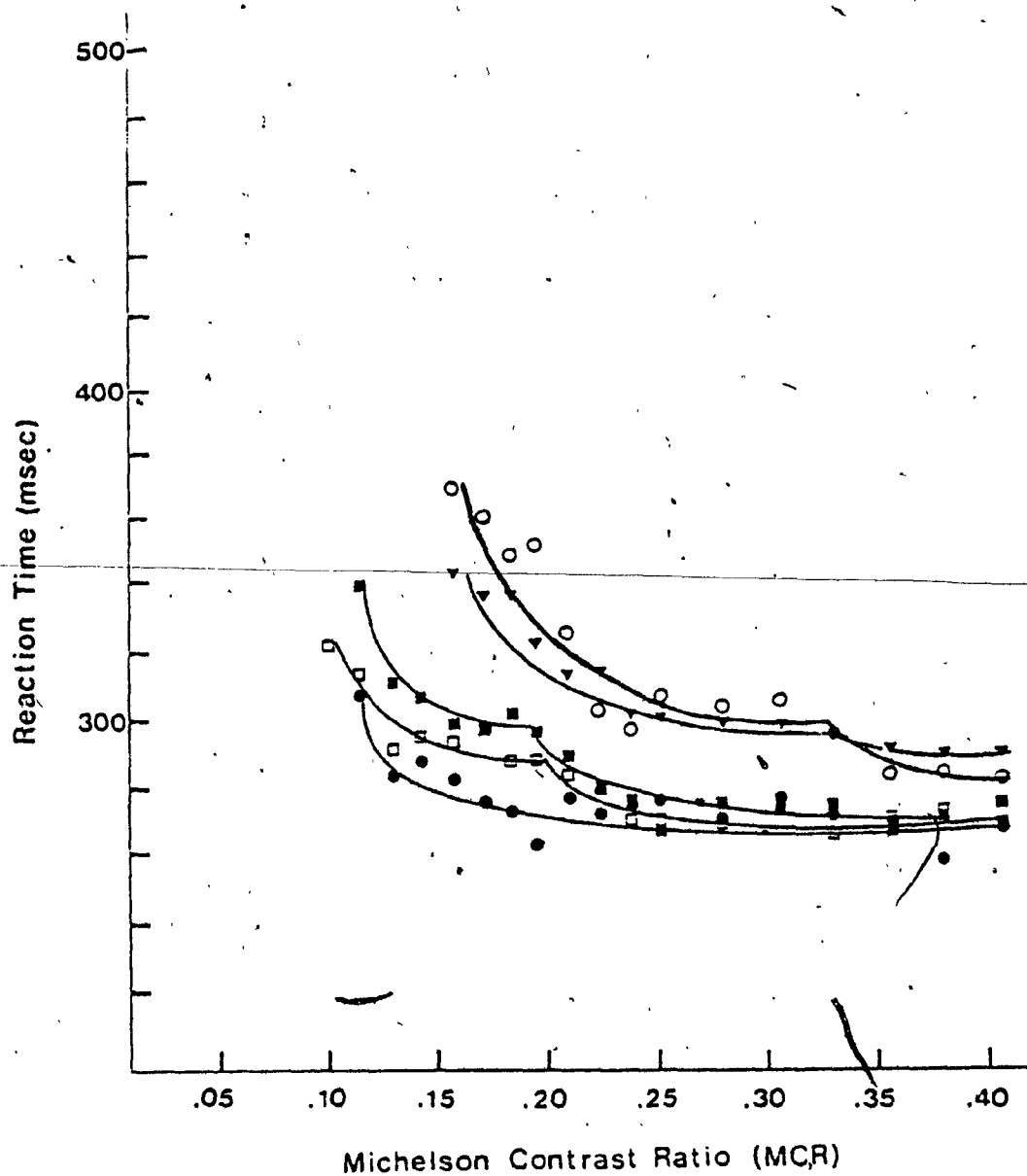


Figure 13a. Reaction Time as a function of target contrast for Observer PB (Replication 1. Target frequency: ●2; □4; ■6; ○8; ▼10.

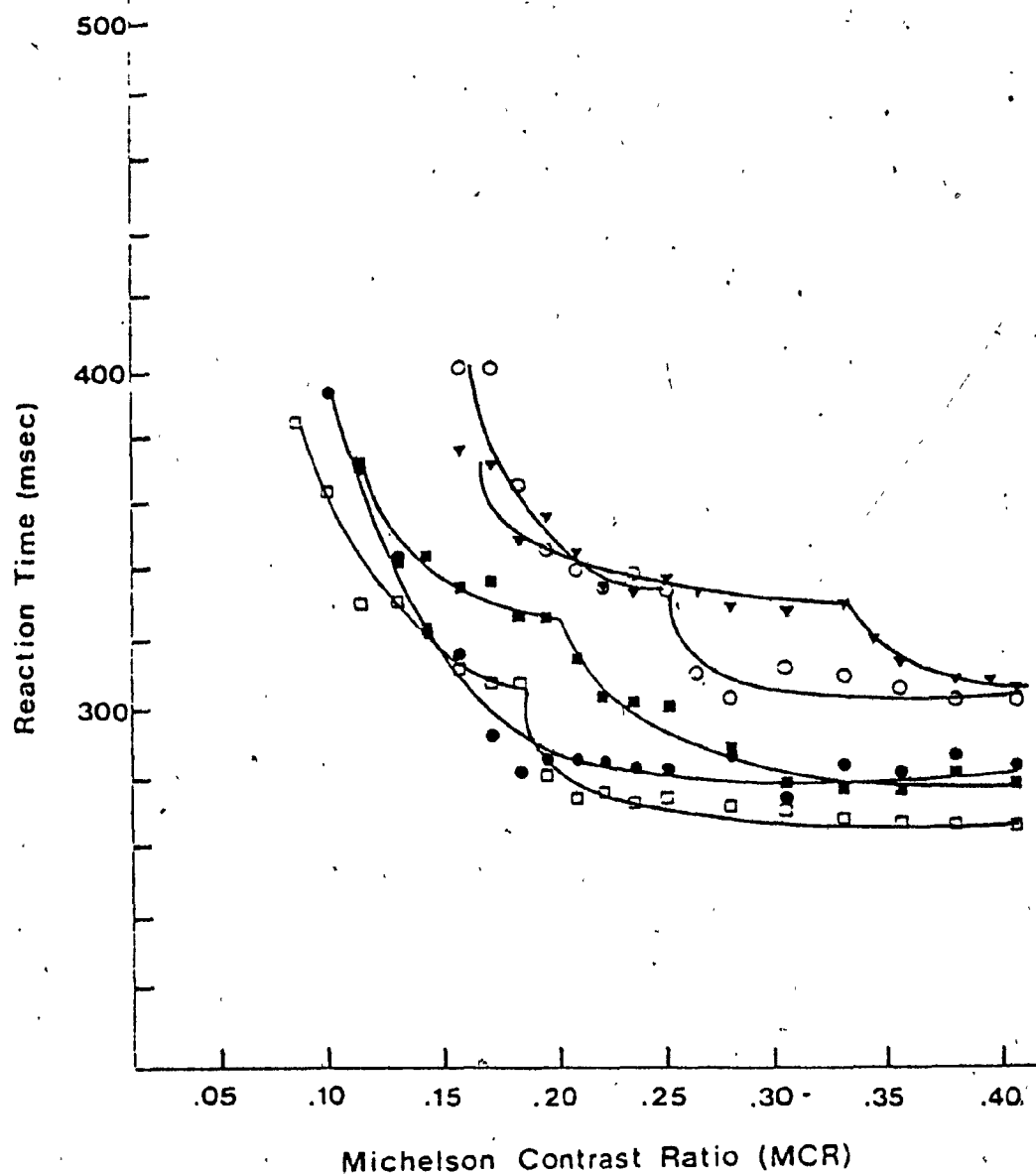


Figure 13b. Reaction Time as a function of target contrast for Observer PB (Replication 2). Target frequency: ● 2; □ 4; ■ 6; ○ 8; ▼ 10.

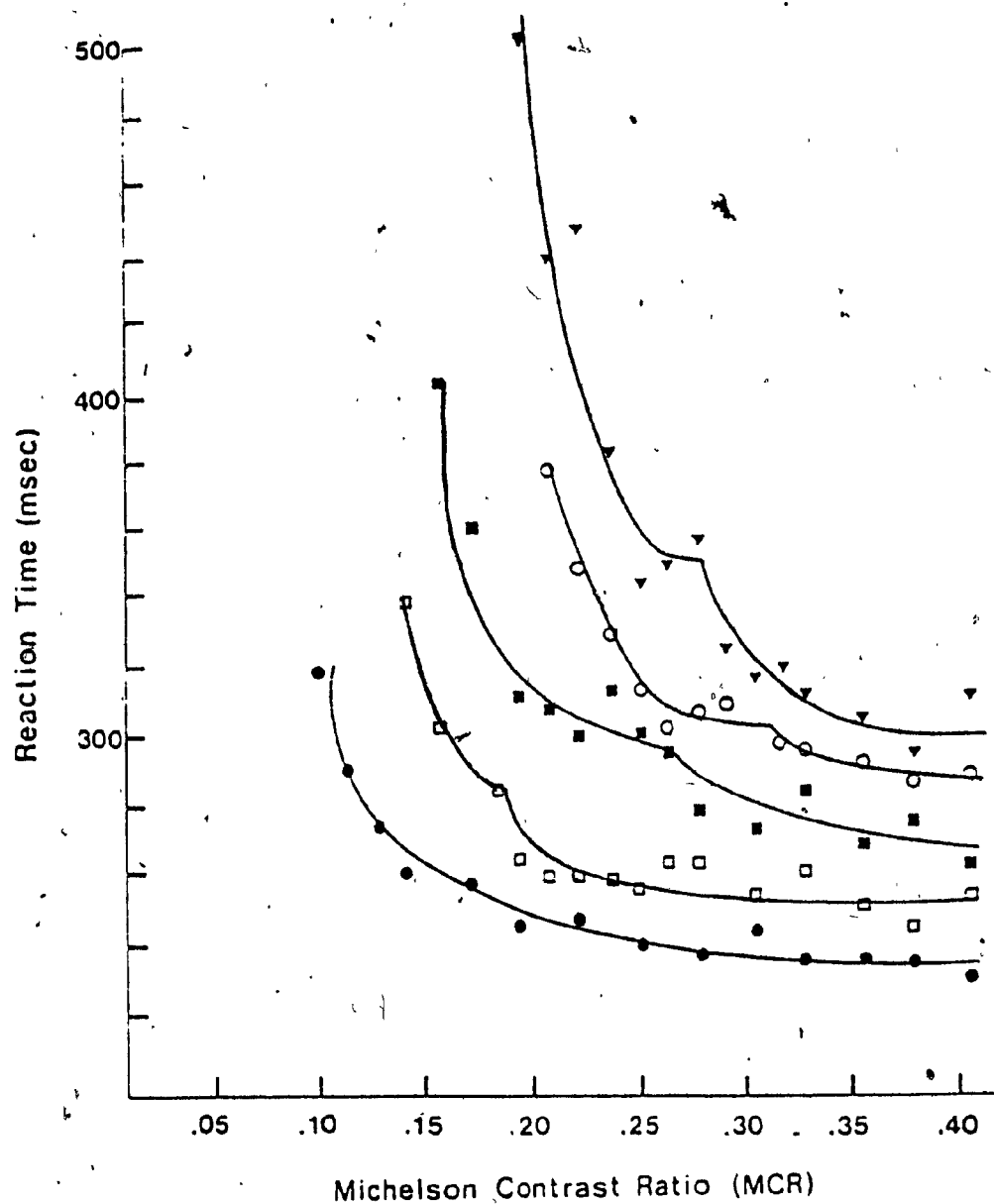


Figure 14a. Reaction Time as a function of target contrast for Observer SS (Replication 1). Target frequency: ● 2; □ 4; ■ 6; ○ 8; ▼ 10.

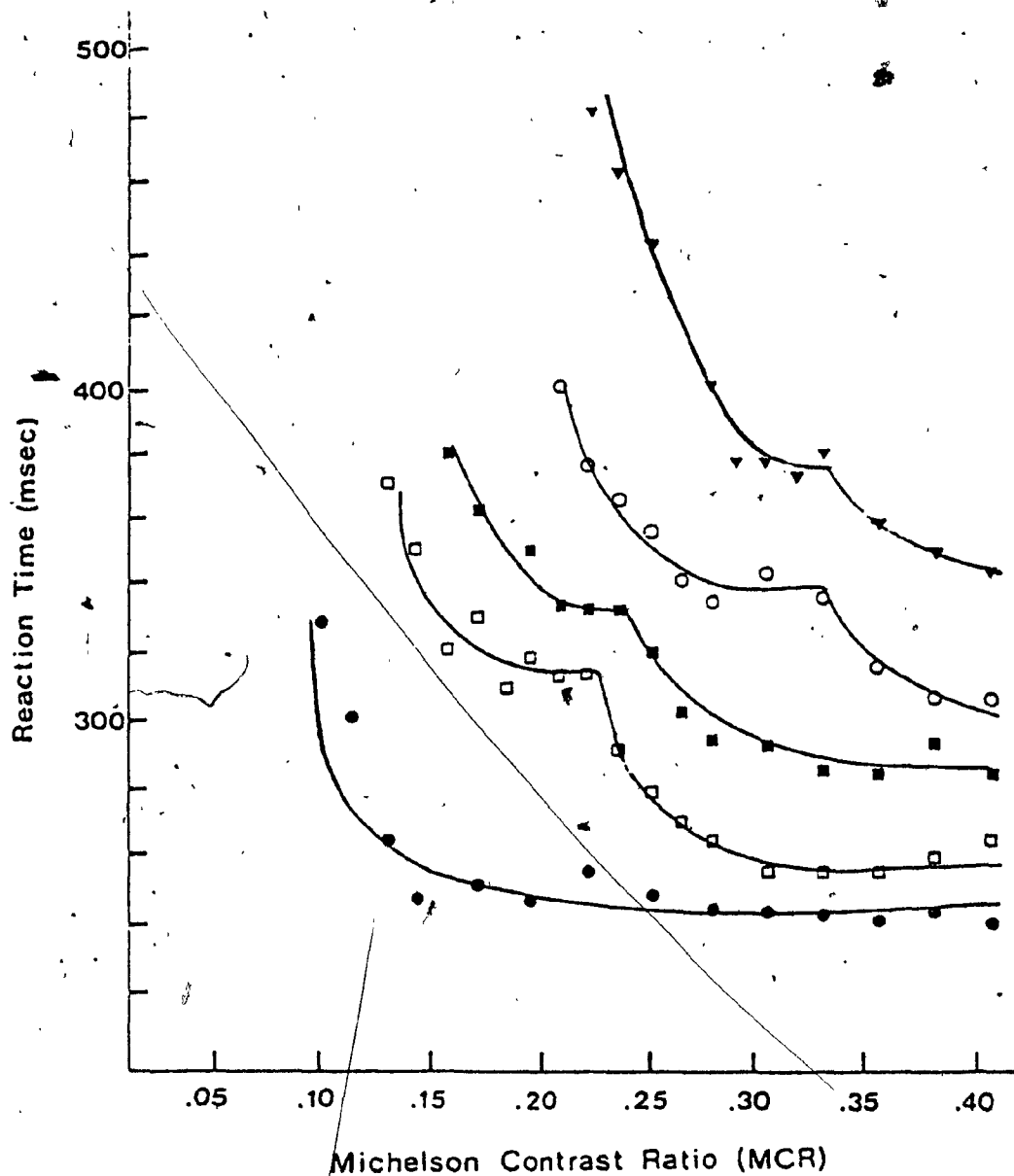


Figure 14b. Reaction Time as a function of target contrast for Observer SS (Replication 2). Target frequency: ●2; □4; ■6; ○8; ▼10.

described. For both subjects, the break occurred at higher contrasts with increasing spatial frequency. Similar to BK's data, RTs to the 8 and 10 c.p.d. gratings did not differ in magnitude, for subject PB. However, like the data depicted in Figure 12a, breaks in the function occurred at different contrasts for the 8 and 10 c.p.d. gratings.

Subject SS's data were similar to those of the other subjects in most respects. As noted above, unlike the data of the other observers, RT differences occurred between the 8 and 10 c.p.d. gratings for both replications.

Discussion

The data reported in this experiment replicated Harwerth & Levi's (1978) findings. Biphaseic RT curves were reported for all observers at the mid to higher spatial frequency gratings. Harwerth & Levi suggested that the discontinuities found in their RT curves were the result of the sustained and transient channels operating within different contrast ranges. The same interpretation of the data reported in this experiment may also be made. To help illustrate this, refer to Figure 12a. For the 4 c.p.d grating, BK's reaction times decreased as the contrast of the grating was increased from threshold until a contrast of .16. RT seemed to asymptote from this point until a grating contrast of .21 was reached. Further increases in the contrast of the grating, resulted in further lowering RT, until an asymptotic level was reached at about a contrast of .27. The "sustained-transient" explanation of the data suggests that at the lower contrasts, the "slower" sustained system mediated RT. At the first asymptote, the response of the sustained system seemed to be maximum, with no further influence on RT. However, at higher contrast levels (beyond .21 in this case), it was proposed that the "quicker" transient system became involved in mediating RT. This resulted with an abrupt reduction in RT. With further increases in contrast, RT decreased until the transient response reached its peak, producing the second asymptotic level.

The prediction that biphasic RT curves may begin at higher spatial frequencies with shorter durations, was supported in these data. Using 500 msec. stimuli, Harwerth & Levi reported that breaks in the RT curves occurred with .5 c.p.d. stimuli. For 50 msec. stimuli, their data revealed that discontinuities occurred for gratings not below 1 c.p.d. In this experiment, the use of 16 msec. stimuli, resulted in the production of biphasic RT curves only beginning at 4 c.p.d. The sustained transient view seems to offer a viable explanation of what may have occurred to produce this result. Since transient cells are more likely to mediate brief stimuli, it is more likely that these, rather than sustained cells may have been responding not only to low spatial frequencies, but also to moderate ones. Therefore, at 2 c.p.d., transient cells alone, may have mediated the RT measure. This was reflected in the production of monophasic RT curves at 2 c.p.d., for all observers. Beyond this, spatial frequency, the sustained system seemed to be operating, as the biphasic RT curves imply. For most observers, biphasic RT curves occurred with 10 c.p.d. gratings, suggesting that even at high spatial frequencies, where transient activity is purported to be rare, high contrast stimuli may activate the transient system.

Although Harwerth & Levi made implications about the activity of sustained and transient neurons in their RT

study, they never described a model that could have accounted for their data. In order to do so, it may be hypothesized that RT is determined by many factors. For instance, Teichner & Krebs (1972) suggested that neural transmission time, neural activity level (which they describe as the intensity or energy level) and cognitive factors, such as motivation and attention seem to mediate RT. If cognitive factors are assumed to be held constant, a model using Teichner & Krebs's proposals, may be offered in order to account for the data produced in this experiment.

Given that RT reflects neural transmission time, we would expect that tissues having quicker transmission times, should produce quicker RTs when compared to slower neurons mediating RT. This suggests that the implication of quicker transient cells would produce faster RTs than the slower sustained cells.

It has been well documented since the work of Pieron (1920), that RT decreases with increases in the intensity of a stimulus. On a cellular level, it is well known that increases in the intensity of a stimulus are accompanied by increases in the firing rate of a responding cell. Thus, it may be argued that increases in the firing rate of a responding cell or responding cells may be associated with decreases in RT. As well, Maffei & Fiorentini (1973) found sustained and transient cells whose activity level increased

as a function of sinusoidal grating contrast. With this in mind, it is hypothesized that RT is inversely related to cellular activity, which can vary as a function of the energy (duration or luminance level) or contrast of a stimulus (grating).

A third component mediating RT, may be related to the number of cells that respond to a stimulus. It may be argued that as more cells respond to a stimulus, the more likely it is, that the stimulus will be detected. Graham (1980) defines this as "Probability Summation" which refers to "...the increase in the detectability of a pattern that results when two or more uncorrelated channels rather than one respond to the pattern".

Given the influence that differential response times, firing rates, and cellular activity level have on RT, a model accounting for these data is proposed in Figure 15. Consider what happens when a 4 c.p.d. grating is displayed. The abscissa represents neurons that are maximally sensitive to individual frequency gratings. The ordinate reflects the response rate of these different cells. Each curve represents the activity level of the responding cells. At a low contrast (depicted in a), neurons maximally sensitive to spatial frequencies near 4 c.p.d. respond to the grating. This may be reflected in long RTs, since few cells are responding and those that are

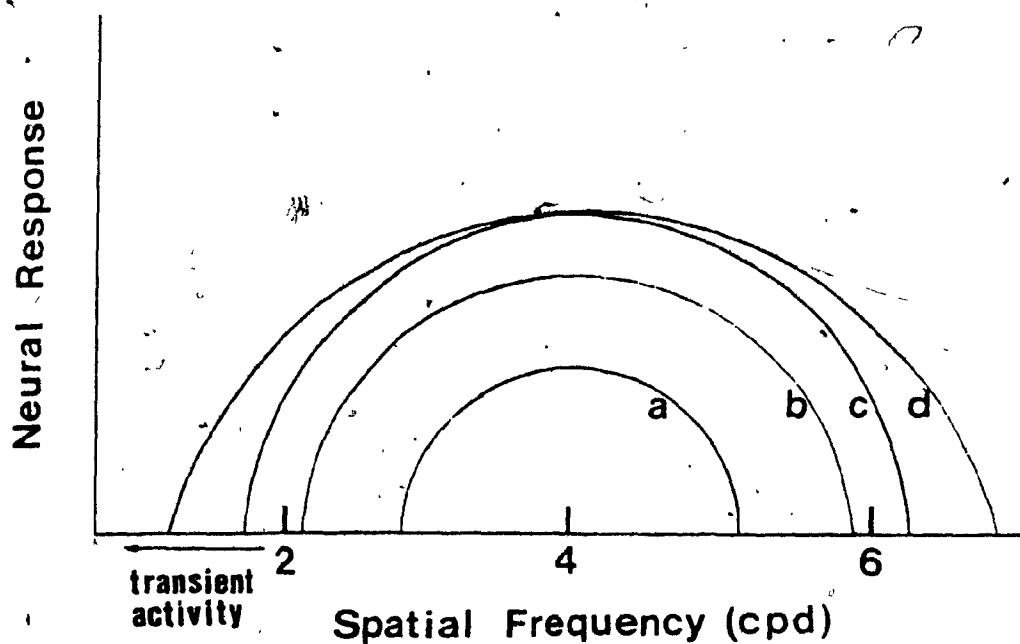


Figure 15. A model is proposed to account for the results of Experiment 1. (See the text for a description.)

active, have low firing rates. As contrast is raised (b), not only does the firing rate of these cells increase in frequency, but other cells begin responding. If probability summation operates in the RT paradigm for individual cells and given that RT varies inversely with the magnitude of neural activity, we would expect a drop in RT with this contrast increase. As contrast is further increased, this would result in the stimulation of other neurons, however, the response rate of the previously responding cells, may stay the same (asymptotes). Evidence for asymptotic firing rates of neurons responding to increases in grating contrast was demonstrated by Maffei & Fiorentini (1973). If at this point, RT is most sensitive to cellular activity level, we might not expect a drop in RT due to the asymptotic firing rate of the previously responding neurons and low firing rate of the newer responding cells. With even further increases in contrast (c), the new cells which begin to respond, may include both the sustained (tuned to higher frequencies) and transient (tuned to lower frequencies) classes. As the transient cells become implicated, their faster transmission times may produce dramatic decreases in RT. As contrast is again increased (d), RT continues to decrease due to probability summation, and increased firing rates of the transient cells. This continues until the transient cells reach their asymptotic level. It can be seen from this description, that a biphasic RT curve would result from the exposure of the 4 c.p.d. grating, as a

function of contrast.

This model may account for other aspects of the data as well. For instance, the discontinuity in the data occurred at higher contrasts as spatial frequency was increased. In this model, it is proposed that as the spatial frequency of the stimulus increases, the sustained cells maximally responding, are tuned to higher frequencies. As a result, those cells which are tuned to higher spatial frequencies are further separated from the low transients. As depicted in Figure 15, the model suggests that for higher spatial frequency gratings, one would need greater contrast levels to stimulate the transient cells, thereby requiring greater contrasts to produce the discontinuity.

The data suggests that overall, RT increased as a function of spatial frequency. The model would account for this, by suggesting that at the lower frequencies, transient involvement is greatest, producing the quickest RTs. As spatial frequency increased, transient involvement and activity level decreased, resulting in longer RTs. To further investigate this hypothesis, the 4, 6 and 8 c.p.d. biphasic RT curves were analysed by comparing the RTs of the stimuli above as well as below the break. That is, if the fact that RT increased as a function of spatial frequency was due to the reduced involvement of the transient system, we would expect this to be so for the transient portion

(below the break) of the curves only. Therefore, when comparing the RTs above the curve, where it is hypothesized that sustained cells were mostly operating, we would expect no differences in RT, as a function of contrast. One-way analyses of variance (ANOVA) tests were computed for each observer and replication for the separate portions of the RT curves above and below the discontinuities, "collapsing" across contrast. The results of these analyses are depicted in Table 1. The ANOVA tests revealed in every comparison, significant differences ($p < .01$) in the "transient portions" of the curves. However, in every analysis except one ($p < .05$), significant differences were not found for the "sustained portions" of the curves. These data thus support the hypothesis that transient activity accounted for the RT differences found as a function of spatial frequency.

One of the most consistent results produced by this study were the variations that occurred between the replications. For instance, if BK's RT curves are compared across trials for the 6 c.p.d. grating (Figures 12a & 12b), it is clear that the break in the curve occurred at different contrasts for the two replications. For instance, in the first replication, the break occurred at a contrast of .23, while in the second, it occurred at .18. It is possible that factors, such as fatigue and alertness could have varied across sessions, influencing the impact of the stimulus on the visual system. For instance, if BK was more

Table 1

One-Way Analysis of Variance Results for the Separate
Portions of the RT curves above and below the Discontinuity
Break for the 4, 6, and 8 c.p.d. Gratings.

"Above" Discontinuity in RT Function

Observer	Replication	df	F	Sig. Level
B.K.	1	(2,19)	.97	>.05
B.K.	2	(2,8)	.58	>.05
P.B.	1	(2,20)	1.87	>.05
P.B.	2	(2,17)	2.52	>.05
S.S.	1	(2,14)	1.55	>.05
S.S.	2	(2,19)	4.00	<.05

"Below" Discontinuity in RT Function

B.K.	1	(2,22)	25.97	<.01
B.K.	2	(2,29)	14.90	<.01
P.B.	1	(2,24)	3.64	<.05
P.B.	2	(2,23)	31.64	<.01
S.S.	1	(2,24)	51.35	<.01
S.S.	2	(2,19)	25.91	<.01

fatigued in replication 1, we might expect that the target had a reduced impact, thus producing both an overall slower RT curve and a shift in the breaking point to a higher contrast, when compared with the RT curve from replication 2. This in fact, occurred not only for BK but also for PB at 2, 6 and 10 c.p.d. and at 4, 8, and 10 c.p.d. for SS.

Although Harwerth & Levi did not report these types of inconsistencies across replications, this phenomenon was consistent enough in this study to make statements about collapsing RT data across replications. As was pointed out earlier, since the collapsed data might have "washed out" the break in the RT function, these data were presented per session. It seems that in the future, other studies sensitive to the shape of the RT function, would also be best served by presenting RT data in a similar fashion.

Experiment 2

One of the eventual goals of this research is to investigate metacontrast in the context of understanding sustained-transient interactions. Experiment 2 was conducted to assess RT to the peripheral stimulus which is eventually used as the mask, in a metacontrast paradigm. Thus, this "peripheral" stimulus will henceforth be referred to as the mask stimulus. As was pointed out earlier, transient cells have been shown to be more concentrated in the periphery than in the fovea of animals (Fukuda & Stone, 1974). Harwerth & Levi (1978) suggested that if this is also true in the human visual system, then RTs tested in the periphery, may reflect enhanced activity of the transient system over the sustained. They found that for a 500 msec. stimulus for instance, RT increased with degree of eccentricity. This however, seems to be inconsistent with the prediction that transient cells are more involved in mediating RTs; one would expect shorter rather than longer RTs. The authors failed to address this problem. They seemed to have put more emphasis on the discontinuity break in the data, which they claimed to have occurred at higher contrasts with degree of eccentricity. This they felt, was "evidence" of differential manipulations of the two systems. However, the basis for making this statement is not clear. The figure representing their data is presented in Figure 16. It seems to be quite evident, that variations in the occurrence of the break as a function of contrast, is not as

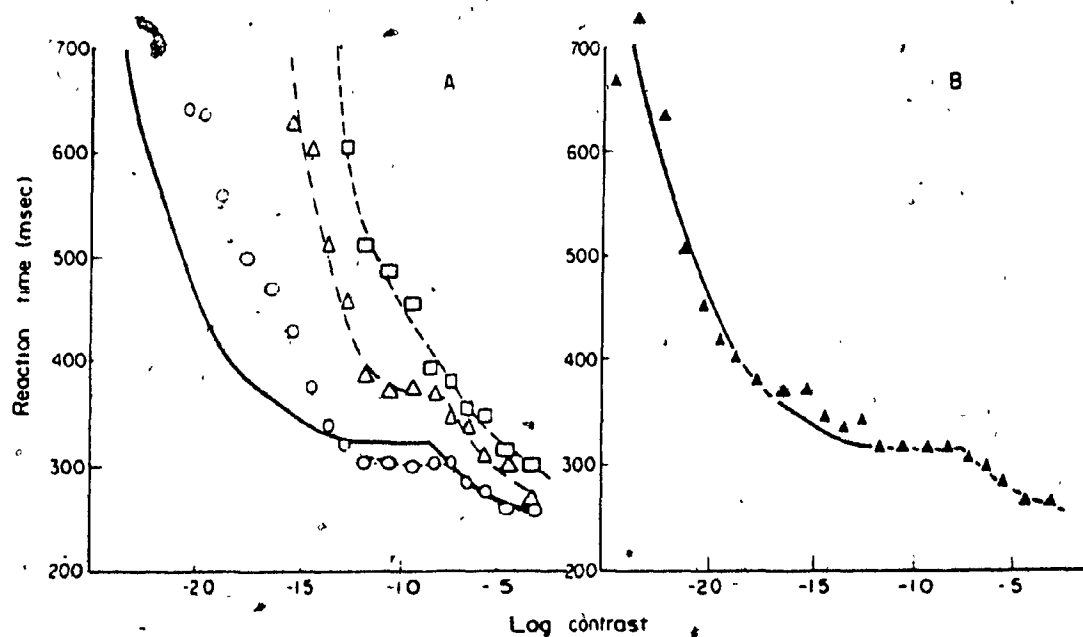


Figure 16. Data from Harwerth & Levi (1978). Effect of field size and retinal location on reaction time data for a 4 c.p.d. stimulus with an exposure duration of 500 msec. (A) Data for a 1° field viewed centrally (circles), 2.5° eccentrically (triangles), and 5° eccentrically (squares). The solid line is the curve drawn through the data (of a previous experiment) to serve as a reference. (B) Data for a 6° field viewed centrally (triangles) compared to data for the 3° field (solid line). (From Harwerth & Levi (1978, pp. 1582).

obvious as the authors had claimed.

Another interpretation of these data is necessary. If it is assumed that in the human visual system, transient activity increases in the periphery and is not sensitive to long durations, we may be able to explain their data. If the 4 c.p.d. target was processed mainly by sustained neurons (the break occurring as a result of the influence of a small number of transient cells), then as it was presented in the periphery, less sustained neurons would be available to mediate the processing. To the extent that the amount of cellular activity is associated with RT, we would expect overall, longer RTs with this long exposure duration, due to the overall decreased activity level.

If this interpretation is correct, then it is proposed that with short duration stimuli, RT to peripheral stimulation may decrease, since the highly concentrated transient system will be implicated to a greater degree.

Procedure. The same observers, apparatus and procedure used in Experiment 1 were employed in this study. The only variable to change were the stimuli. This time instead of presenting the foveal target, the mask stimulus, consisting of the two 1.5 X 1.0 areas adjacent to the target, was used. These stimuli were each located .5 peripherally from the fovea. The two adjacent areas to the target consisted

of the mask stimulus. Just prior to the foreperiod, the observers were signalled to fixate in the middle of the target mean luminance area. At the end of this period, the masks were presented for 16 msec, at which time the RT clock commenced. The observers were instructed to depress the RT lever as soon as they noticed any perceptual changes in the mask area. The luminance of the target area did not alter from the mean level during the time of the mask presentation. Three spatial frequency masks were presented in random order (2, 6 and 10 c.p.d.).

Results.

Figures 17a and 17b represent BK's data for replication one and two, respectively. The most apparent aspect of these data is the absence of the discontinuity break for spatial frequencies of 6 c.p.d. and the longer RTs for the 10 c.p.d. grating. Figures 18a and 18b compare BK's RTs to the central target and peripheral masks, for replication one and two, respectively. The standard errors ranged between 5 and 22 msec for all of the observers. Overall, for BK, RTs to the 6 c.p.d. grating were faster when it was presented in the periphery. RTs to the 10 c.p.d. grating however, were slower. PB's data are presented in figures 19a and b where comparisons between the central and peripheral stimuli are presented for both replications. In only one replication were faster RTs evident at 6 c.p.d. However, as with BK, the 10 c.p.d. grating produced slower RTs. SS's data are similarly presented in figures 20a and b. The data were consistent with those of the other two subjects, with faster RTs to the 6 c.p.d. mask and longer RTs to the 10 c.p.d. peripherally presented grating. It was also evident for all three observers, that RT did not differ between the 2 c.p.d. foveally presented target and peripheral mask.

Discussion

The results of this experiment seem to support the

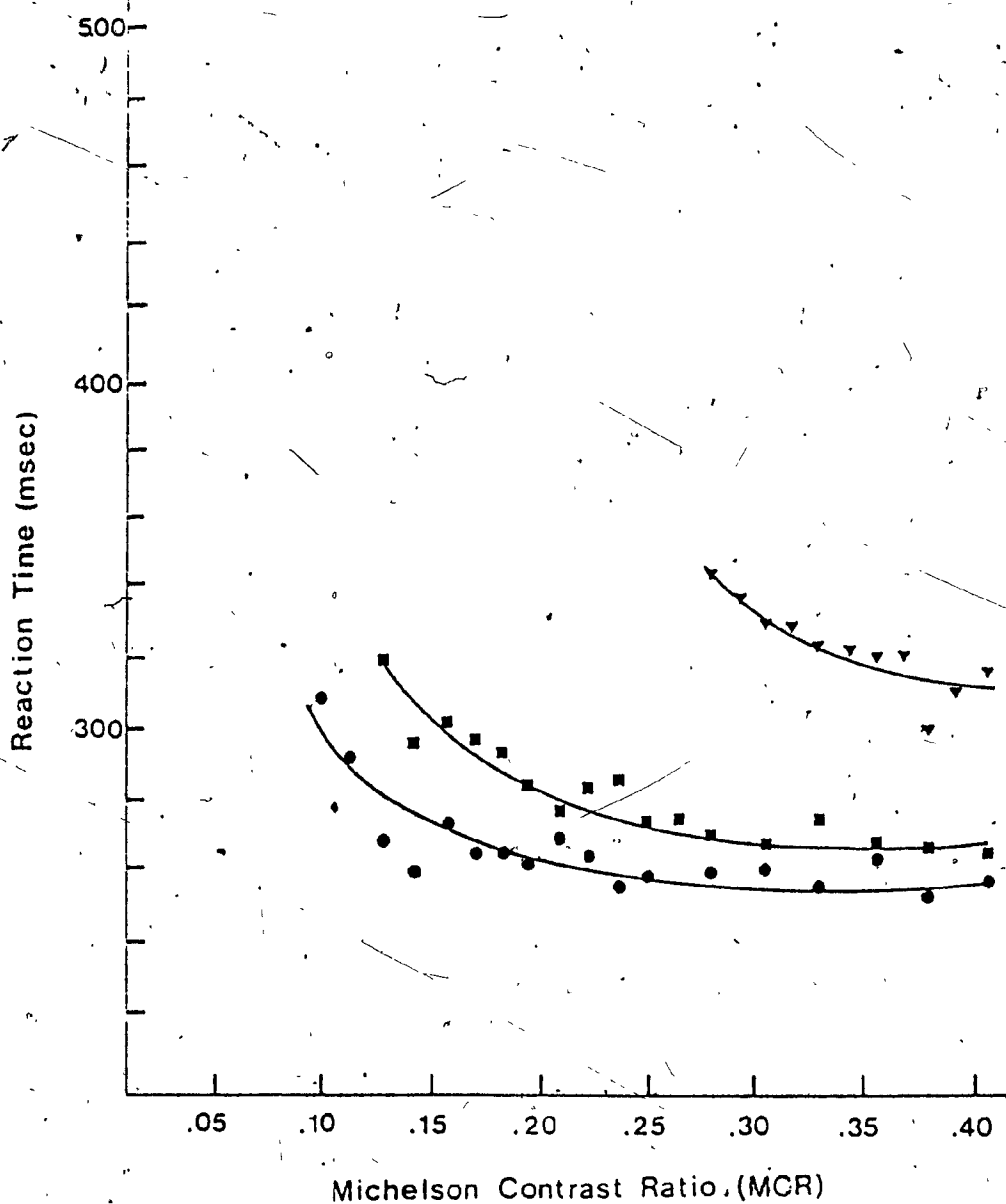


Figure 17a. Reaction Time as a function of the peripheral contrast for Observer BK. (Replication 1). Target frequency (c.p.d.): • 2; ■ 5; ▼ 10.

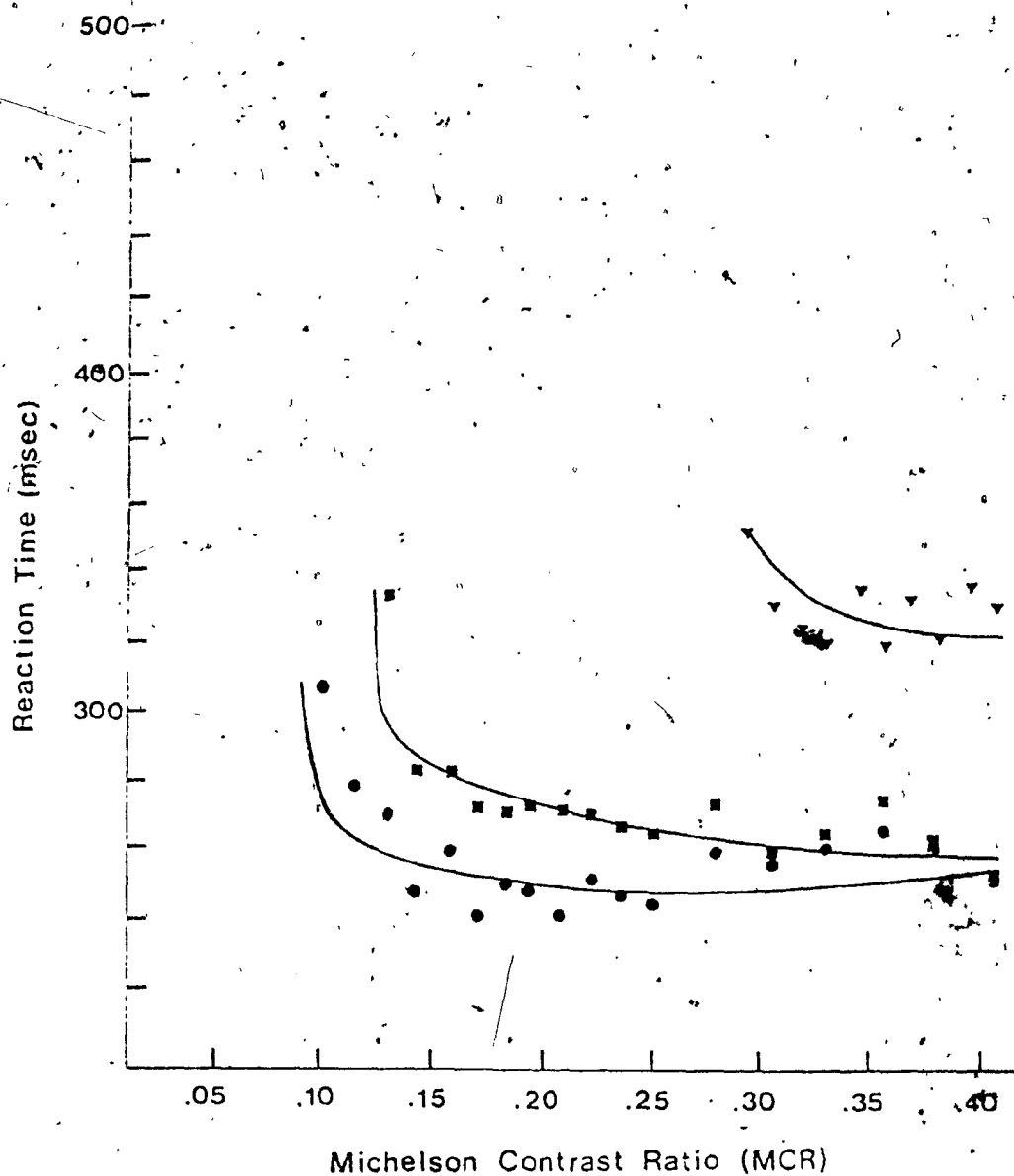


Figure 17b. Reaction Time as a function of the peripheral contrast for Observer BK (Replication 2). Target frequency (c.p.d.): ● 2; ■ 6; ▼ 10.

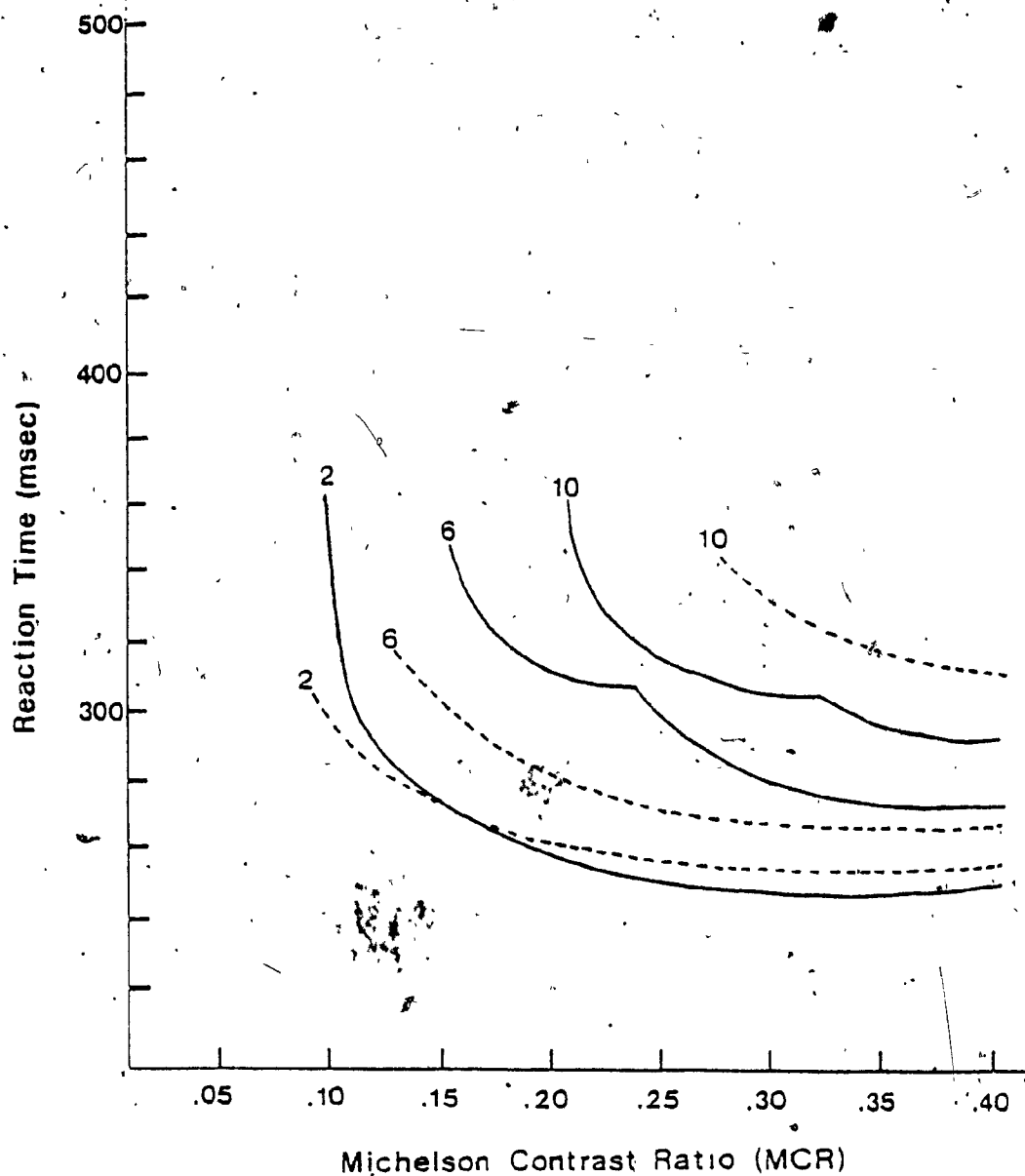


Figure 18a. Mean Reaction Time to central (solid lines) and peripheral (dashed lines) for observer B.K. (Replication 1) spatial frequency is illustrated (c.p.d.).

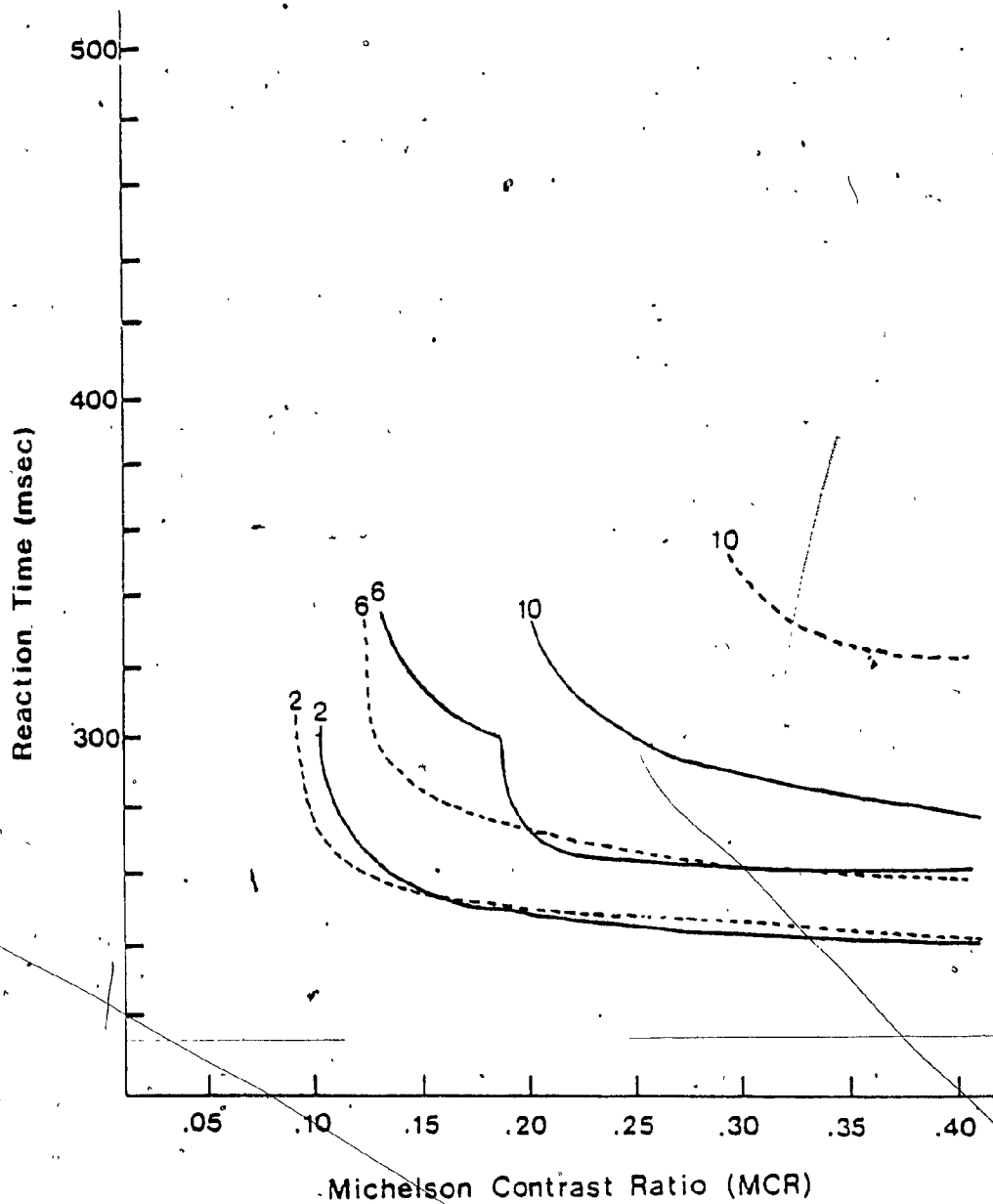


Figure 18b. Mean Reaction Time to central (solid lines) and peripheral (dashed lines) for observer B.K. (Replication 2). Spatial frequency is illustrated (c.p.d.).

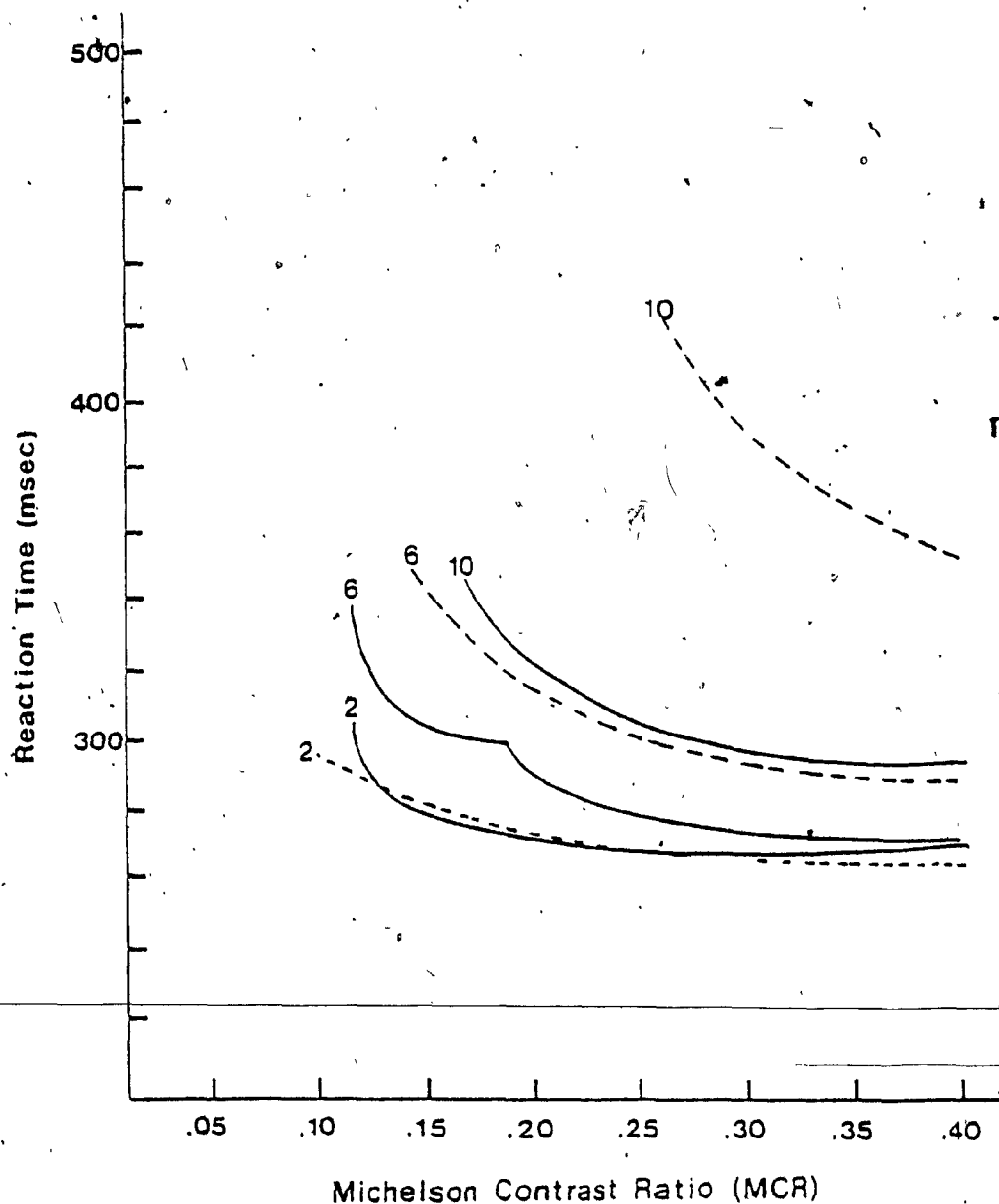


Figure 19a. Mean Reaction Time to central (solid lines) and peripheral (dashed lines) for observer P.B. (Replication 1). Spatial frequency is illustrated (c.p.d.).

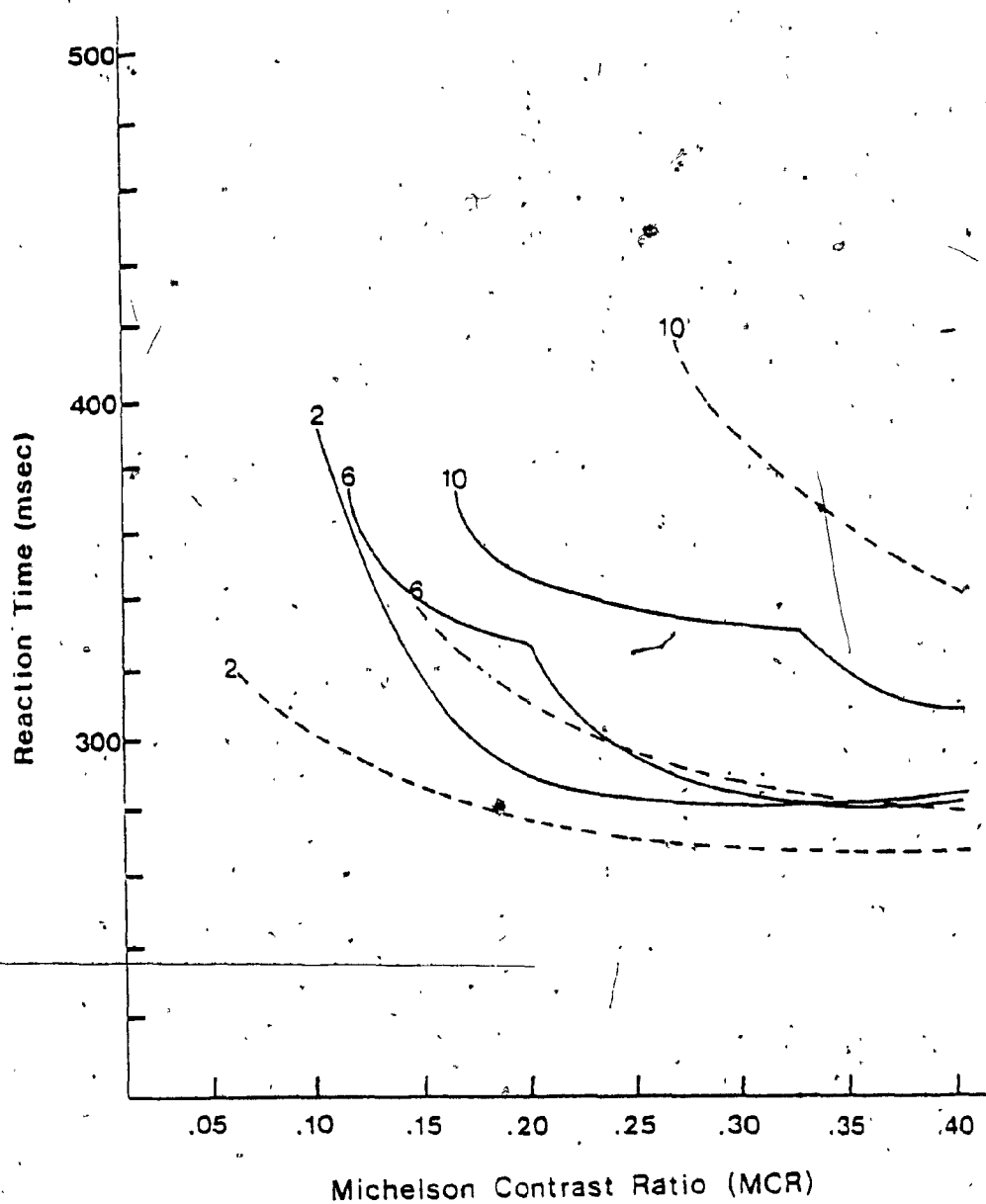


Figure 19b. Mean Reaction Time to central (solid lines) and peripheral (dashed lines) for observer P.B. (Replication 2). Spatial frequency is illustrated (c.p.d.).

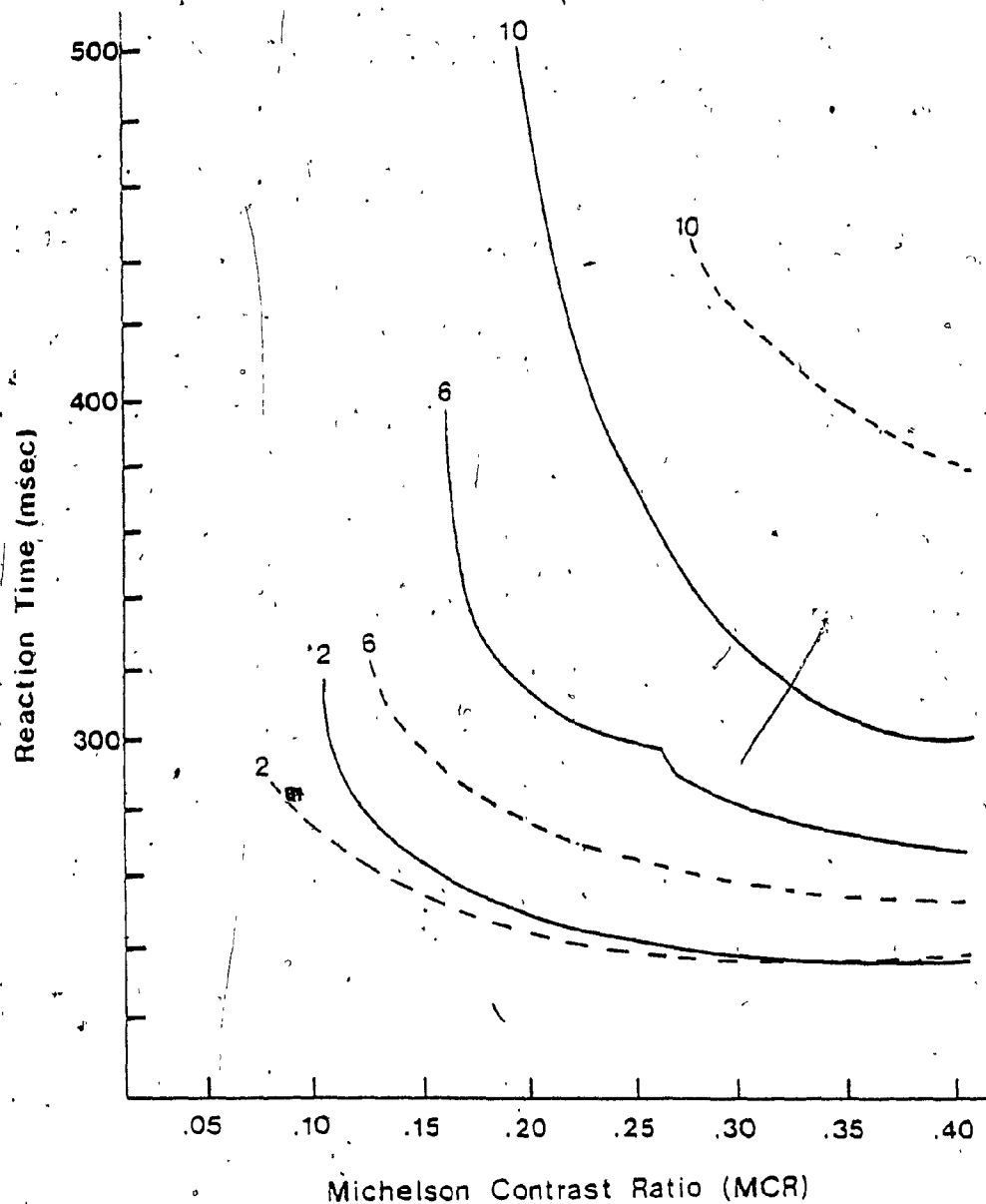


Figure 20a. Mean Reaction Time to central (solid lines) and peripheral (dashed lines) for observer S.S. (Replication 1). Spatial frequency is illustrated (c.p.d.).

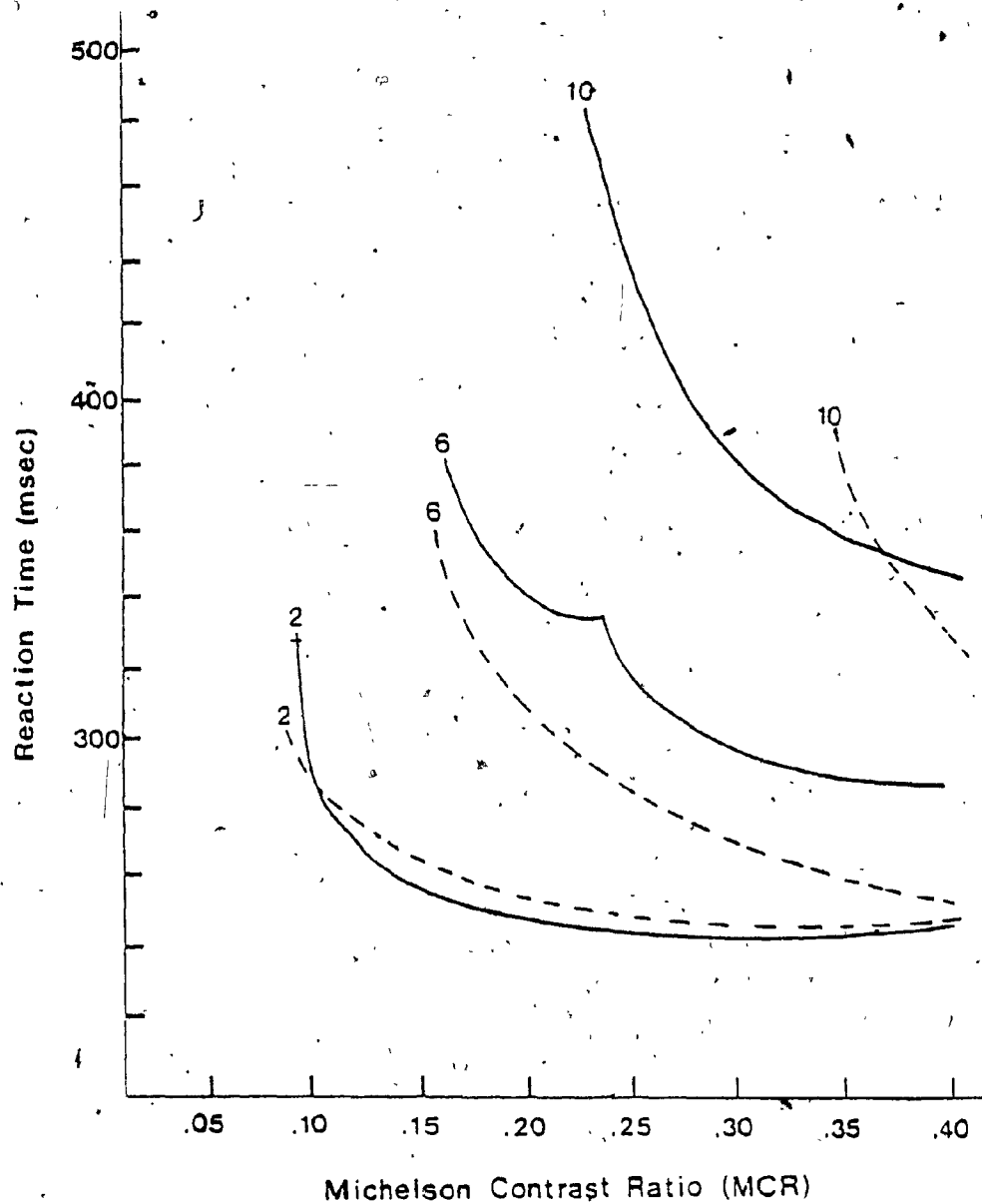


Figure 20b. Mean Reaction Time to central (solid lines) and peripheral (dashed lines) for observer S.S. (Replication 2). Spatial frequency is illustrated (c.p.d.).

predictions concerning the 6 c.p.d. peripherally presented mask. That is, generally the RTs for the mask were faster than those for the foveally presented target. As discussed earlier, these data seem to be consistent with the idea that when the peripheral area of the retina is stimulated, there is a greater likelihood that transient cells are involved in visual processing. The data from this experiment suggested that in this case, RT seemed to be mediated by these cells.

The 2 c.p.d. grating produced short RTs for both the foveal and peripheral stimuli. RT, however, did not appreciably decrease in the periphery, suggesting that implicating more transient cells did not offer more information (i.e., quicker processing time) to the visual system. This interpretation is consistent with the idea that transient cells were already processing the 2 c.p.d. grating as quickly as possible and further stimulation of other transients made little difference,

If RT to a 10 c.p.d. stimulus is mediated mostly by sustained cells, one would expect that when presenting the grating in the periphery, fewer sustained cells would be available, since their numbers generally fall off in this area. Due to the reduced population of sustained cells, we would expect that a 10 c.p.d. grating presented in the periphery would result with an increase in the RT (if we assume that RT is associated with neural activity). This

was evident in the results of this experiment for all subjects.

In conclusion, Experiments 1 and 2 were conducted in an attempt to investigate sustained and transient activity with a RT procedure. The results generally supported Harwerth & Levi's (1978) proposal that whether sustained or transient neurons mediate RT seems to be determined by many variables, including the spatial frequency, duration, contrast and location of a sinusoidal grating.

Experiment 3

One of the main direction of this thesis is an attempt to understand the mechanisms that mediate metacontrast. Specifically, a number of investigators have recently proposed that the interaction of sustained and transient neurons, may be responsible for the production of this type of masking. In the first experiment, it was proposed that the RT paradigm offers a way to measure the action of sustained and transient neurons. It was found that the activity of these two channels may be differentially manipulated, by varying stimulus parameters. If this interpretation of the data is correct, then a direct investigation of the influence of sustained and transient mechanisms in the production of the metacontrast function may be possible. Specifically, if the same mechanisms mediating RT are involved in metacontrast, then by using the same gratings as in Experiments 1 and 2, the sustained and transient cells mediating these stimuli may be differentially manipulated. For instance, the results from Experiments 1 and 2 suggested that varying contrast, and spatial frequency of the grating stimuli, will affect the contribution of sustained and transient activity. Based on at least three models (Weisstein et al., 1975; Breitmeyer & Ganz, 1976; White & Lorber, 1976) of metacontrast, predictions about the shape of the metacontrast function may be made, with respect to the proposed interaction of the sustained and transient mechanisms, mediating the processing

of the target and mask.

White & Lorber proposed that maximum metacontrast should occur when the target and mask are of the same spatial frequency. They suggested that neurons maximally inhibit each other, if they are similar in spatial frequency, and close to each other in proximity. That is, within the context of spatial frequency sensitive channels mediating metacontrast, White & Lorber would predict that neurons responding to the same spatial frequency may greatly inhibit each other, producing maximum metacontrast effects. Weisstein et al. (1975) and Breitmeyer & Ganz (1976), however, disagree with this description. They believe that metacontrast is the result of sustained neurons being inhibited by transient ones. Both models would predict that maximum metacontrast effects, would occur when low spatial frequency gratings (mask), which presumably stimulate the transients, would inhibit higher spatial frequency gratings (target) which is believed to implicate sustained neurons. Furthermore, Weisstein et al. and Breitmeyer & Ganz differ as to what mediates paracontrast. As reviewed earlier, Weisstein et al. argue that paracontrast is the result of transient cells responding to the target, being inhibited by sustained cells reacting to the mask. Breitmeyer & Ganz however, argue that paracontrast is the result of intrachannel inhibition, whereby sustained cells responding to the target, are inhibited by sustained cells responding

to the mask. Thus, Weissstein et al. would predict that maximum paracontrast effects should occur with lower spatial frequency targets (in which maximum transient cells are involved) and higher spatial frequency masks (where sustained cells are mostly operating). Breitmeyer & Ganz however, would predict that maximum paracontrast might occur when both the target and mask were of higher spatial frequency, thereby predominantly implicating the sustained system, providing a basis for sustained intrachannel inhibition.

Independent and Dependent Variables.

Table 2 displays the 18 conditions that were used in this experiment. Target and mask spatial frequencies of 2, 6 and 10 c.p.d. were employed. High contrast masks were used, while both high and low contrast targets were implemented. The rationale for using these stimuli, is described below.

These stimuli were derived from the results of Experiments 1 and 2. For all observers in those experiments, fast monotonic RT functions were produced for the 2 c.p.d. grating. It was suggested that these results reflected the action of the transient system. For all three observers, the 6 c.p.d. grating produced biphasic RT curves, which was interpreted as reflecting the operation of both

Table 2

Conditions of Experiment 3

MASKING SPATIAL FREQUENCY (C.P.D.) - High Contrast	TARGET SPATIAL FREQUENCY (C.P.D.)					
	2		6		10	
	Contrast		Contrast		Contrast	
	Low	High	Low	High	Low	High
2						
6						
10						

the sustained and transient systems. By manipulating the contrast variable, it was suggested that the activity of sustained and transient cells could be differentially manipulated. The 10 c.p.d. grating mainly produced slower monophasic RT curves which was interpreted as reflecting the operation of the sustained system.

In order to differentially involve the sustained and transient systems, a high and low contrast level was used for all targets. High contrast masks were employed to maximize the effectiveness of this stimulus. The contrast level of the targets was determined from the results of Experiment 1. These contrast levels are found in Table 3. The data showed for instance, that for the 6 c.p.d. target grating, breaks in the curve for all observers, occurred at or beyond a target contrast of .18. Thus, for this stimulus, the low contrast condition was set at a contrast of .16, while the high contrast condition was set at .41. Using these different contrast levels, it was proposed that in the low contrast conditions, sustained cells were being implicated, while at the high contrast conditions, transient cells were mostly involved. As control conditions, high and low contrast targets were used for the 2 and 10 c.p.d. stimuli, since at these spatial frequencies, it is argued from the data of experiment 1, that the implication of sustained and transients was determined by spatial frequency alone, and not contrast. However, if the degree of neural

Table 3

Contrast Levels (MCR) Associated with Breaks in
the RT Curves in Experiment 1 for All Three Observers

Observer	Replication	Frequency	MCR
B.K.	1	2	No Break
		4	.20
		6	.23
		8	.29
		10	.31
B.K.	2	2	No Break
		4	.15
		6	.18
		8	.25
		10	No Break
P.B.	1	2	No Break
		4	.19
		6	.18
		8	.31
		10	.31
P.B.	2	2	No Break
		4	.18
		6	.21
		8	.25
		10	.33
S.S.	1	2	No Break
		4	.18
		6	.24
		8	.31
		10	.28
S.S.	2	2	No Break
		4	.22
		6	.24
		8	.33
		10	.33

activity is critical in metacontrast, contrast may serve to increase the impact of the stimuli. That is, the higher contrast, 2 and 10 c.p.d. targets may evade masking more effectively than when presented at the lower contrasts. All masks were presented at the higher contrast in order to maximize their masking effectiveness.

Subjective rating methods have often been employed to measure the metacontrast effect (Werner, 1935; Kahneman, 1967; Weisstein, 1970, 1971; Growney, 1976). Brightness, clarity of contours, as well as degree of motion have often been the basis for which subjects have made their magnitude estimates. Stober (1977) however, demonstrated that subjects may have a tendency to confuse perceptual qualities in their estimates. For instance, brightness and clarity estimates were confounded in his investigation of metacontrast. He also argued that subjects using magnitude estimates, would often use the same numbers as a result of habit, rather than accurately reflecting their perceptions. As a result of these criticisms, a more objective dependent measure was employed in this study. Subjects were instructed to match the contrast of a comparison stimulus to the target grating.

Predictions. From the theoretical based predictions made earlier, the following outlines the expected results for these stimulus conditions. If the White & Lorber

hypothesis is correct, one would expect maximum metacontrast to occur when the target and mask share both the same spatial frequency and contrast. According to the Weisstein et al. (1975) and Breitmeyer & Ganz (1976) models however, it would be predicted that maximum metacontrast would occur with a 2 c.p.d. mask and a 10 c.p.d. low contrast target. As well, the theories would also predict that the high contrast 6 c.p.d. target would evade metacontrast, since the data reported by Harwerth & Levi and that of Experiment 1, suggested that this stimulus is mediated by transient neurons. According to these theories, it is also predicted that the 2 c.p.d. target, would evade masking due to its implication of transient cells. As well, the 10 c.p.d. stimulus might not be seen as an effective mask, since it is believed that this stimulus is mediated by sustained cells.

According to the Breitmeyer & Ganz model, paracontrast would have been predicted to occur, with the higher 10 c.p.d. target and mask condition. According to Weisstein et al. however, paracontrast might be most effective when a low contrast, low spatial frequency target (2 c.p.d.) is presented with the high spatial frequency (10 c.p.d.) mask.

Method

Subjects. The three observers, BK, PB and SS from Experiments 1 and 2 were also employed in this study.

Apparatus. The same apparatus from the earlier experiments was used in this study. An additional function generator (Tektronix, FG 501) provided a sinusoidal waveform for the comparison stimulus. Its spatial frequency and contrast could be independently adjusted. This signal was fed into an analog gate, which could be triggered by the Coulbourn logic system. The output from this analog gate converged onto the summing amplifier, which fed into the Z-axis of the oscilloscope. When triggered, the perceptual result was a full screen sinusoidal grating. The subject controlled an external 10-turn potentiometer which manipulated the amplitude of the sinusoid, thereby affecting its contrast. The contrast of the comparison grating was measured using the same procedure as outlined in Experiment 1. All the stimuli were presented for 16 msec.

Procedure. For each session, one of the 18 conditions was randomly selected for each observer. Within each condition the stimuli were separated by 12 SOAs of varying durations. They were: -50, -25, 0, 20, 40, 60, 80, 100, 120, 140, 180, and 250 msec. The luminance remained at the mean level during the ISI.

The timing schematic for the experimental procedure is depicted in Figure 21. Prior to the beginning of the experiment, the observers dark adapted for 5 minutes. They then freely viewed (monocularly) the three adjacent 10 cd/m^2 blank fields (light adapted) for another five minutes. The beginning of each trial was signaled to the observer with a warning tone. At this signal, the observer was told to fixate in the middle of the central target area. The target and mask combination was then presented with a random SOA separation. 500 msec following the offset of the last stimulus, a comparison grating set at the same spatial frequency as that of the target, was presented. Its contrast had been previously adjusted by the observer via an external potentiometer, to its lowest position prior to each SOA block. As soon as the subject saw the target, he was instructed to adjust the potentiometer such that the comparison stimulus contrast matched that of the target. For the first trial, the subject would move the potentiometer dial in an upward direction, thereby increasing the contrast of the comparison grating. During the next trial, the dial would remain in the same position, and after the presentation, the observer would move the dial in the desired direction. In order to reduce the possibility that the observer would extract information from the position of the potentiometer dial, the gain of the sinusoid was randomly adjusted from trial to trial by the experimenter. For instance, on one trial, it may have taken

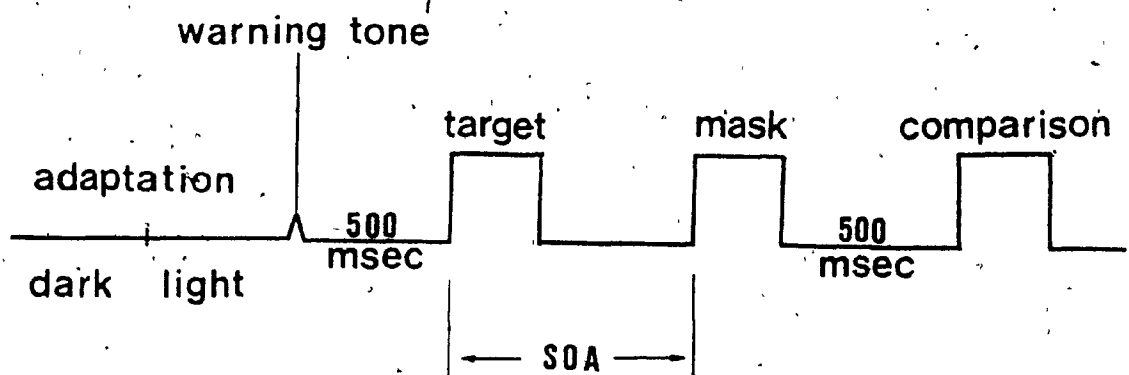


Figure 21. The timing schematic for the procedure of Experiment 3 is illustrated.

three turns to reach maximum contrast, while on the next trial, it could have taken 10. On the average, approximately eight contrast manipulations were required by the observers to reach contrast equality between the target and comparison stimulus. It would take approximately one and a half minutes to make a match.

For each of the 18 conditions, the SOAs were randomly presented within each block. Three replications of SOA were administered. Prior to each block, the observer was presented with two replications of a target-alone condition. These six replications consisted of the baseline measure of the perceptual impact of the target, in the absence of the mask. The observer was instructed to adjust the contrast of the comparison grating to match that of the target, in a similar fashion as when the target was presented with the mask. The trials were separated by 10 second intervals at which time the observer freely viewed the lit screen. Each session, which consisted of the three SOA replications and six baseline measurements, required approximately one hour to complete. The observers practised this task for at least five hours prior to collecting the data.

Results and Discussion

The data were averaged across the three replications for each SOA. The baseline measurements were also averaged

for the six replications. Figures 22 through 27 represent BK's data for three of the 18 conditions each. SOA is presented on the abscissa, while the comparison matching contrast, depicted in Michelson contrast ratio units, is shown on the ordinate. The baseline matching contrast is displayed on the right-hand side of each graph. Standard error bars are shown.

BK's data were representative of the other observers. Tables depicting PB & SS's data for these conditions can be found in appendix A. The most prominent feature of these data is the absence of the metacontrast effect. Only in one condition (6 c.p.d. mask and a 6 c.p.d. high contrast target) was metacontrast evident, and even in this case, the effect was not large and was not described by the typical U-shaped or monotonic metacontrast functions. This condition however, did not produce metacontrast for the other observers. For the other two observers, variability was minimal, with average standard errors ranging between contrast values of .01 and .02. The remainder of this discussion will be addressed to those parameters that might have accounted for these results.

Growney (1976) and White & Lorber (1976) employing metacontrast paradigms using grating stimuli, were able to produce typical metacontrast results. The main difference between this experiment and theirs, was the contrast

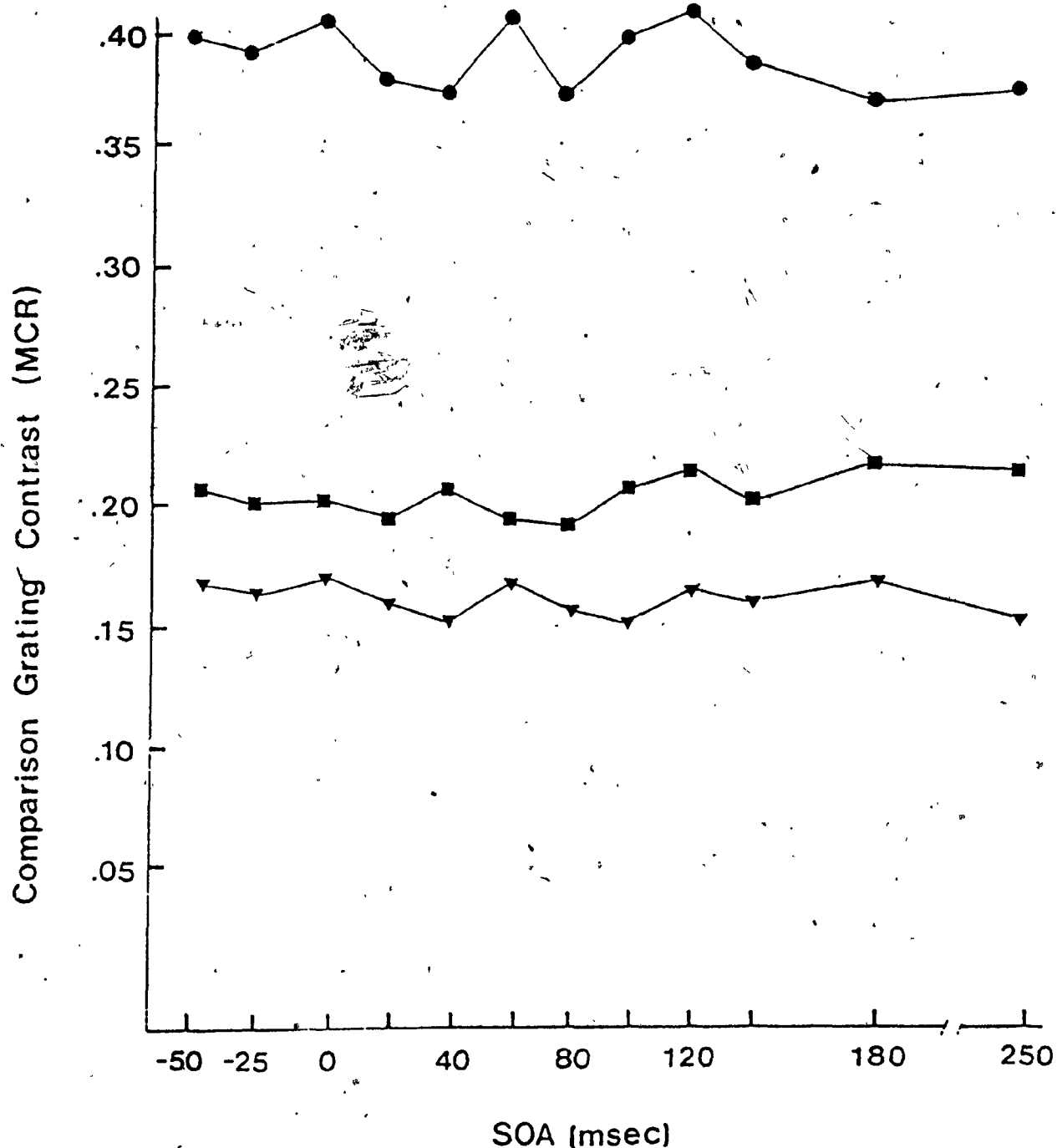


Figure 22. Comparison Grating Contrast (MCR) as a function of SOA (msec), for observer B.K. Each function represents 1 condition in Experiment 3. ● = 2 c.p.d. high contrast target; 2 c.p.d. mask. ■ = 6 c.p.d. low contrast target; 2 c.p.d. mask. ▼ = 2 c.p.d. low contrast target, 2 c.p.d. mask. The baseline matching contrast values (with standard error bars) are displayed on the right-hand side of each function.

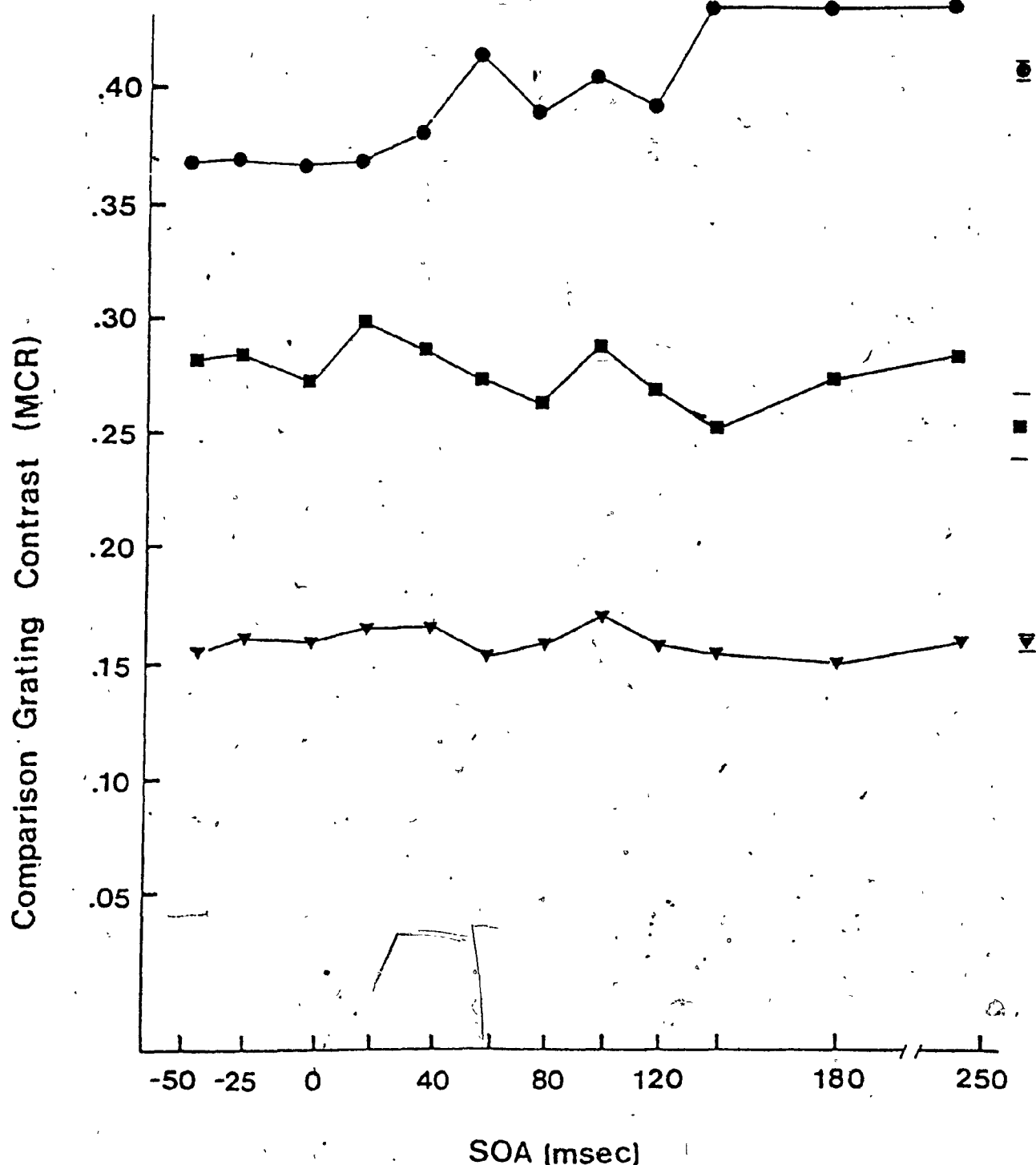


Figure 23. Comparison Grating Contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 condition in Experiment 3. ● = 6 c.p.d. high contrast target, 2 c.p.d. mask; ■ = 10 c.p.d. low contrast target, 2 c.p.d. mask; ▼ = 2 c.p.d. low contrast target, 6 c.p.d. mask. The baseline matching contrast values (with standard error bars) are displayed on the right-hand side of each function.

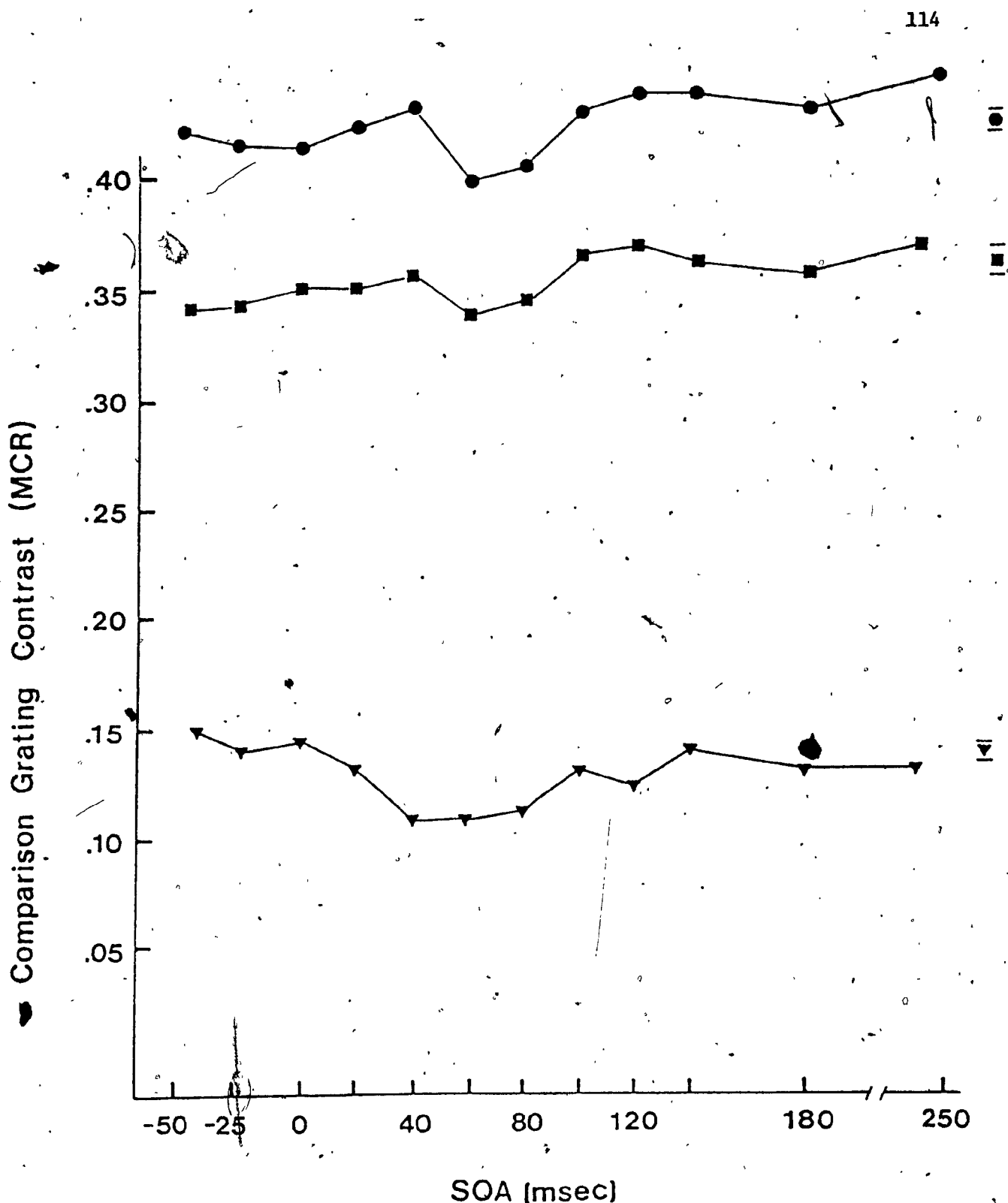


Figure 24 Comparison Grating Contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 condition in Experiment 3. ● = 10 c.p.d. high contrast target, 6 c.p.d. mask; ■ = 6 c.p.d. high contrast target, 10 c.p.d. mask; ▼ = 2 c.p.d. low contrast target, 10 c.p.d. mask. The baseline matching contrast values (with standard error bars) are displayed on the right-hand side of each function.

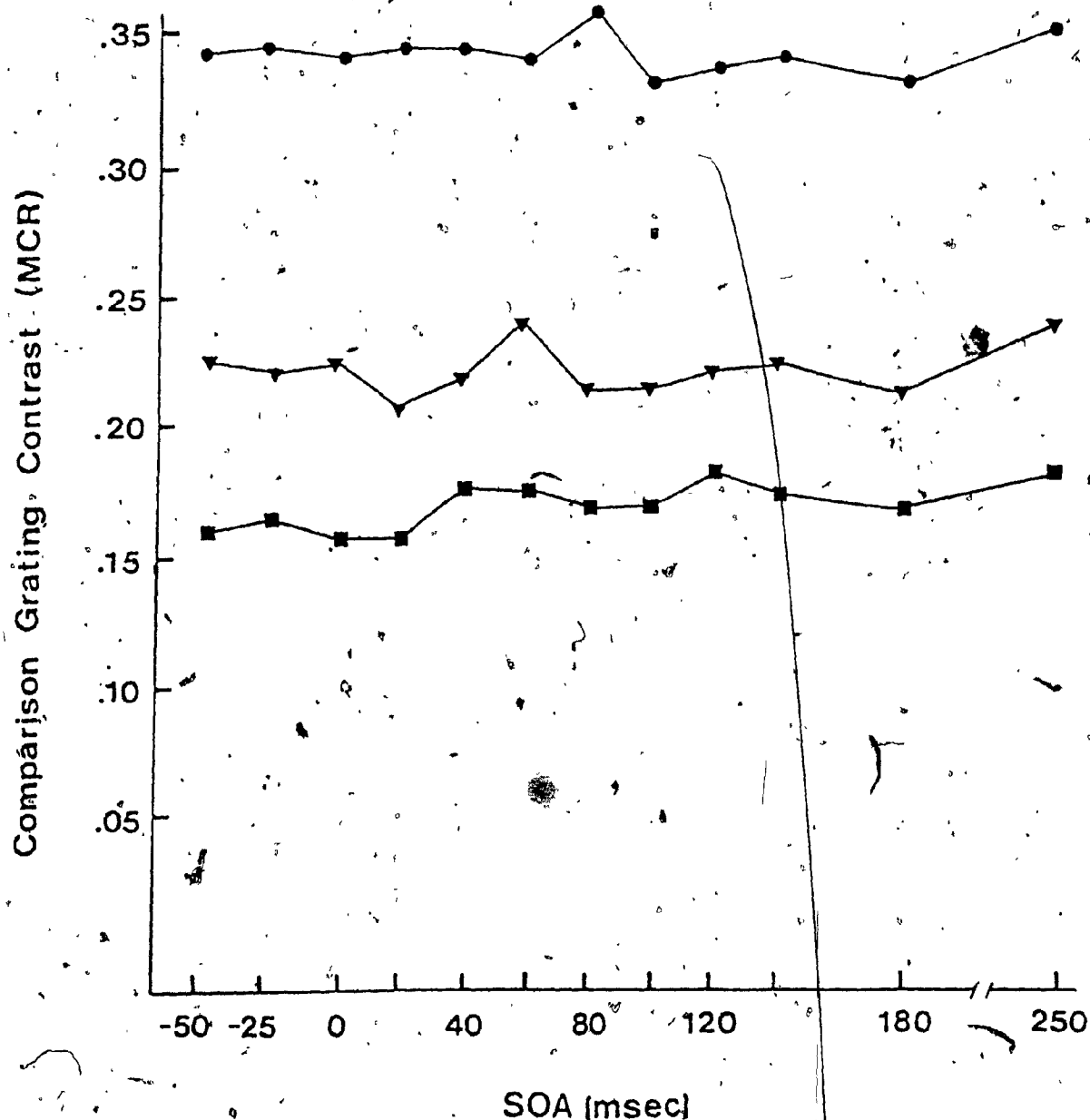


Figure 25. Comparison Grating Contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 condition in Experiment 3. ● = 6 c.p.d. high contrast target, 6 c.p.d. mask; ■ = 6 c.p.d. low contrast target, 6 c.p.d. mask; ▼ = 6 c.p.d. low contrast target, 10 c.p.d. mask. The baseline matching contrast values (with standard error bars) are displayed on the right-hand side of each function.

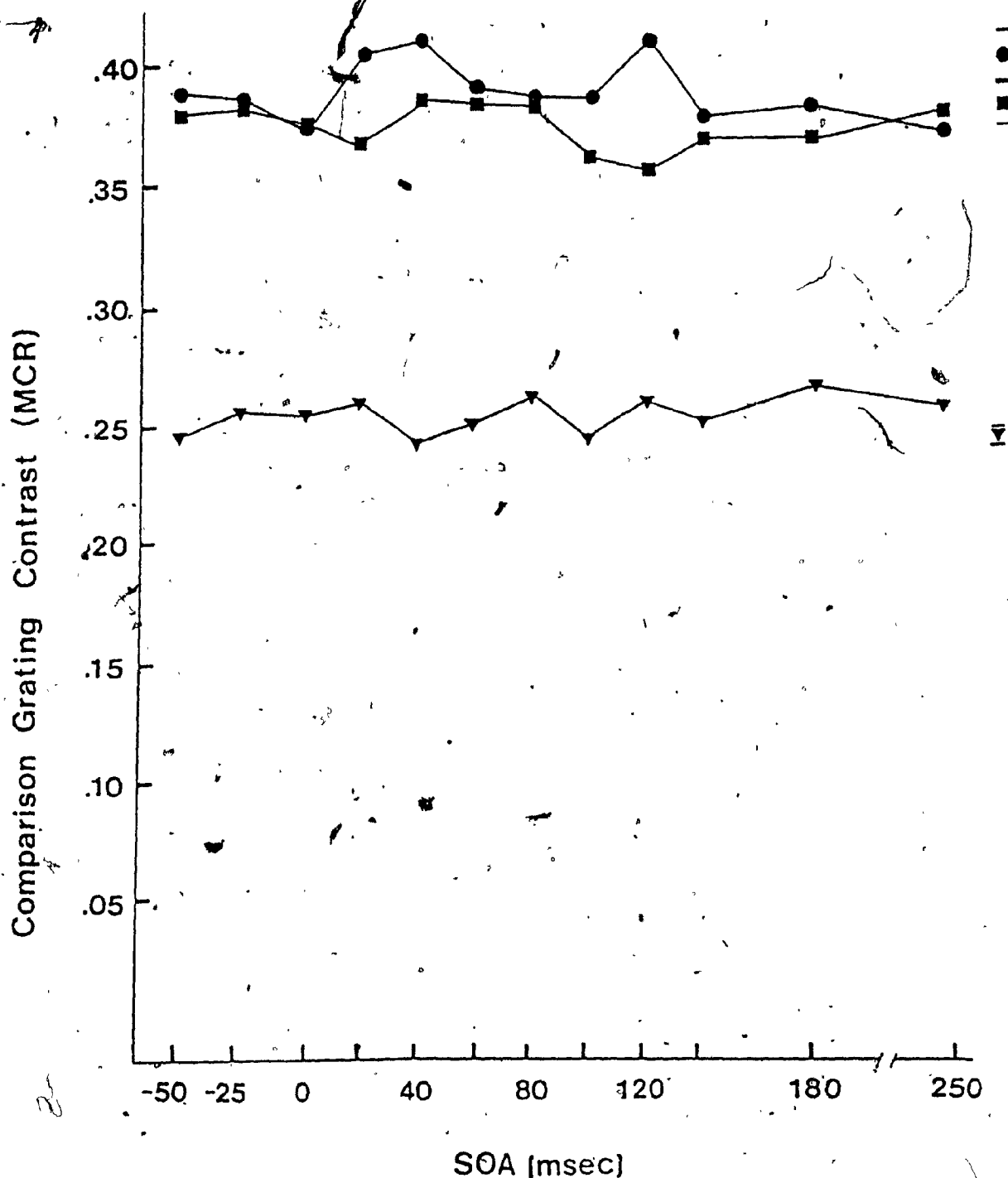


Figure 26. Comparison Grating Contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 condition in Experiment 3. ● = 2 c.p.d. high contrast target, 10 c.p.d. mask; ■ = 2 c.p.d. high contrast target, 6 c.p.d. mask; ▼ = 10 c.p.d. low contrast target 10 c.p.d. mask. The baseline matching contrast values (with standard error bars) are displayed on the right-hand side of each function.

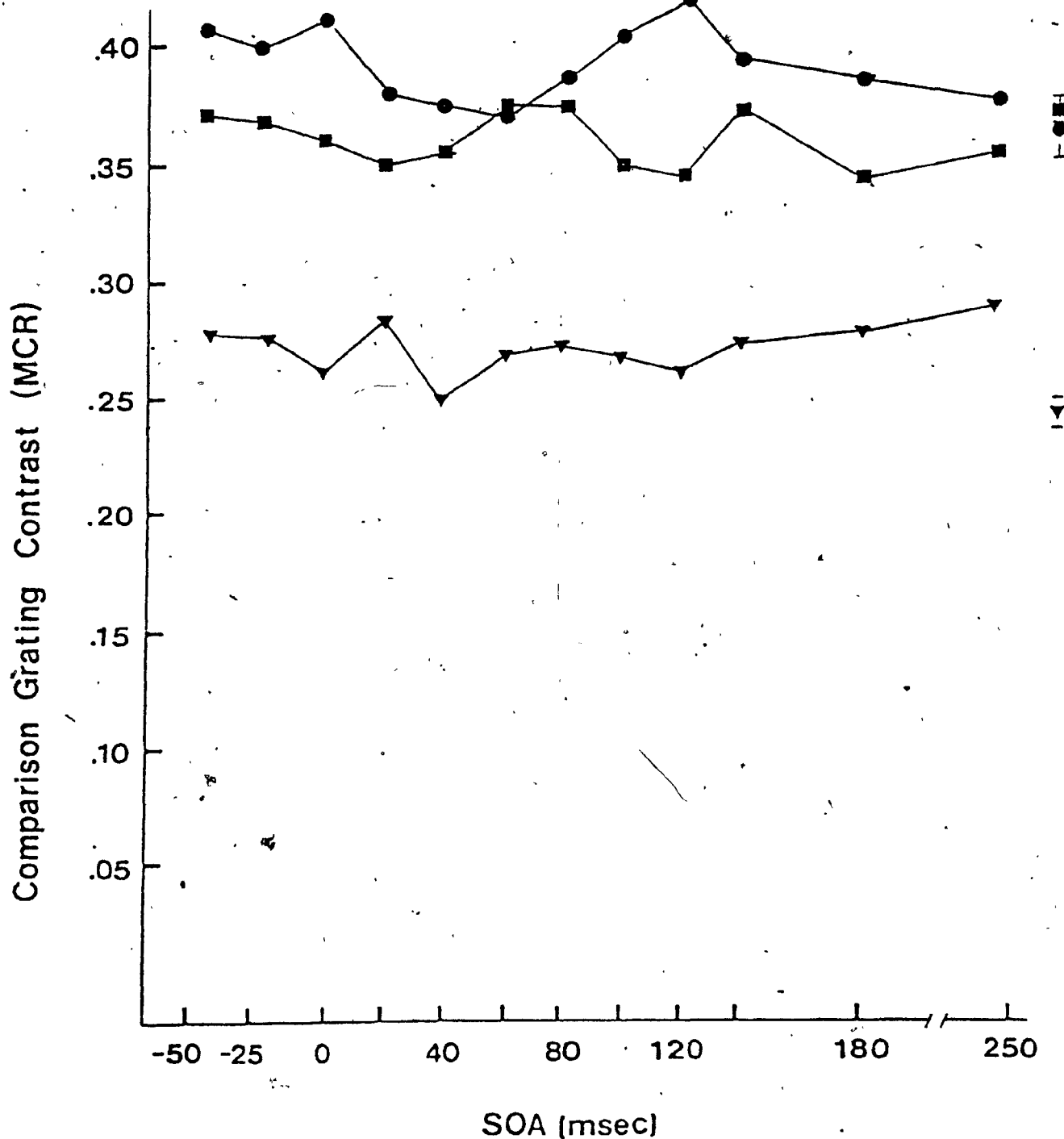


Figure 27. Comparison Grating Contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 condition in Experiment 3. ● = 10 c.p.d. high contrast target, 10 c.p.d. mask; ■ = 10 c.p.d. high contrast target, 2 c.p.d. mask; ▼ = 10 c.p.d. low contrast target, 6 c.p.d. mask. The baseline matching contrast values (with standard error bars) are displayed on the right-hand side of each function.

variable. In this experiment, the maximum contrast used, was .41; In the Growney and White & Lorber studies, the stimuli had contrasts of .64 and .78, respectively. Since it has been shown that grating contrast level directly affects neural stimulation (Maffei & Fiorentini, 1973), it is believed that in this study, the cells responding to the mask were not effectively stimulated in order to produce masking. The use of the Tektronix 5403 (P-32 phosphor) oscilloscope limited the contrast range of the gratings; the higher contrasts were accompanied with luminance distortions.

One recent study has shown how important a variable contrast is, in the production of metacontrast. Looking at the effectiveness that mask contrast manipulations had on the metacontrast effect, Ims (1980) reported that the effect was strongly influenced by mask contrast level. Using a letter-orientation identification task, Ims employed masks with 3 contrast levels; .35, .55 and .75. It was evident in the data, that errors in the identification task only began to occur when the annular mask was at its highest contrast level (within the range of contrasts used by Growney and White & Lorber).

It seems from this discussion, that one possible explanation for the absence of metacontrast may have been due to the low contrast levels used. Due to the limitations

of this apparatus however, it appears that if metacontrast was going to be generated with these types of stimuli, factors other than contrast may have had to be manipulated.

It has been argued (Boynton & Kandel, 1957) that light adaptation may reduce a mask's effectiveness by reducing the magnitude of the neurological response it produces. In fact, the results from Enroth-Cugell & Shapley (1973), Enroth-Cugell, Hertz & Lennie (1977) as well as Harding & Enroth-Cugell (1978), indicated that transient cells found in the cat's retina lose their responsiveness to stimulation as the eye becomes more light adapted. Psychophysically, Boynton & Kandell (1957) as well as Purcell, Stewart & Brunner (1974) reported that light adaptation could reduce the effectiveness of a masking stimulus. White & Lorber (1976) using dark adapted observers in their study successfully produced metacontrast with grating stimuli. Although Growney used light adapted observers, they adapted to a relatively low luminance (17 cd/m^2) compared to the peak luminance of the grating stimuli (78 cd/m^2). Thus, it is conceivable that in this study, not only did low contrast masks contribute to the results, but possibly, so did the state of adaptation of the eye.

Experiment 4

This study, was identical to Experiment 3, except for a change in the the state of adaptation of the eye. After initially dark adapting for 5 minutes, the observer viewed a dimly lit (1 cd/m^2) field for an additional 5 minutes. This luminance level was maintained for all of the fields, except during the stimulus presentations, at which time, the gratings modulated around a mean luminance level of 10 cd./m^2 . BK and PB were used as the observers.

Results and Discussion

As in Experiment 3, the data were averaged across replications. PB's data are presented in Figures 28 - 33 and are representative of BK's results, which are presented in appendix B. Similar to the results of Experiment 2, metacontrast was not produced in any of the conditions. The variability, as indicated by the standard error bars was generally very small for both observers.

Since the state of adaptation of the eye was the only variable to change from Experiment 3, it seems from these results, that the state of adaptation of the eye alone, was not the significant variable precluding the metacontrast effect. In furthering the attempt to understand why metacontrast was not produced, the dependent measure was scrutinized.

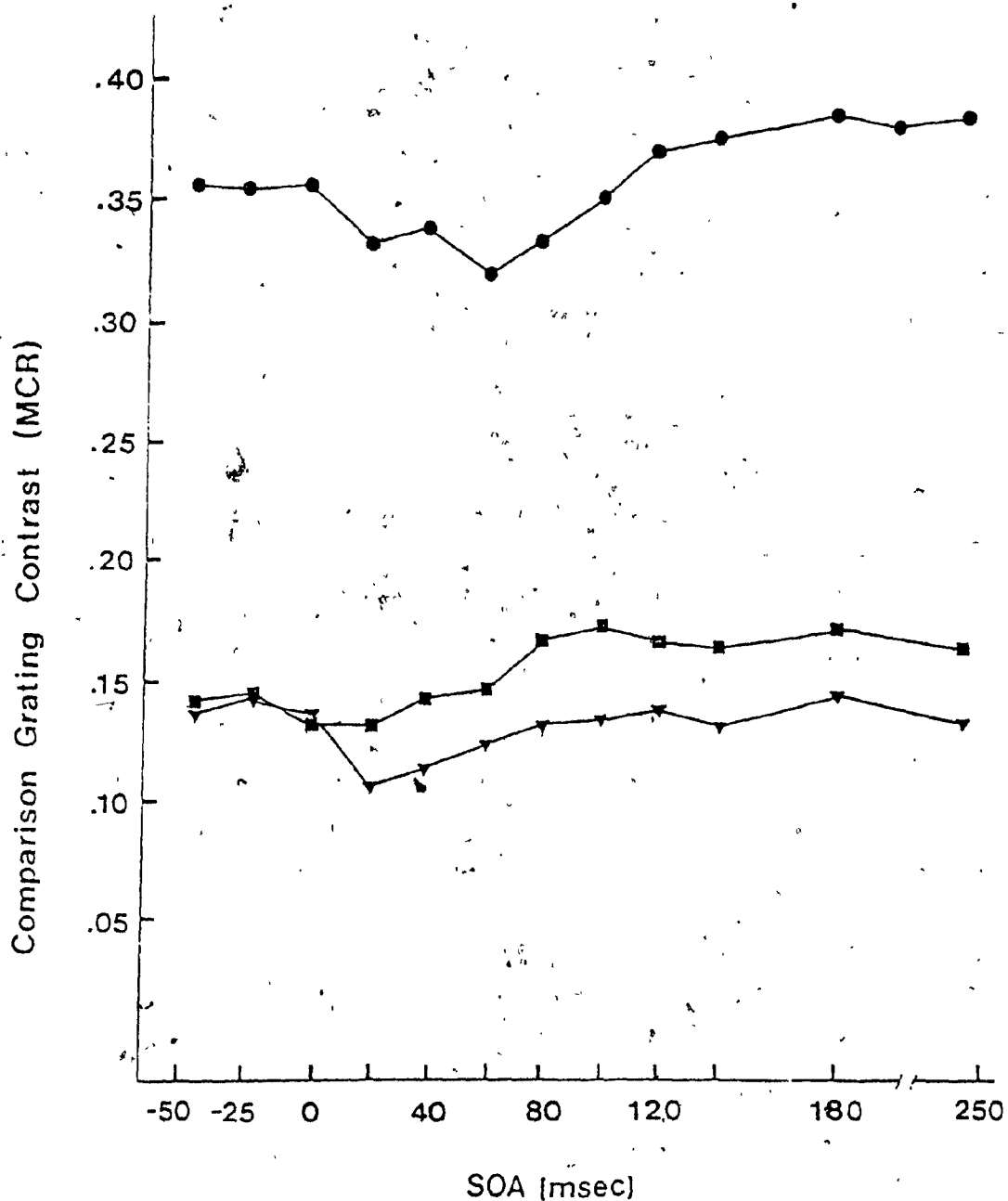


Figure 28. Comparison Grating Contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 dark adapted condition in Experiment 4.
 ● = 2 c.p.d. high contrast target, 2 c.p.d. mask;
 ■ = 6 c.p.d. low contrast target, 2 c.p.d. mask;
 ▼ = 2 c.p.d. low contrast target, 2 c.p.d. mask.
 The baseline matching contrast values (with standard error bars) are displayed on the right-hand side of each function.

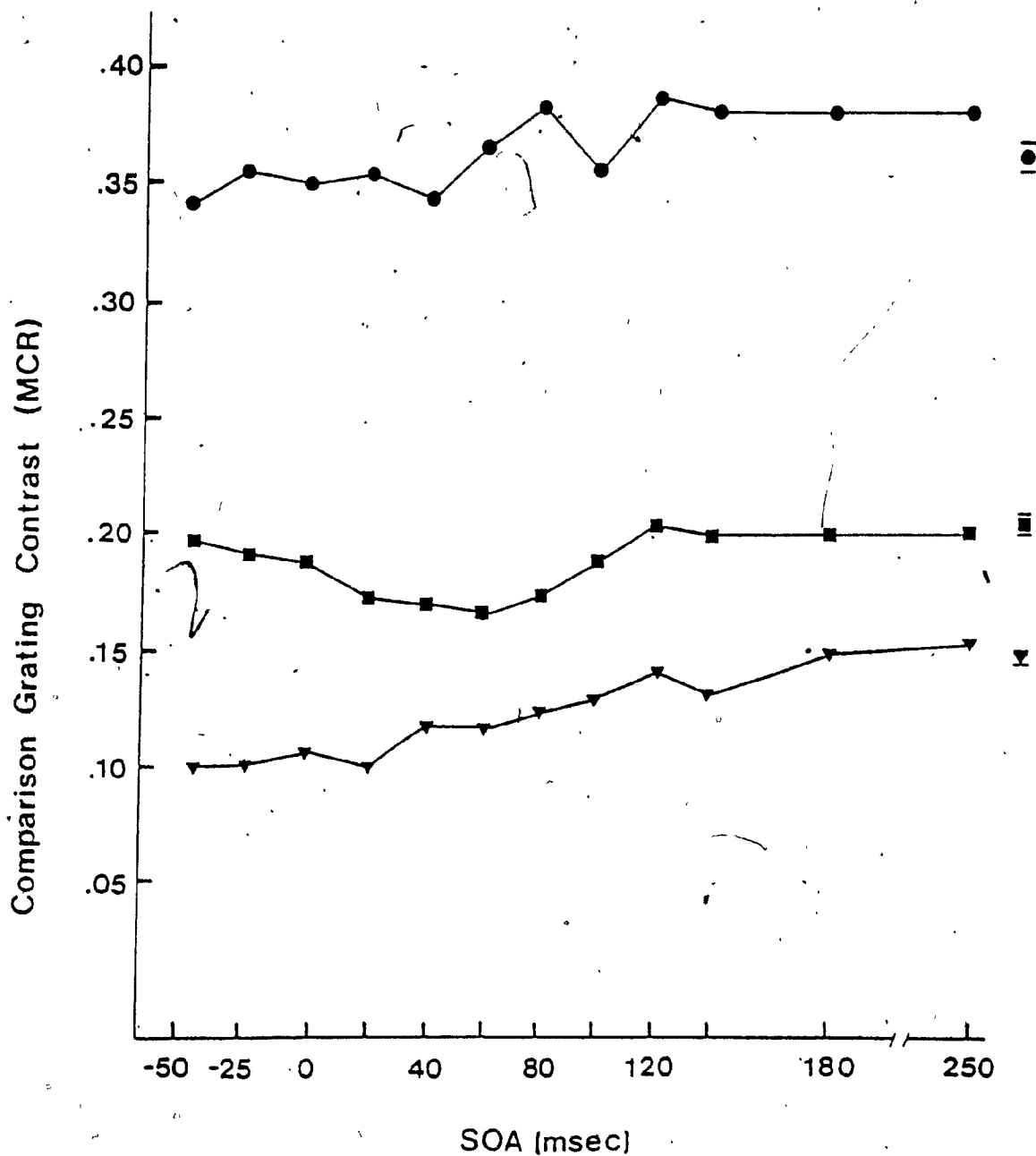


Figure 29. Comparison Grating Contrast (MCR) as a function of SOA (msec) for observer R.K. Each function represents 1 dark adapted condition in Experiment 4.

- = 6 c.p.d. high contrast target, 2 c.p.d. mask;
- = 10 c.p.d. low contrast target, 2 c.p.d. mask;
- ▼ = 2 c.p.d. low contrast target, 6 c.p.d. mask.

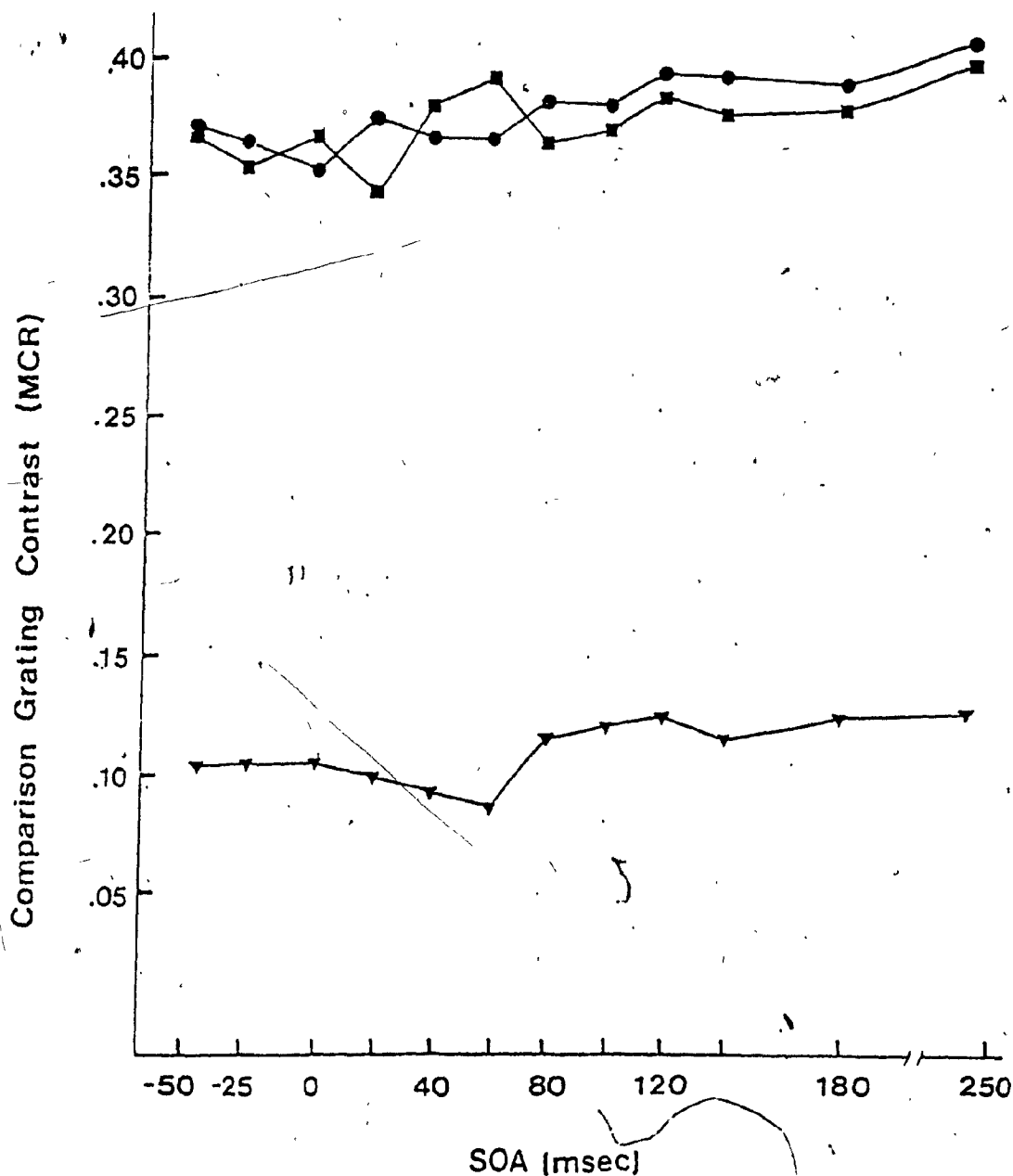


Figure 30. Comparison grating contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 dark adapted condition in Experiment 4.

- = 10 c.p.d. high contrast target, 6 c.p.d. mask;
- = 6 c.p.d. high contrast target, 10 c.p.d. mask;
- ▼ = 2 c.p.d. low contrast target, 10 c.p.d. mask.

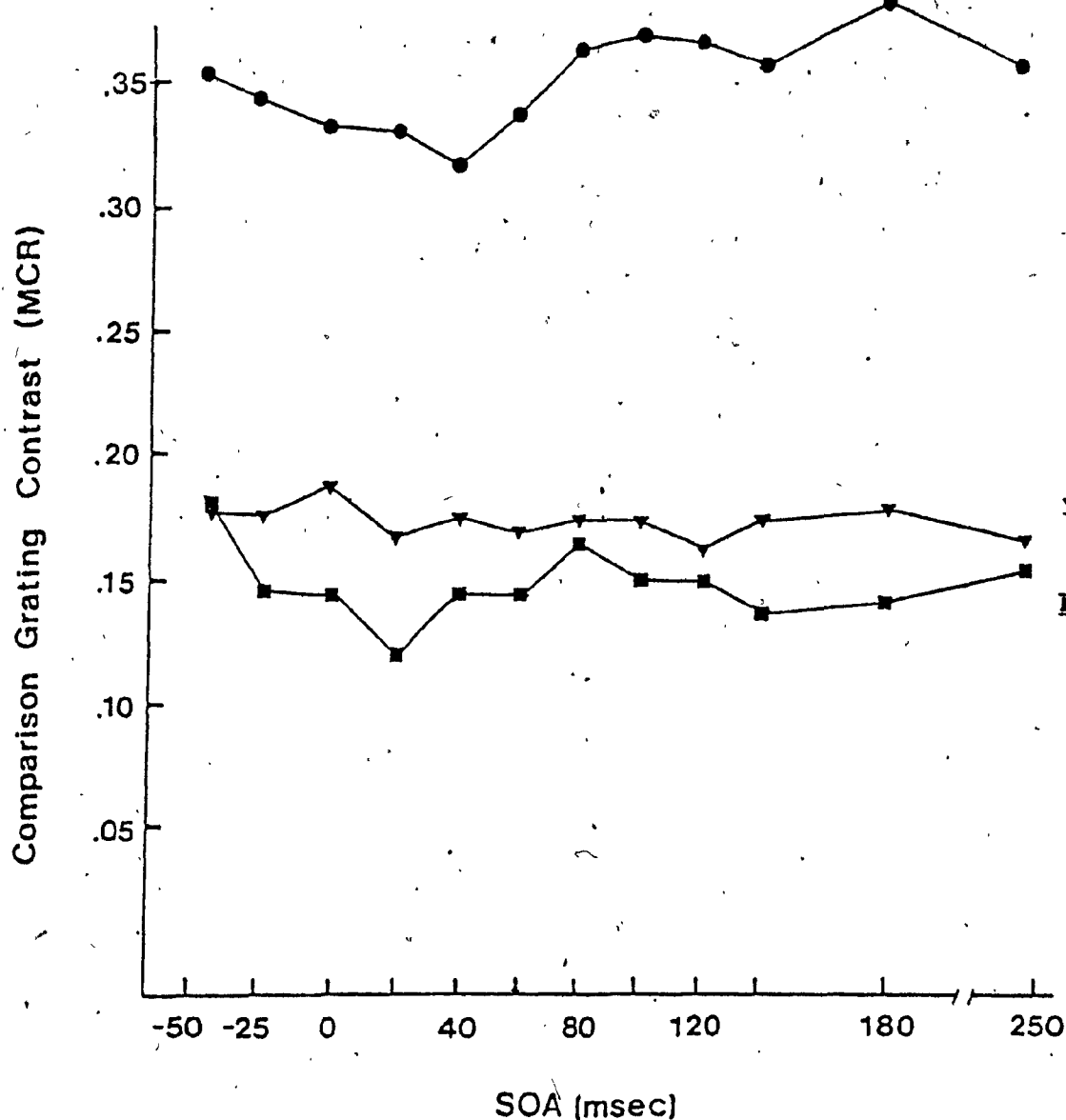


Figure 31. Comparison grating contrast (MCR) as a function of SOA (msec) for observer E.K. Each function represents 1 dark adapted condition in Experiment 4.

- = 6 c.p.d. high contrast target, 6 c.p.d. mask;
- = 6 c.p.d. low contrast target, 6 c.p.d. mask;
- ▼ = 6 c.p.d. low contrast target, 10 c.p.d. mask.

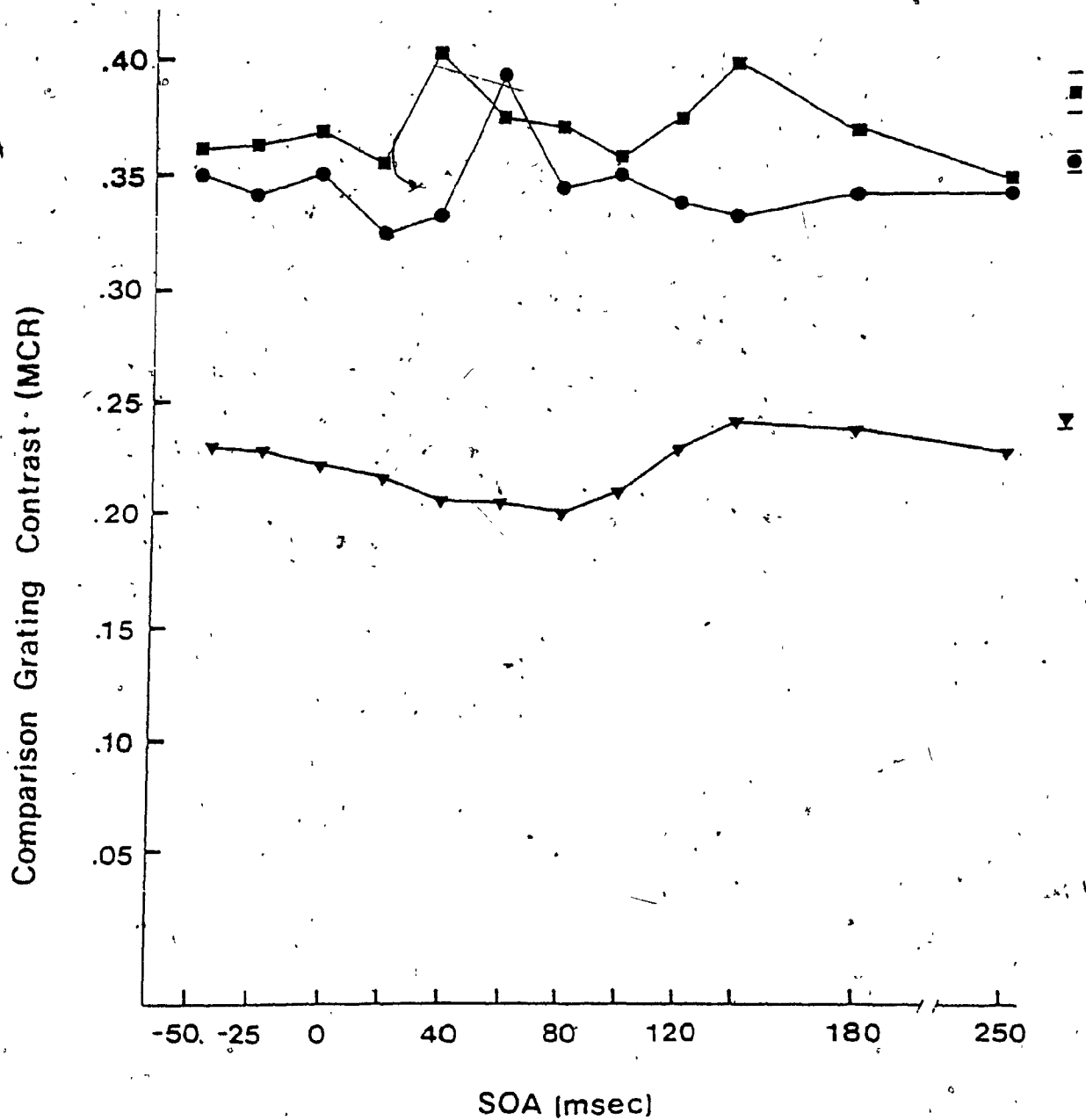


Figure 32. Comparison grating contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 dark adapted condition in Experiment 4.
 ● = 2 c.p.d. high contrast target, 10 c.p.d. mask;
 ■ = 2 c.p.d. high contrast target, 6 c.p.d. mask;
 ▼ = 10 c.p.d. low contrast target, 10 c.p.d. mask.

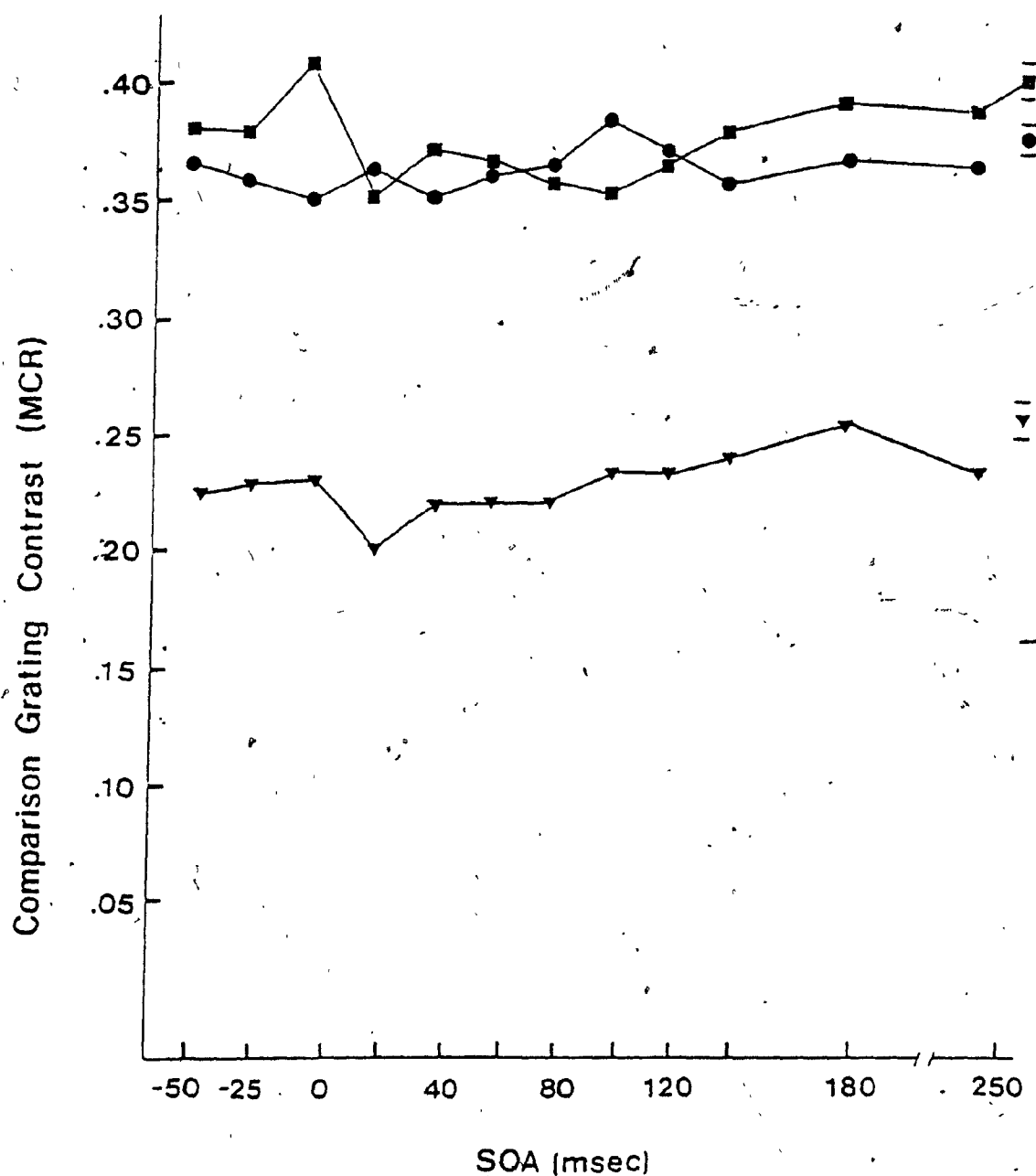


Figure 33. Comparison grating contrast (MCR) as a function of SOA (msec) for observer B.K. Each function represents 1 dark adapted condition in Experiment 4.

- = 10 c.p.d. high contrast target, 10 c.p.d. mask;
- = 10 c.p.d. high contrast target, 2 c.p.d. mask.
- ▼ = 10 c.p.d. low contrast target, 6 c.p.d. mask.

Pilot work indicated that the dependent measure, may have not been sensitive to perceptual changes in the target. In these preliminary studies, uniform high luminance (88 cd./m^2) nonmodulated stimuli were presented as masks.

Metacontrast was produced, reducing the perceptual effectiveness of the target. However, the observers in the pilot work all reported that adjusting the contrast of the comparison stimulus, was not effective in reducing its perceptual impact to match that of the target stimulus.

They claimed that although the comparison contrast may have matched the apparent contrast of the target, the brightness was not the same. It may be possible that in Experiments 3 and 4, the brightness of the target was attenuated due to metacontrast, yet its perceptual contrast remained the same.

In the pursuit of finding another dependent measure that would be sensitive to all perceptual variations of the target, we may turn to the White & Lorber study. In their investigation, a comparison stimulus was presented to the observers, which varied in duration. The observers made comparisons based on "the apparent contrast between the light and dark bars of the gratings, the sharpness of the contours, and whether any bars or pieces of bars appeared to missing from the TS (target stimulus)". Using a similar dependent measure as White & Lorber, pilot work using the high luminance masks was conducted. The observers

participating in this work indicated that they were confident in matching the perceptual effectiveness of the masked target. That is, they were now able to make matches that they considered to be perceptually equivalent.

Experiment 5

This study was similar to Experiments 3 and 4, except for a change in the dependent measure, and a reduction in the number of conditions and SOAs. Table 4 displays the 12 conditions that were used in this experiment. Since the main thrust of this study was to try to maximize the effect of metacontrast, the 2 and 10 c.p.d. high target contrast conditions were eliminated, since it was believed that these targets would have a high likelihood of evading masking.

Dependent and Independent Variables

In order to assess the effective perception of the target stimulus, the duration of the comparison grating was adjusted, until the observer matched it to the effective perception of the target. Because of the physical outlay of the Coulbourn logic system, it was necessary for the experimenter to manipulate the duration variable as instructed by the observer. Prior to an SOA block, the duration of the comparison stimulus would be adjusted by the experimenter to 0 msec. After the first trial, the observer would indicate to the experimenter, that he should increase the duration of the comparison (if he saw the target). The experimenter would then increase the duration by a variable amount. During the following trials, the observer instructed the experimenter as to the direction of the duration manipulation, until he was satisfied that a

Table 4

Conditions of Experiment 5

		TARGET SPATIAL FREQUENCY (C.P.D.)			
		2	6		10
			Contrast		
MASKING SPATIAL FREQUENCY (C.P.D.) - High Contrast	Low	Low	High	Low	Low
	2				
	6				
	10				

match had occurred.

PB and SS were exposed to the 12 conditions for SOAs of 0, 30, 60 and 90 msec. The state of adaptation of the eye was manipulated by presenting these conditions to both the dark and light adapted eye (using the same parameters as in the previous experiments).

Results and Discussion

The data were averaged across the three replications within each adaptation condition. PB's light and dark adaptation data are presented in Figures 34 - 37, and 38 - 41, respectively. They are representative of SS's results, which are presented in appendix C. Again, in all conditions, metacontrast was not observed. The variability remained very low for both observers in all conditions.

It was becoming quite evident from these studies, that due to the low contrast level of the mask, metacontrast might be unobtainable using these stimuli. If however, the effect of contrast was to minimize the neural activity of the mask, it is possible to increase this activity using another variable.

It is well known that below a critical duration, decreasing the duration of a stimulus will lead to decreases

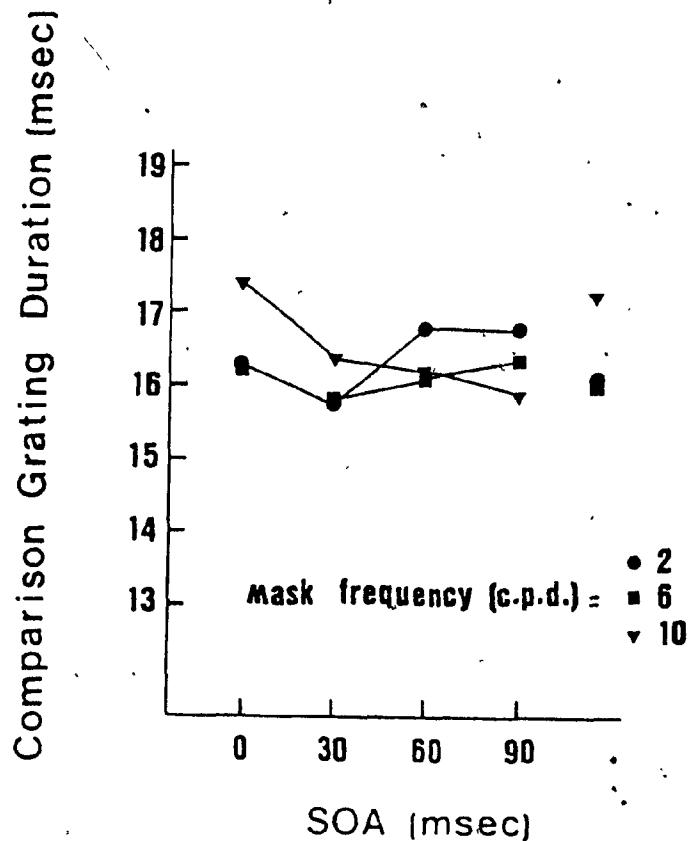


Figure 34. Comparison grating duration (msec) as a function of SOA (msec) for observer P.B. Each function represents one light-adapted condition of Experiment 5. The baseline matching durations are shown on the right-hand side of each function. Standard errors ranged between .2 - 1.5 msec. Target condition = 2 c.p.d. (low contrast).

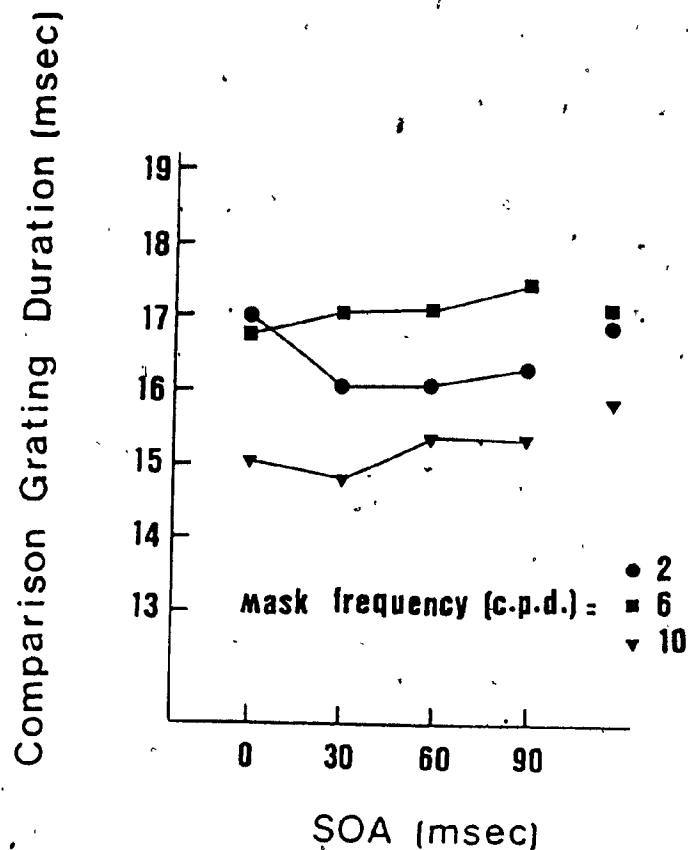


Figure 35. Comparison grating duration (msec) as a function of SOA (msec) for observer P.B. Each function represents one light-adapted condition of Experiment 5. The baseline matching durations are shown on the right-hand side of each function. Standard errors ranged between .2 - 1.5 msec. Target condition = 6, c.p.d. (low contrast).

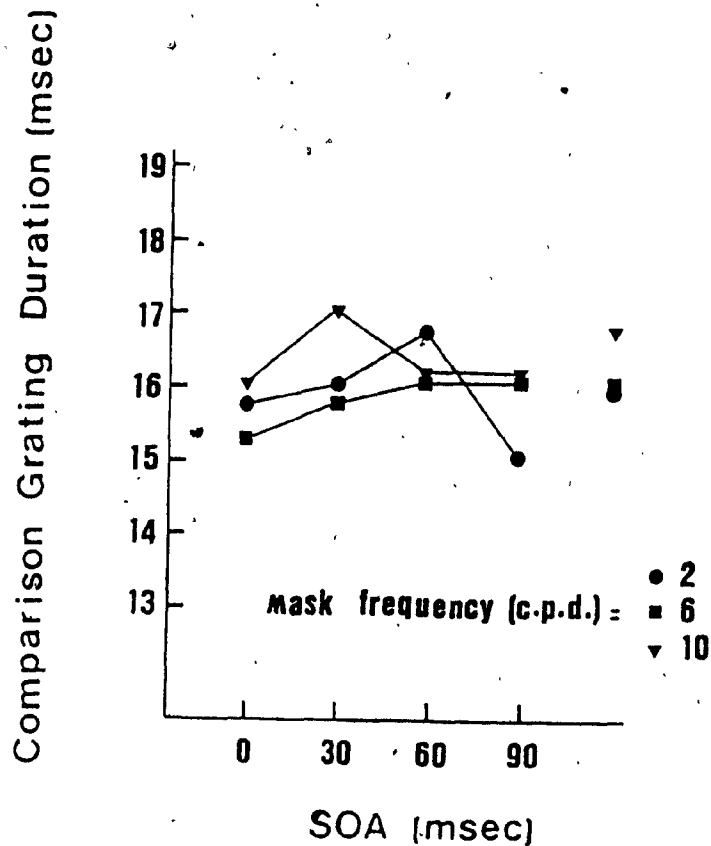


Figure 36. Comparison grating duration (msec) as a function of SOA (msec) for observer P.B. Each function represents one light-adapted condition of Experiment 5. The baseline matching durations are shown on the right-hand side of each function. Standard errors ranged between .2 - 1.5 msec. Target condition = 6, c.p.d. (high contrast).

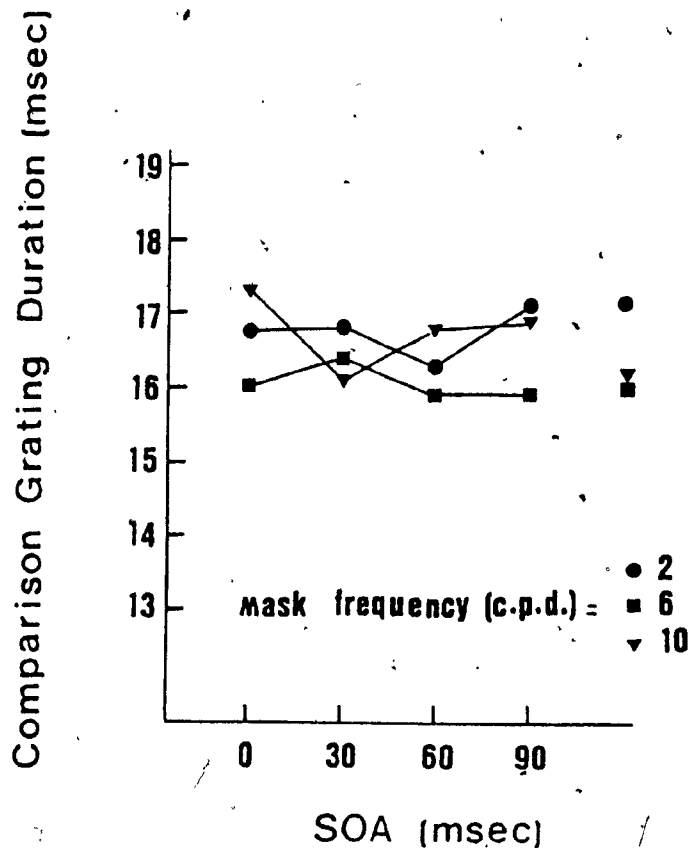


Figure 37. Comparison grating duration (msec) as a function of SOA (msec) for observer P.B. Each function represents one light-adapted condition of Experiment 5. The baseline matching durations are shown on the right-hand side of each function. Standard errors ranged between .2 - 1.5 msec. Target condition = 10 c.p.d. (low contrast)

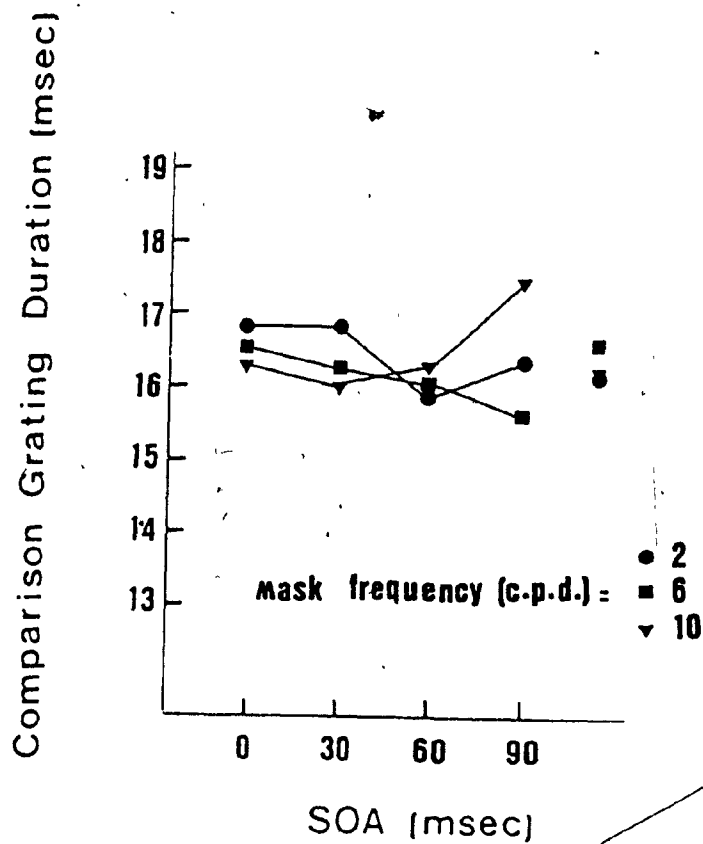


Figure 38. Comparison duration (msec) as a function of SOA (msec) for observer P.B. Each function represents one dark-adapted condition of Experiment 5. The baseline matching durations are shown on the right-hand side of each function. Standard errors ranged between .2 - 1.5 msec. Target condition = 2 c.p.d. (low contrast).

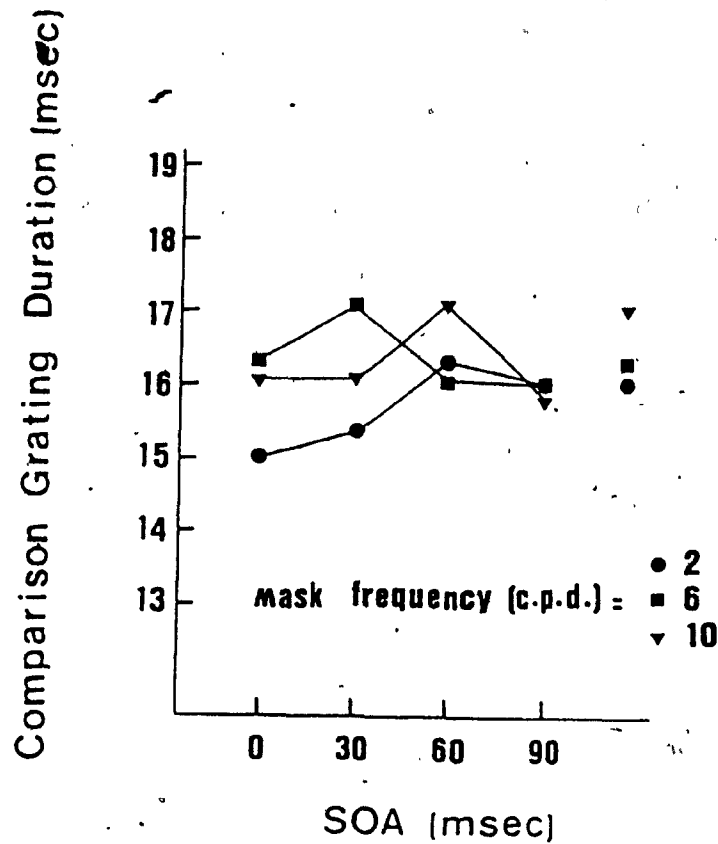


Figure 39. Comparison duration (msec) as a function of SOA (msec) for observer P.K. Each function represents one dark-adapted condition of Experiment 5. The baseline matching durations are shown on the right-hand side of each function. Standard errors ranged between .2 - 1.5 msec. Target condition = 6 c.p.d. (low contrast).

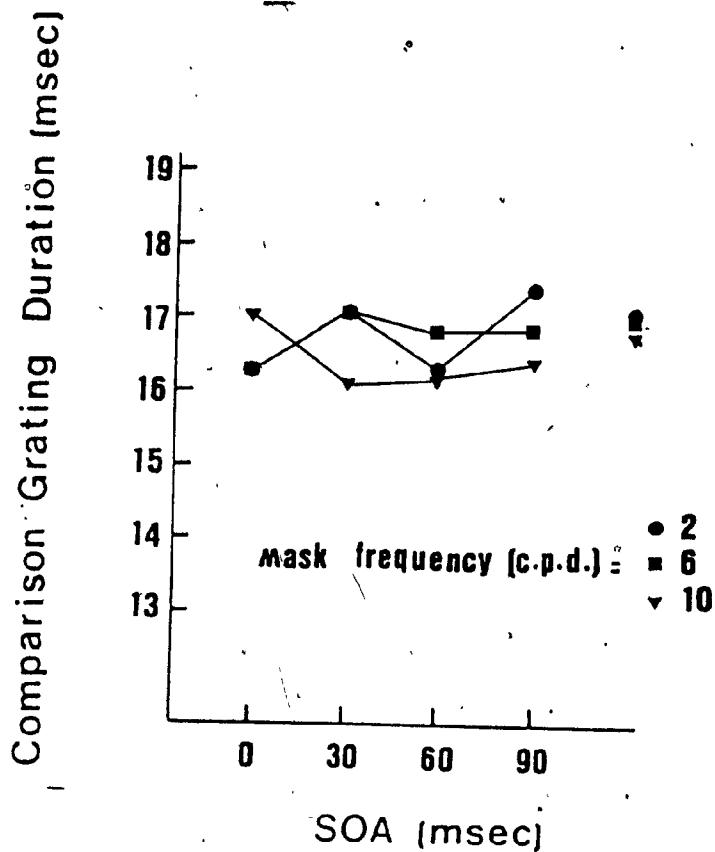


Figure 40. Comparison duration (msec) as a function of SOA (msec) for observer P.B. Each function represents one dark-adapted condition of Experiment 5. The baseline matching durations are shown on the right-hand side of each function. Standard errors ranged between .2 - 1.5 msec. Target condition = 6 c.p.d. (high contrast).

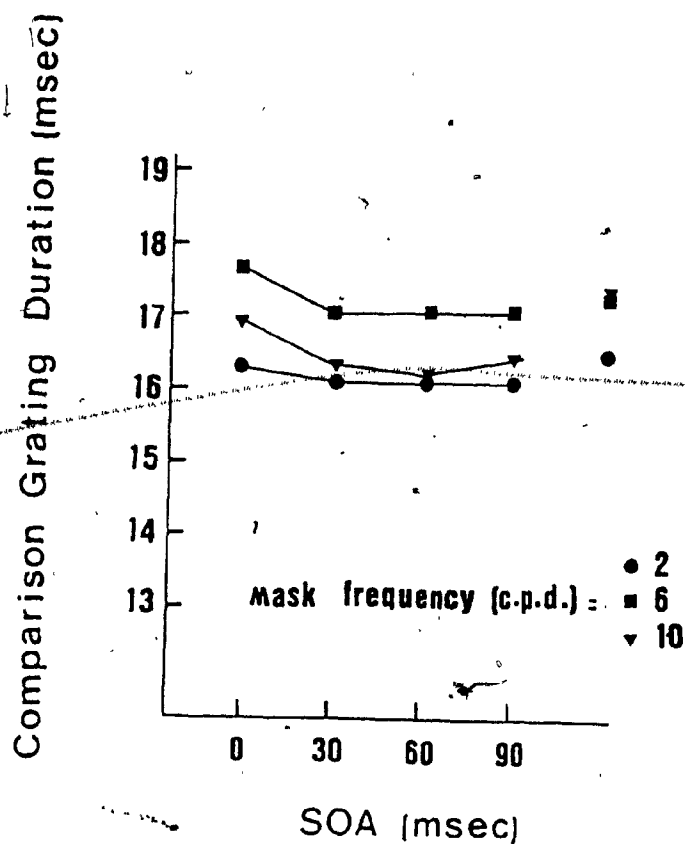


Figure 41. Comparison duration (msec) as a function of SOA (msec) for observer P.B. Each function represents one dark-adapted condition of Experiment 5. The baseline matching durations are shown on the right-hand side of each function. Standard errors ranged between .2 - 1.5 msec. Target condition = 10 c.p.d. (low contrast).

in the firing rate of a responding neuron (Ganz, 1975). If the activity level of neurons responding to the mask is related to its masking effectiveness, then it is possible that changes in mask duration may be as effective on masking, as changes in its contrast. Alpern (1953), Kinsbourne & Warrington (1962), Kahneman (1966), Dochin (1967) and Turvey (1973) all reported that masking effects were attenuated as the duration of the mask was decreased.

Since duration manipulations have been shown to affect the magnitude of masking, it was expected that similar variations in target and or mask duration with these grating stimuli, would have an influence on the production of metacontrast.

Experiment 6

Pilot work indicated that varying the duration of the stimuli affected whether metacontrast was produced, only if the energy (defined as the product of duration and luminance) of the mask increased relative to that of the target. It was found for instance, that when higher energy targets and masks were employed (when they were presented for 50 msec. each) metacontrast was still not produced. However, when the mask energy doubled that of the target (the target and mask were presented for 16 and 32 msec. respectively), metacontrast became evident, yet only in the dark adaptation condition.

Experiment 6 was conducted to thoroughly investigate this sole situation, which could produce metacontrast with these stimuli. Table 5 presents the nine stimulus conditions that were used. Pilot work indicated that the higher contrast 6 c.p.d. target evaded masking. Therefore, this stimulus condition was not used in the experiment. The target and mask were presented for 16 and 32 msec respectively, to the dark adapted eye. Each condition was replicated 3 times for SOAs of -60, -40, -20, 0, 20, 40, 60, 80, and 100 msec. The dependent variable was the comparison duration manipulation. PB, SS and LL served as the observers.

Table 5

Conditions of Experiment 6

TARGET SPATIAL FREQUENCY
(C.P.D.)

Low Contrast

	2	6	10
2			
6			
10			

MASK
SPATIAL FREQUENCY
(C.P.D.)
- High Contrast

Results

The data were averaged across the three replications. LL's data are presented in Figures 42 - 44 and are consistent with the data of PB and SS, whose data are presented in appendix D. In these figures SOA is represented on the abscissa, while the matched durations, are shown on the ordinate. In each figure the effect of the three masks (2, 6 and 10 c.p.d.) are depicted for each target (2, 6 and 10 c.p.d.). The average baseline measures for the target-alone condition, are found on the right-hand side of the functions. The displayed standard errors, represented the low variability found for all observers.

The most apparent finding was the production of dramatic metacontrast monotonic functions. Figure 42 displays LL's results for the 2 c.p.d. grating. Maximum metacontrast appeared to occur at an SOA of 0 for the 2 c.p.d. mask condition. As well, in Figures 43 and 44 which display LL's data for target frequencies of 6 and 10 c.p.d. respectively, the same trends were evident. That is, maximum masking occurred both, at an SOA of 0, and in the conditions in which the target and mask shared the same spatial frequency. This trend was also evident in PB and SS's data. In summary, these data showed metacontrast to vary as a function of the spatial frequency similarity between the target and mask.

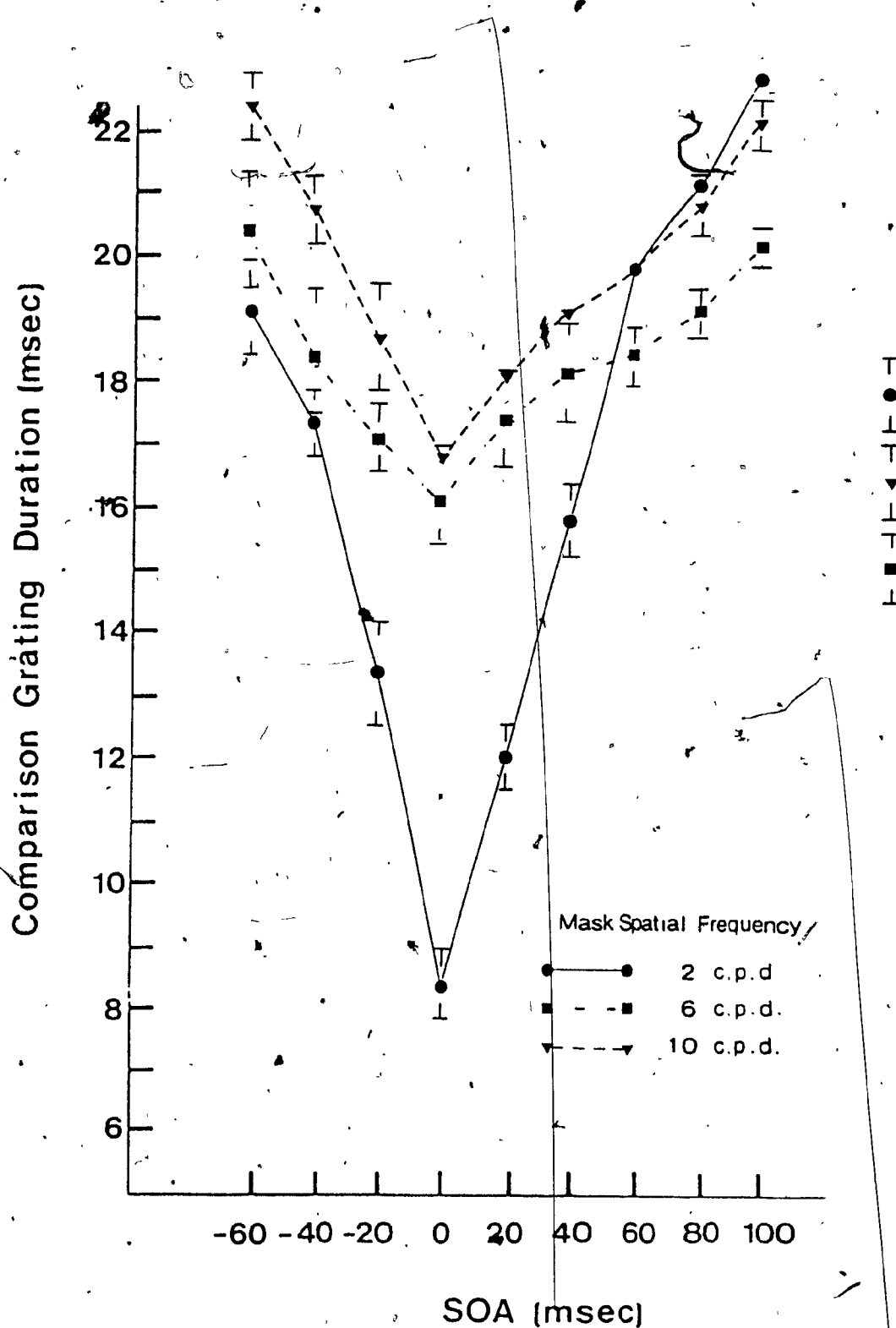


Figure 42. Comparison duration (msec) as a function of SOA (msec) for observer L.L. Each function represents one condition of Experiment 6. The baseline matching durations are shown with standard error bars on the right-hand side of the graph. Target spatial frequency = 2 c.p.d.

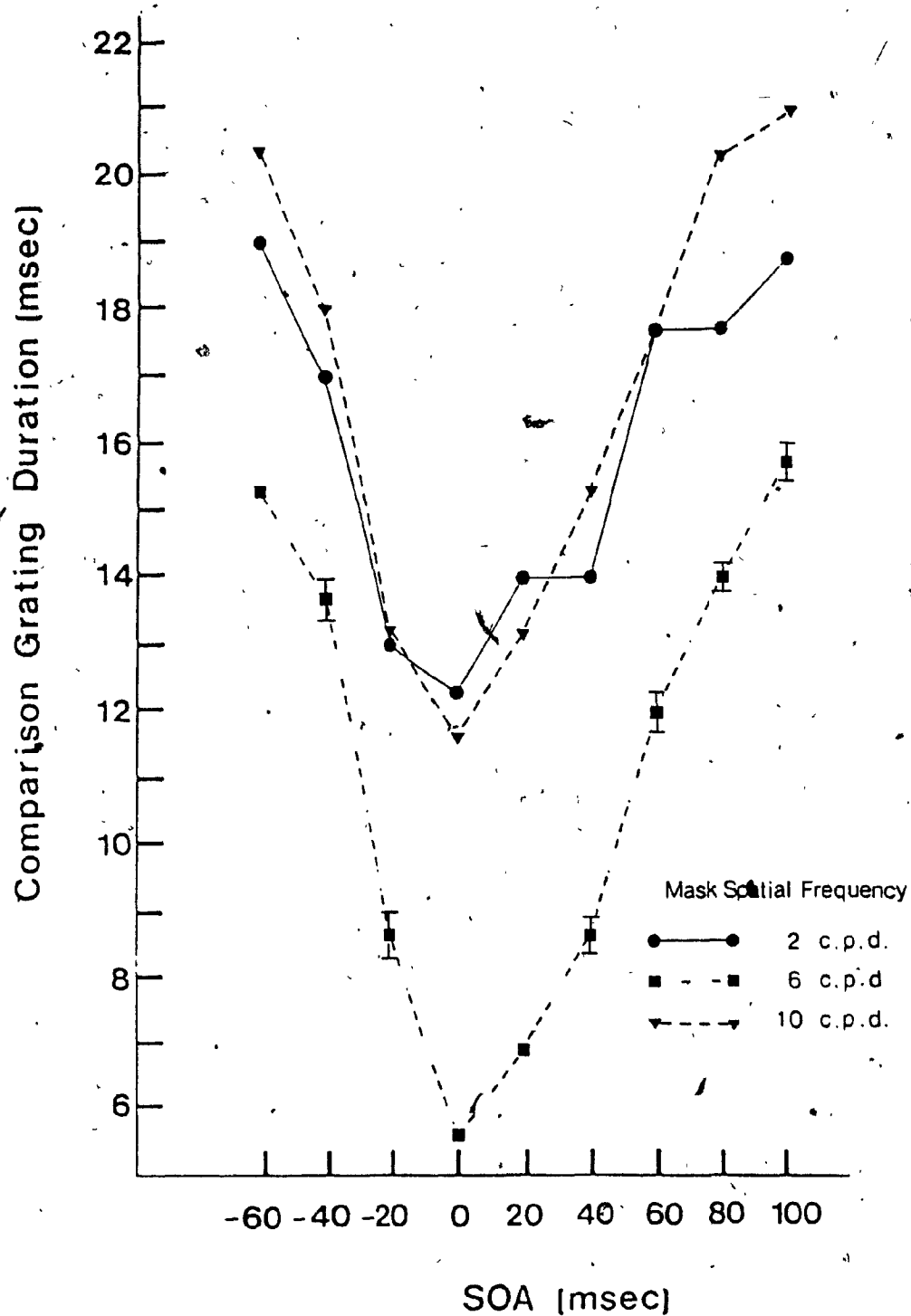


Figure 43. Comparison duration (msec) as a function of SOA (msec) for observer L.L. Each function represents one condition of Experiment 6. The baseline matching durations are shown with standard error bars on the right-hand side of the graph. Target spatial frequency = 6 c.p.d.

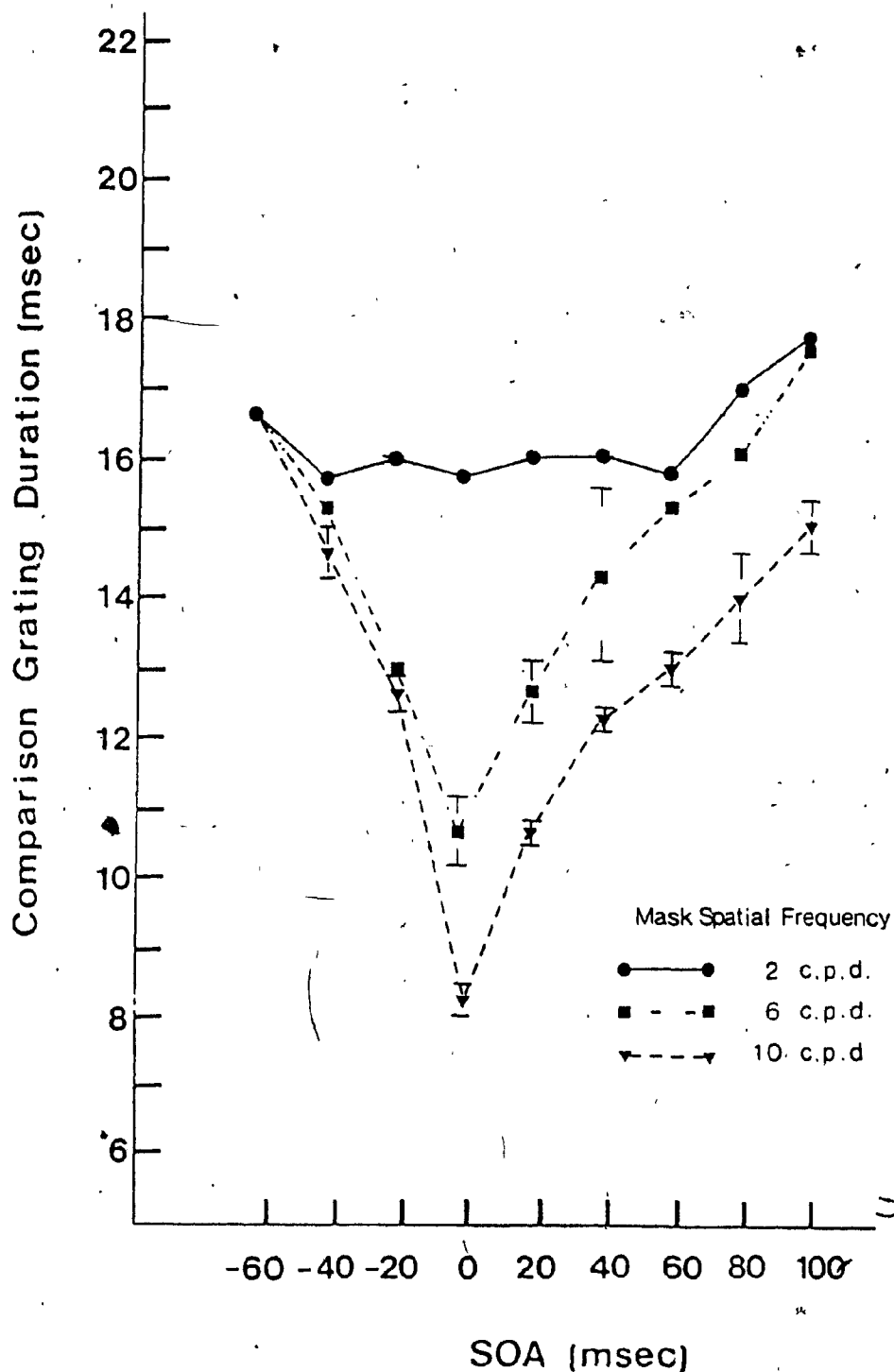


Figure 44. Comparison duration (msec) as a function of SOA (msec) for observer L.L. Each function represents one condition of Experiment 6. The baseline matching durations are shown with standard error bars on the right-hand side of the graph. Target spatial frequency = 10 c.p.d.

Discussion

From the data of experiment 6, it is clear that monotonic metacontrast functions may be generated using these low energy stimuli. It was not suprising that these types of functions were produced, since as was indicated earlier, this is an expected finding with relatively higher energy masks and lower energy targets. It seems that these overall low energy stimuli are marginally effective as masking stimuli. Not only are they unable to produce U-shaped metacontrast functions, but they require dark adapted conditions to produce monotonic curves.

The White & Lorber (1976), Weisstein et al. (1975) and Breitmeyer & Ganz (1976) models have placed great importance in describing what may be mediating U-shaped metacontrast functions. That notwithstanding, differential predictions about the conditions which produce monotonic functions may be extrapolated from their theories.

White & Lorber (1976) for instance, predicted that maximum masking (whether it be monotonic or U-shaped) should occur when the target and mask share the same spatial frequency. This prediction was confirmed by the data.

Weisstein et al. (1975) however, suggested that a high energy mask smears-out its transient response, necessitating less temporal separation between the target and mask to

create metacontrast. If metacontrast is strictly a function of the transient system inhibiting the sustained, with lower spatial frequency gratings maximally stimulating the transient system, then we might have expected maximum masking to have occurred at both an SOA of 0 and with the low spatial frequency mask. Although maximum masking did occur at an SOA of 0, it was evident that the low spatial frequency mask condition did not produce more masking when compared to the other conditions.

Breitmeyer & Ganz envisioned monotonic functions occurring due to intrachannel inhibition, whereby sustained cells responding to the mask, inhibit sustained cells reacting to the target. From their theory, one would have expected greatest masking to occur with the 10 c.p.d. target and 10 c.p.d. mask. The results however did not show this.

To summarize, White & Lorber's (1976) "similarity hypothesis" seems to have accurately predicted the data. The sustained-transient view of metacontrast, as it has been conceptualized by Weisstein et al. (1975) and Breitmeyer & Ganz (1976) however, is not adequate in describing the neural mechanisms that produced these data. In the General Discussion section, an attempt to explain the mechanisms mediating the results of these experiments is discussed.

GENERAL DISCUSSION

The initial aim of this thesis was to elucidate the characteristics of the proposed sustained and transient channels in the human visual system. Experiment 1 was conducted in light of a study conducted by Harwerth & Levi (1976) where they claimed that a RT paradigm to grating stimuli, offered a way to observe the results of sustained and transient activity. This study was conducted both as a replication of their RT data, as well as an investigation of how these two processing channels may be affected by shorter stimulus durations. Similar to Harwerth & Levi's interpretation of their data, the results of Experiment 1 were interpreted as giving evidence for the existence of sustained and transient mechanisms mediating RT to gratings. Specifically, it was proposed that the spatial frequency and contrast level of a grating was associated with the differential involvement of these two processing channels. Consistent with the neurophysiological research cited earlier, the results supported the proposal that low spatial frequency gratings maximally involved the transient system, while higher spatial frequencies implicated the sustained system.

The shape of the RT curves were seen to be an important variable in the assessment of sustained and transient

activity. It was argued that the biphasic RT curves produced with the middle spatial frequency gratings, gave evidence that for a given spatial frequency, RT may be mediated by either the sustained or transient channels. RTs to high contrast gratings were seen to be mediated by transient cells, with RTs to lower contrast gratings being mediated by sustained tissues.

A model accounting for these RT functions was described. Three neural properties were viewed as being critical to this model. It was proposed that RT was sensitive to neural transmission time, neural responding rate as well as the number of tissues responding to the stimulus. Overall, the model explained the data, by assuming that contrast manipulations affected these three variables. The model accounted for the shape of the RT curves as well as for the effect of varying the spatial frequency and stimulus duration of the gratings.

Experiment 2 was conducted to further describe the characteristics of the sustained and transient channels. Gratings which varied in spatial frequency and contrast were presented in the periphery. The results were consistent with predictions that were extrapolated from the neurophysiological literature, which described an increase of transient activity in the periphery. These results suggested that sustained and transient activity can also be

differentially manipulated by varying the location of the stimulus.

In an attempt to describe the interactive characteristics of the sustained and transient channels, further studies investigated the paradigm of metacontrast. In recent years, a number of theorists have implicated the sustained and transient systems in accounting for this phenomenon. Specifically, Weisstein et al. (1975) as well as Breitmeyer & Ganz (1976) proposed that these channels interact in a way, such that one channel (transient) inhibits the other (sustained) in a nonmonotonic manner, to produce the degradation of the target stimulus.

Experiment 3 was conducted with two important assumptions in mind. From the results of the first two experiments, it was proposed that RT offered a sensitive way to measure the action of sustained and transient activity. It was assumed that if the same mechanisms mediating RT are also involved in the production of metacontrast, then from the results of Experiments 1 and 2, it may be possible to differentially manipulate the sustained and transient influences on the production of metacontrast. If the Weisstein et al. and Breitmeyer & Ganz descriptions of the neural interactions underlying metacontrast were correct, then it was assumed that by using the same foveal and peripheral stimuli as in Experiment 1 and 2, various degrees

of the metacontrast effect may be observed under the different stimulus conditions. It was proposed that by varying the spatial frequency and contrast of the stimuli, the implication of sustained and transient cells would be differentially manipulated. That is, according to these theories, the strongest metacontrast effect would be expected under conditions which created maximum stimulation of the transient cells and therefore, maximum inhibition of the sustained system.

The data, however, did not bear this out. In fact, metacontrast was not observed for all of the conditions in the experiment. Two possible explanations of these results became apparent. Firstly, if the mechanisms mediating RT and metacontrast were different, then using the spatial frequency and contrast parameters derived from Experiments 1 and 2, might not have had any bearing on manipulating the cells which normally produce metacontrast. Secondly, it was possible that RT and metacontrast are mediated by the same neurons, however the stimulus parameters were not ideal for producing strong metacontrast effects. This latter possibility was experimentally investigated before the first possible explanation was considered.

Experiments 4 and 5 were conducted in an attempt to assess why metacontrast was not produced in Experiment 3. Factors which have been known to strongly affect the

metacontrast function were investigated. It was found that the state of adaptation of the eye (Experiment 4) or the dependent measure (Experiment 5) alone, were not responsible for the absence of metacontrast. Pilot work indicated that increasing the energy of the mask relative to that of the target however, would produce metacontrast in the dark adapted eye.

Experiment 6 was conducted to investigate this condition. In this study, masks with twice the energy of the targets were used. Stimulus conditions with spatial frequency manipulations similar to Experiment 3 were employed. Monotonic metacontrast functions were produced in all conditions. From the results of all the observers, the most salient aspect of these data, was the fact that maximum metacontrast varied directly as a function of the spatial frequency similarity between the target and mask. This finding is consistent with the White & Lorber contention that maximum metacontrast should occur when metacontrast stimuli share the same spatial frequency. However, these findings are in conflict with Weisstein et al.'s prediction that monotonic metacontrast should be maximal with the low spatial frequency mask. As well, Breitmeyer & Ganz's description of sustained-sustained inhibition accounting for monotonic functions was not fully supported, in that maximum metacontrast was not found in the higher spatial frequency target and mask condition.

These data may be explained by first considering the results of Maffei & Fiorentini (1973). They conducted a study which showed that sustained neurons found in the cat LGN were not as sensitive to changes in stimulus contrast as transient cells. Specifically, as the contrast of the grating stimulus decreased, the response of the transient cells grew weaker, while that of the sustained cells remained relatively constant. If this evidence typifies the activity of sustained and transient cells in the human visual system, then it may be possible to describe what may have occurred neurologically, to account for these data.

It is possible that in Experiment 3, the low energy masks were not stimulating either the sustained or transient neurons to a degree sufficient enough, to foster inhibition. In Experiment 6 the energy of the mask was increased relative to that of the target. However, this stimulus was still weak (considering that it was presented for 32 msec, while the stimuli used by Maffei & Fiorentini were presented for 250 msec). As well, Maffei & Fiorentini showed that a grating with a contrast of approximately .40 (a contrast of .41 was used in Experiment 6) resulted in the somewhat reduced activity level of a transient cell. They showed that the response rate of the sustained cell however, was not affected by lowering contrast, until a level of approximately .15 was reached. It is possible that if at

low contrast levels (.15 - .50, as depicted in the Maffei & Fiorentini study), sustained activity is relatively stronger than the transient response, then sustained-sustained inhibition may be more likely to occur than that of sustained-transient inhibition. In fact, this type of inhibition is what Breitmeyer & Ganz described as mediating monotonic metacontrast functions. The criticism made about this interpretation of the data however, was that if sustained-sustained inhibition mediated the monotonic metacontrast effects of Experiment 6, then it would be expected that the higher frequency stimuli should have produced maximum inhibition, since it has been shown both physiologically and psychophysically that these stimuli are most likely to be processed by sustained cells. However, as was pointed out earlier, the high frequency condition did not produce maximum metacontrast. This leads to another description of the neural processes that may have mediated these results.

As shown by Harwerth & Levi and the results of Experiments 1 and 2, RT measures seem to indicate that there exists both sustained and transient cells which may respond to most spatial frequency gratings. Using a 50 msec stimulus duration, Harwerth & Levi presented evidence suggesting that sustained activity may have been mediating RT for their 1 c.p.d. grating. In Experiment 1, it was shown that the short 16 msec stimulus only produced biphasic

RT functions for gratings above 4 c.p.d., suggesting that sustained cells were not involved in mediating RT for the 2 c.p.d. grating. However, the results of this experiment and that of Harwerth & Levi, demonstrated that sustained cells become implicated in mediating RT as duration is increased. Thus, it is possible that the 2 c.p.d., 32-msec mask used in Experiment 6 could have produced a biphasic RT curve, indicating the presence of sustained cells. Inasmuch as sustained-sustained inhibition mediated metacontrast in Experiment 6, this would imply that sustained cells were involved in the processing of the 2 c.p.d. target. The results of Experiment 1, however, suggested that for all observers, sustained activity was not evident in mediating RT for the 2 c.p.d. grating. This result presents a problem in describing sustained-sustained inhibition mediating the results of these experiments.

In order to support the explanation that this type of inhibition underlied the metacontrast results, the data from Experiment 1 and 6 must be reconciled. In order to do so, the first proposal presented in this section must be addressed: That is, whether or not the cells mediating RT are exclusively involved in the production of metacontrast seems to be questionable. It is possible that the only important result of the RT experiments, was that they showed both sustained and transient activity involved in the processing of most spatial frequency gratings. It is

conceivable then, that metacontrast may be mediated by other cells not involved in the processing of RT. Thus, the RT measure may not be sensitive to all of the sustained or transient activity mediating the perception of a grating.

It is proposed that for each of the spatial frequency gratings, both sustained and transient cells respond. The monotonic metacontrast functions may have been the result of intrachannel inhibition. Inhibition may have involved either sustained cells from the mask inhibiting the sustained cells processing the target or implicated the interaction of transient cells responding to the two stimuli.

The above description of low energy intrachannel inhibition supports White & Lorber's (1976) "similarity" hypothesis as well as Breitmeyer & Ganz's (1976) portrayal of monotonic metacontrast functions. However, it is possible that with higher energy stimuli, transient inhibition of sustained cells may become implicated. Whether or not the sustained-transient interactions described by Weisstein et al. and Breitmeyer & Ganz can adequately account for the metacontrast functions produced with these higher energy stimuli, is a question that remains to be answered. Although Ims (1980) most recently investigated the role mask contrast played in the metacontrast and backward masking paradigms, he did not

investigate this matter in the context of differentially manipulating sustained and transient involvement. This is a necessary step in further reconciling the different theories of metacontrast.

In conclusion, the RT and metacontrast paradigms may both involve sustained and transient activity. However, from the results of these experiments, it seems unlikely that the data from one paradigm can be used to predict variations in the other.

Metacontrast with low energy stimuli produced monotonic metacontrast functions, which was interpreted as being the result of sustained-sustained or transient-transient intrachannel inhibition. If transient inhibition of sustained responses describes the mechanism that mediates type B metacontrast, then the occurrence of this cellular interaction may not represent a robust phenomenon in the visual system. That is, the results of this investigation suggest that this type of interaction may only occur under limited experimental conditions such as those consisting of high energy stimulation presented to the dark adapted eye. In retrospect, this general limitation of a luminance differential during and between trials has also characterised metacontrast paradigms using conventional stimuli. For example, dark intertrial intervals are usually associated with the presentation of lit stimuli, whereas lit

intertrial intervals accompany the presentation of dark stimuli (Purcell, Stewart & Dember, 1969). This seems to indicate that those conditions producing metacontrast in general are experimentally contrived, since this type of stimulation does not characterize events that occur during normal visual experience. Therefore, although sustained-transient interactions may be involved in type B metacontrast, they may not play an important role in normal visual processing.

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Appendix A

P.B.'s Data from Experiment 3. Mean Contrast (MCR) of
Comparison Grating for each Condition and SOA

		Target Spatial Frequency (c.p.d.)					
		2		6		10	
		CONTRAST					
	SOA	Low	High	Low	High	Low	High
Mask Spatial Frequency (c.p.d.)	-50	.16	.36	.17	.36	.17	.40
	-25	.14	.34	.18	.35	.17	.42
	0	.16	.36	.17	.37	.18	.42
	20	.17	.35	.17	.36	.18	.40
	40	.15	.37	.18	.36	.17	.41
	60	.15	.40	.16	.38	.17	.42
	80	.16	.42	.15	.37	.18	.41
	100	.17	.41	.15	.35	.17	.42
	120	.14	.37	.14	.38	.16	.42
	140	.18	.38	.13	.37	.18	.43
	180	.16	.39	.15	.38	.17	.41
	250	.17	.42	.15	.39	.18	.42
	Baseline	.17	.43	.14	.38	.18	.42
	-50	.18	.38	.12	.33	.16	.35
	-25	.17	.38	.13	.32	.16	.32
0	.17	.39	.13	.34	.17	.38	
20	.18	.40	.13	.34	.17	.37	
40	.17	.40	.15	.37	.18	.37	
60	.16	.43	.14	.38	.16	.38	
80	.15	.42	.17	.37	.15	.38	
100	.15	.38	.15	.40	.18	.38	
120	.18	.36	.16	.40	.17	.39	
140	.14	.35	.16	.40	.16	.35	
180	.16	.38	.15	.39	.15	.34	
250	.18	.38	.15	.37	.14	.38	
Baseline	.17	.37	.17	.38	.15	.38	

Appendix A - 2

Target Spatial Frequency (c.p.d.)

2

6

10

CONTRAST

		SOA	Low	High	Low	High	Low	High
Mask Spatial Frequency (c.p.d.)	10	-50	.16	.40	.14	.38	.18	.38
		-25	.14	.41	.13	.38	.17	.38
		0	.15	.42	.15	.39	.19	.34
		20	.14	.40	.14	.38	.18	.39
		40	.13	.40	.16	.37	.17	.40
		60	.16	.43	.17	.36	.18	.40
		80	.17	.42	.17	.36	.19	.39
		100	.18	.38	.16	.35	.19	.39
		120	.18	.38	.17	.38	.16	.39
		140	.17	.39	.15	.38	.15	.37
		180	.18	.38	.14	.39	.16	.38
		250	.18	.35	.15	.37	.19	.37
Baseline		.16	.32	.16	.37	.18	.38	

Appendix A - 3

S.S.'s Data from Experiment 3. Mean Contrast (MCR) of
Comparison Grating for each Condition and SOA

Target Spatial Frequency (c.p.d.)							
		2		6		10	
		CONTRAST					
	SOA	Low	High	Low	High	Low	High
2	-50	.10	.36	.16	.33	.13	.40
	-25	.10	.38	.15	.34	.15	.40
	0	.11	.38	.17	.35	.14	.40
	20	.12	.39	.16	.34	.15	.41
	40	.13	.38	.16	.34	.16	.40
	60	.13	.37	.16	.32	.15	.42
	80	.13	.39	.18	.32	.17	.40
	100	.12	.40	.17	.31	.14	.39
	120	.11	.38	.17	.33	.17	.38
	140	.10	.37	.17	.35	.14	.38
	180	.12	.36	.18	.36	.15	.40
	250	.13	.37	.18	.35	.16	.41
	Mask	Baseline	.12	.35	.18	.35	.17
Spatial							
Frequency							
(c.p.d.)							
6	-50	.13	.37	.15	.34	.17	.40
	-25	.15	.36	.15	.35	.16	.41
	0	.14	.38	.16	.36	.18	.40
	20	.13	.36	.17	.37	.18	.38
	40	.13	.35	.18	.36	.16	.38
	60	.14	.36	.18	.35	.17	.37
	80	.14	.35	.18	.37	.18	.36
	100	.13	.38	.19	.37	.18	.35
	120	.12	.37	.19	.36	.16	.34
	140	.10	.37	.17	.35	.15	.34
	180	.10	.36	.17	.33	.14	.32
	250	.10	.35	.16	.32	.14	.30
		Baseline	.11	.35	.16	.37	.17

Appendix A - 4

Target Spatial Frequency (c.p.d.)

2

6

10

CONTRAST

Mask Spatial Frequency (c.p.d.)	SOA	2		6		10	
		Low	High	Low	High	Low	High
10	-50	.08	.35	.16	.35	.16	.40
	-25	.07	.36	.16	.34	.17	.40
	0	.10	.37	.17	.36	.18	.41
	20	.11	.36	.17	.36	.17	.42
	40	.12	.35	.17	.35	.18	.40
	60	.12	.34	.18	.34	.18	.42
	80	.11	.33	.18	.33	.18	.40
	100	.11	.33	.19	.32	.16	.38
	120	.12	.31	.19	.32	.17	.38
	140	.12	.36	.19	.31	.18	.37
	180	.13	.35	.20	.30	.17	.38
	250	.13	.36	.20	.29	.17	.36
	Baseline	.13	.35	.21	.32	.17	.35

Appendix B

PB's data from Experiment 4. Mean Contrast (MCR) of Comparison Grating for each Condition and SOA

		Target Spatial Frequency (c.p.d.)					
		2		6		10	
		CONTRAST					
Mask Spatial Frequency (c.p.d.)	SOA	Low	High	Low	High	Low	High
2	-50	.15	.41	.17	.42	.25	.38
	-25	.16	.42	.17	.43	.26	.38
	0	.15	.42	.18	.44	.26	.39
	20	.16	.43	.18	.44	.26	.38
	40	.16	.43	.17	.41	.25	.39
	60	.14	.41	.17	.42	.24	.36
	80	.15	.42	.19	.41	.26	.38
	100	.15	.43	.16	.42	.26	.40
	120	.16	.39	.17	.45	.29	.39
	140	.16	.41	.18	.44	.25	.39
	180	.16	.41	.17	.41	.26	.39
	250	.16	.39	.16	.42	.26	.40
	Baseline	.14	.42	.17	.44	.23	.41
6	-50	.15	.38	.17	.41	.21	.39
	-25	.10	.37	.18	.40	.22	.38
	0	.16	.39	.18	.42	.22	.40
	20	.15	.43	.17	.42	.23	.39
	40	.15	.43	.19	.44	.24	.41
	60	.15	.41	.17	.41	.22	.42
	80	.15	.41	.18	.44	.24	.43
	100	.16	.41	.19	.44	.23	.41
	120	.14	.40	.17	.45	.22	.42
	140	.15	.39	.16	.43	.24	.46
	180	.15	.43	.17	.44	.25	.43
	250	.15	.42	.17	.41	.24	.44
	Baseline	.15	.39	.15	.42	.23	.41

Appendix B - 2

Target Spatial Frequency (c.p.d.)

CONTRAST

		SOA	Low	High	Low	High	Low	High
Mask Spatial Frequency (c.p.d.)	10	-50	.14	.40	.16	.42	.26	.43
		-25	.15	.41	.17	.43	.27	.42
		0	.15	.40	.16	.44	.27	.43
		20	.15	.41	.17	.43	.25	.38
		40	.15	.39	.18	.39	.25	.39
		60	.14	.41	.18	.41	.25	.41
		80	.15	.42	.15	.39	.25	.41
		100	.14	.38	.18	.38	.25	.40
		120	.16	.41	.16	.39	.26	.40
		140	.14	.39	.16	.43	.24	.44
		180	.16	.42	.16	.42	.24	.43
		250	.15	.44	.17	.42	.25	.43
Baseline		.14	.40	.17	.40	.26	.42	

Appendix C

SS's Data from Experiment 5 (light Adaptation Condition). Mean duration of Comparison Grating for each condition and SOA.

		Target Spatial Frequency (c.p.d.)				
		2	6	10		
		CONTRAST				
		SOA	Low	Low	High	Low
2	0	16.3	15.3	16.3	17.0	
	30	17.0	17.0	17.7	16.0	
	60	17.3	17.7	14.7	16.3	
	90	16.3	17.7	15.7	17.3	
	Baseline	16.0	15.7	15.0	17.3	
Mask Spatial Frequency (c.p.d.)	0	15.7	17.3	15.7	17.7	
	30	16.0	17.3	16.3	16.7	
	60	15.7	18.0	14.7	16.7	
	90	16.7	17.7	15.0	15.7	
	Baseline	16.3	16.0	16.7	16.7	
10	0	16.3	14.7	17.3	16.7	
	30	16.3	16.7	16.7	15.7	
	60	17.3	16.7	16.7	18.3	
	90	15.7	14.0	15.7	16.3	
	Baseline	16.0	16.0	17.0	17.0	

Appendix C - 2

SS's Data from Experiment 5 (Dark Adaptation Condition). Mean duration of Comparison Grating for each condition and SOA.

		Target Spatial Frequency (c.p.d.)			
		2	6	10	
		CONTRAST			
Mask Spatial Frequency (c.p.d.)	2	SOA	Low	Low	High Low
		0	15.7	14.3	17.0 17.3
		30	14.7	14.7	17.0 16.7
		60	14.7	15.3	17.3 16.7
		90	16.7	15.0	16.7 17.3
		Baseline	15.0	15.0	16.7 16.7
6		0	17.7	16.7	16.7 17.0
		30	16.3	15.3	16.7 17.0
		60	15.7	16.7	16.0 16.7
		90	16.0	15.3	16.0 17.0
		Baseline	16.7	16.0	16.3 16.3
10		0	16.0	16.7	17.3 16.7
		30	16.0	16.3	16.7 15.7
		60	17.3	17.0	17.0 15.7
		90	17.7	16.0	17.0 17.6
		Baseline	16.7	16.0	16.7 15.7

Appendix D

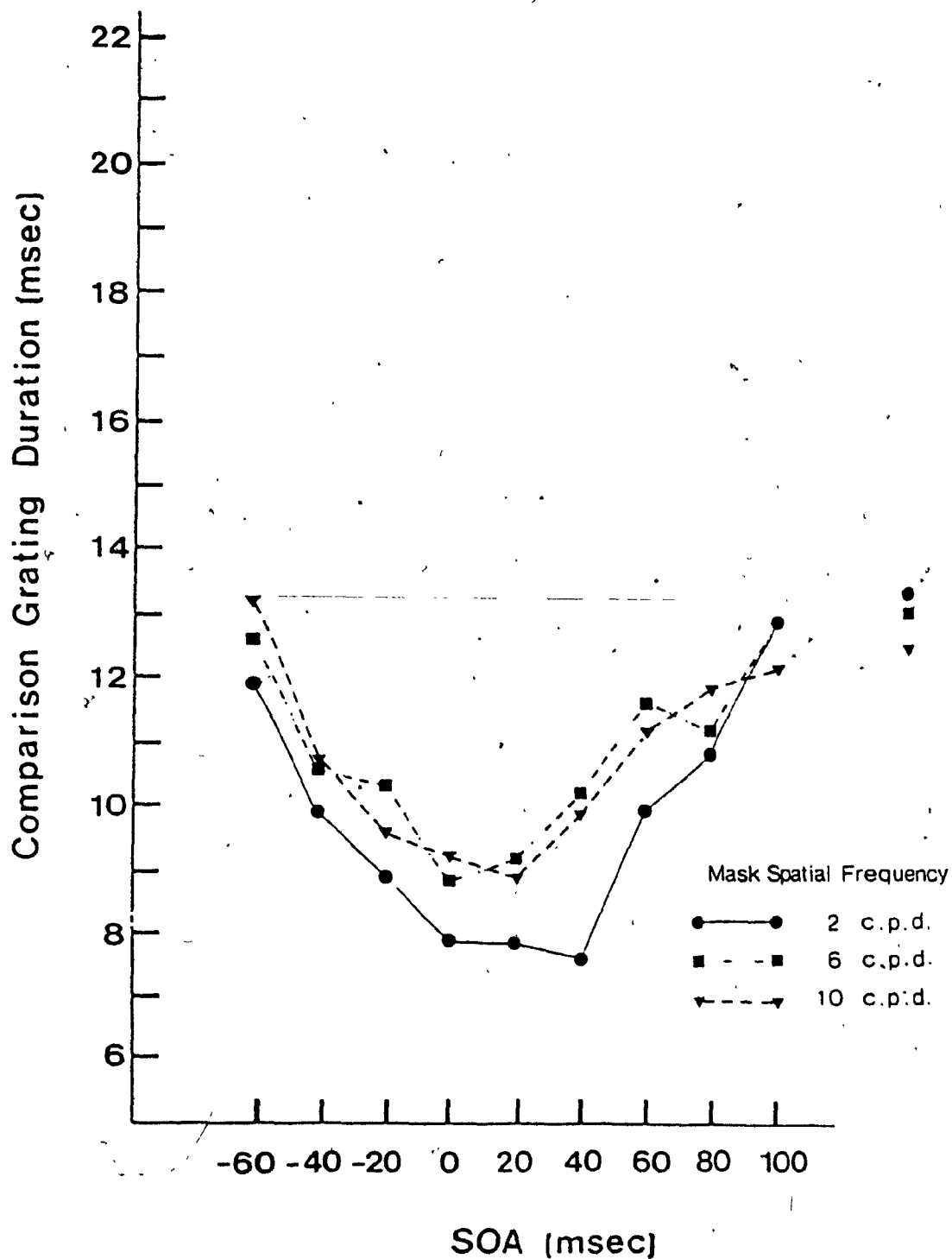


Figure 1: Observer PB's data for 3 conditions in Experiment 6. Comparison grating duration as a function of SOA for a 2 c.p.d. target.

Appendix D - 2

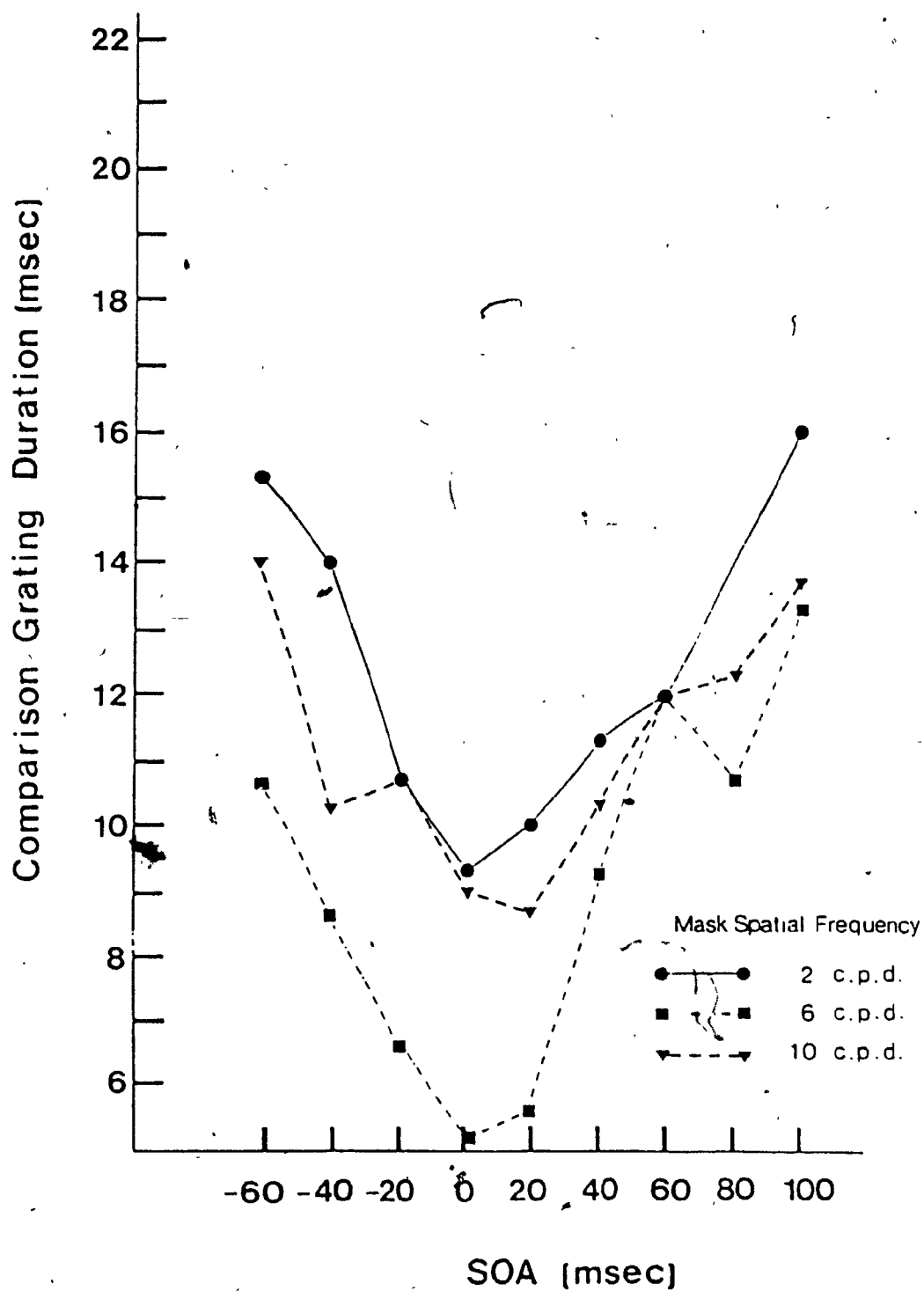


Figure 2. Observer PB's data for 3 conditions in Experiment 6. Comparison grating duration as a function of SOA for a 6 c.p.d. target.

Appendix D - 3

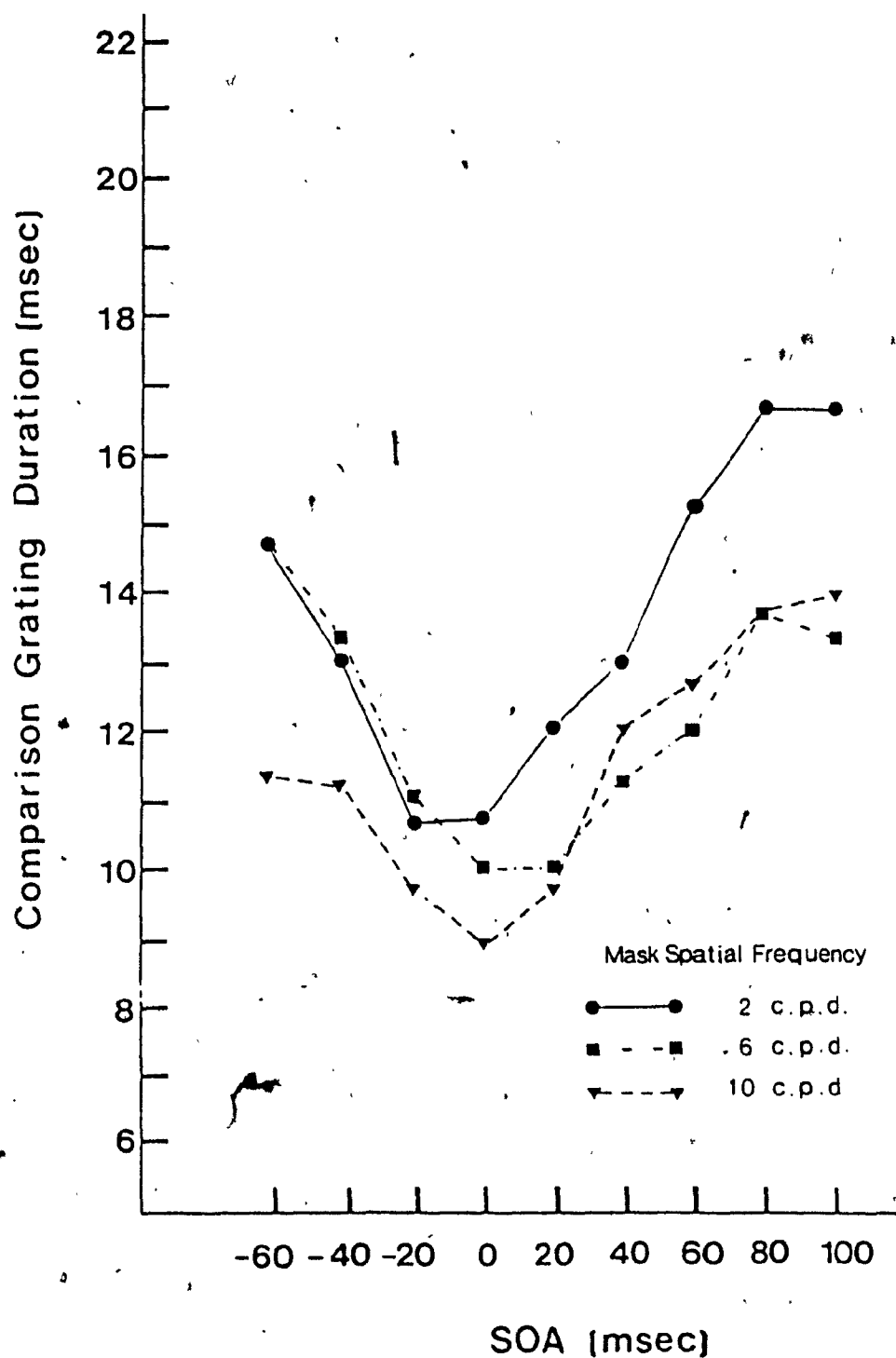


Figure 3. Observer PB's data for 3 conditions in Experiment 6. Comparison grating duration as a function of SOA for a 10 c.p.d. target.

Appendix D - 4

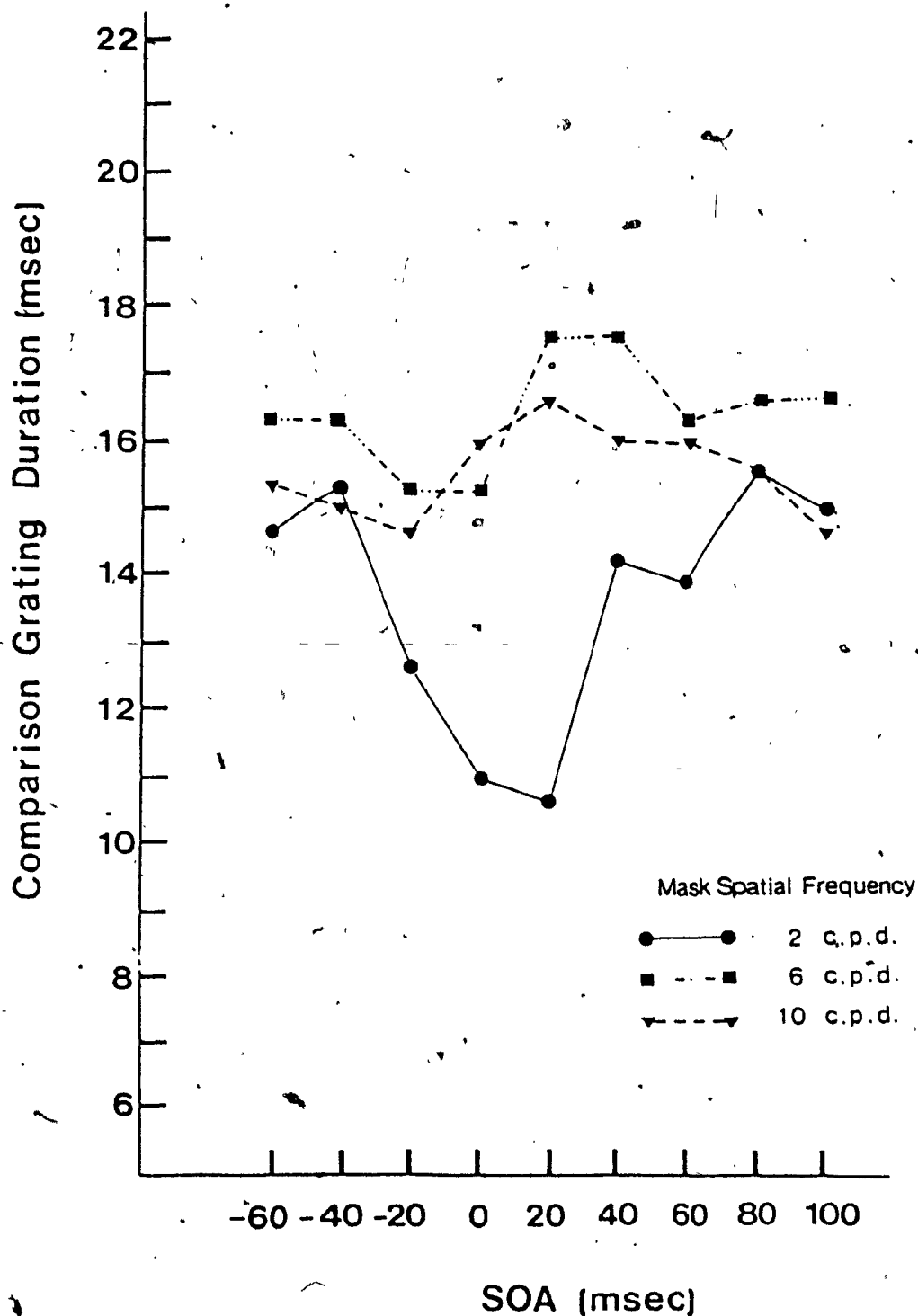


Figure 4. Observer SS's data for 3 conditions in Experiment 6. Comparison grating duration as a function of SOA for 2 c.p.d. target.

Appendix D - 5

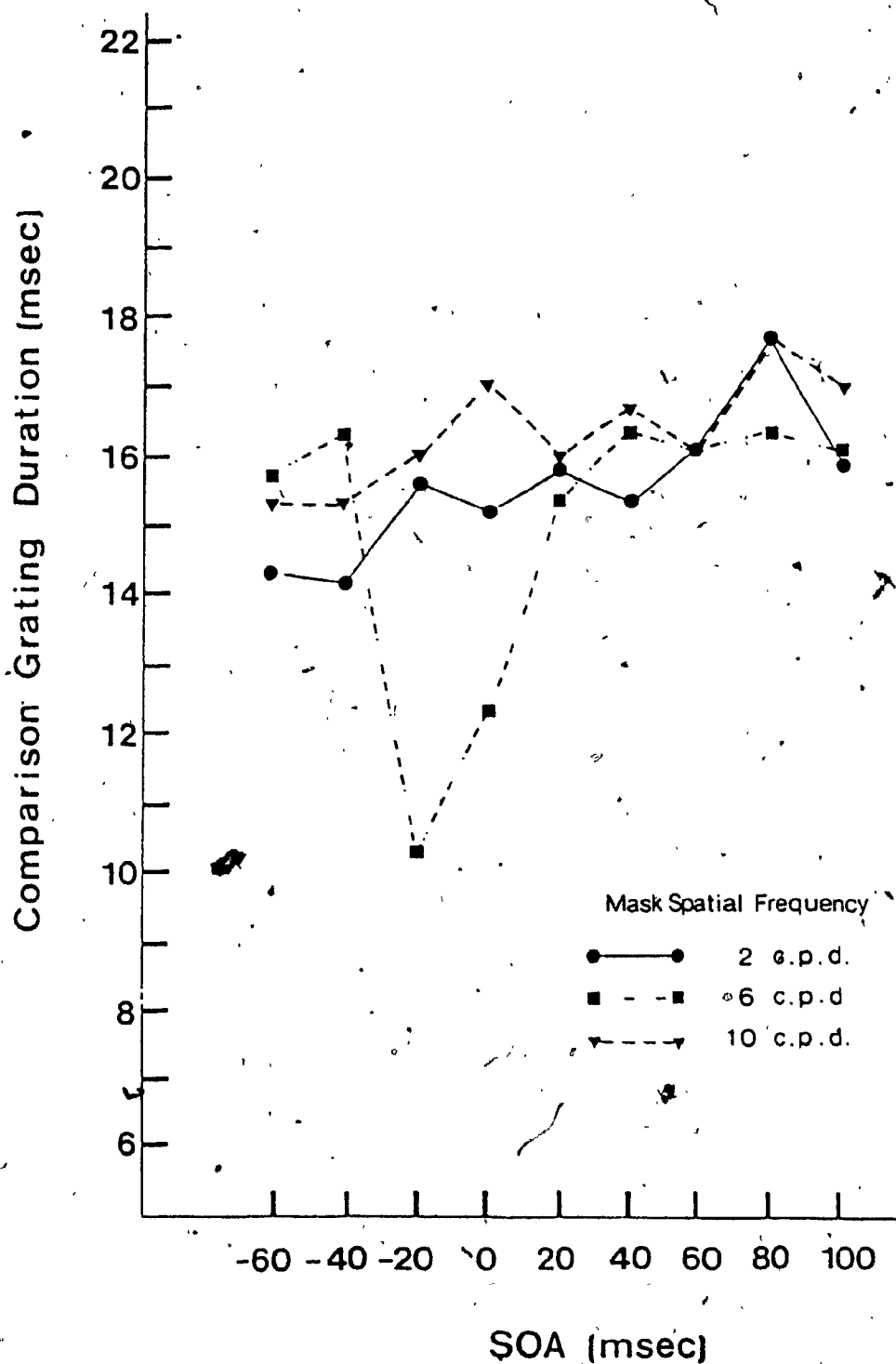


Figure 5. Observer SS's data for 3 conditions in Experiment 6. Comparison grating duration as a function of SOA for a 6 c.p.d. target.

Appendix D - 6

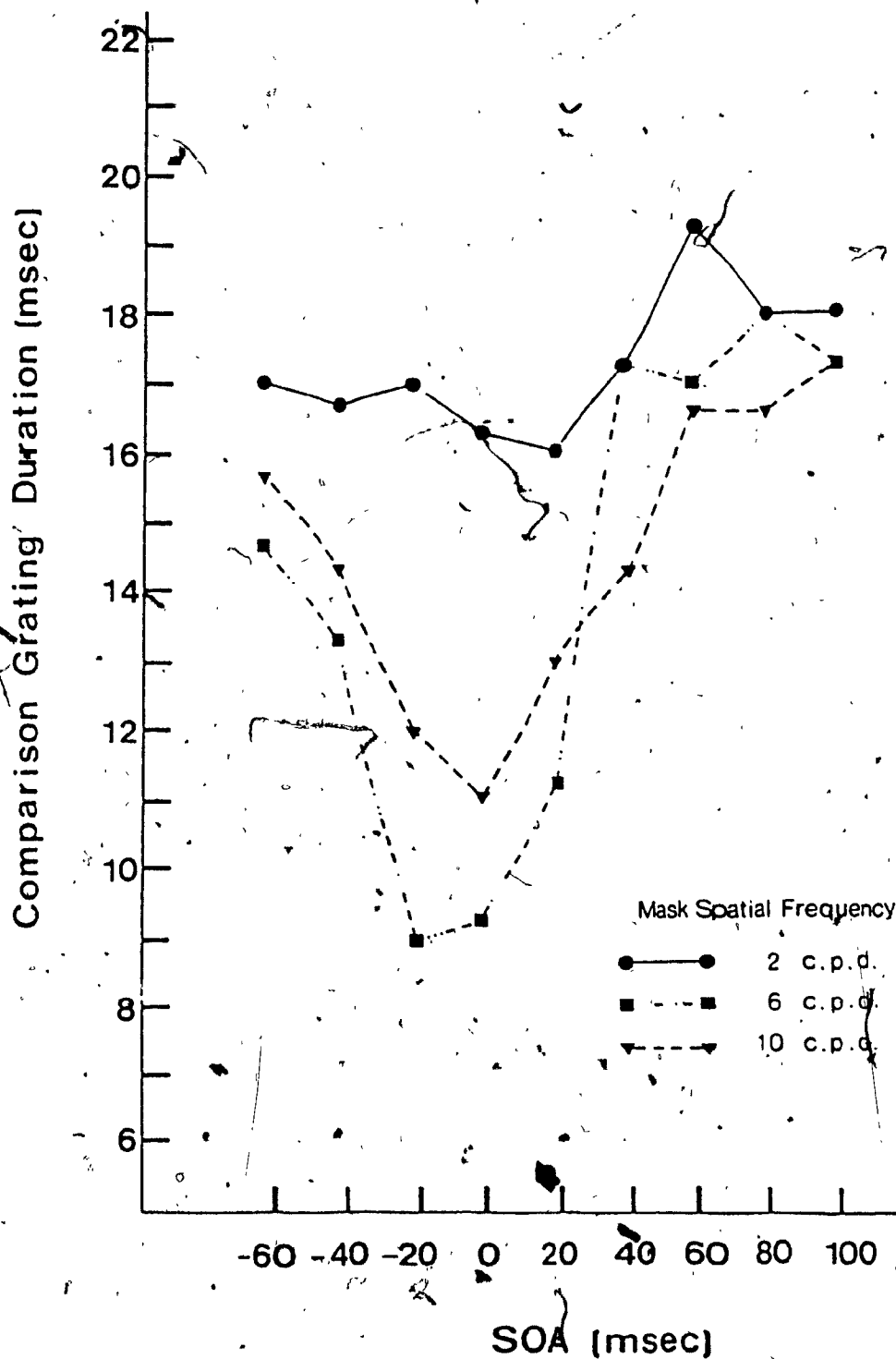


Figure 6. Observer SS's data for 3 conditions in Experiment 6. Comparison grating duration as a function of SOA for a 10 c.p.d. target.