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**Comparisons between Electrophysiologically and Psychophysically
Determined Contrast Sensitivity Functions in Humans**

by

Mary M. Conte

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

1995

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This manuscript has been read and accepted for the Graduate Faculty
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8/31/95

Date

James Gordon

Chair of Examining Committee

8/31/95

Date

Kay Deaux

Executive Officer

Dr. Vance Zemon

Dr. Stanley Novak

Dr. Eric Heinemann

Dr. Jonathan Victor

Supervisory Committee

THE CITY UNIVERSITY OF NEW YORK

ABSTRACT

**Comparisons between Electrophysiologically and Psychophysically
Determined Contrast Sensitivity Functions in Humans**

by

Mary M. Conte

Advisers: Professor James Gordon

Professor Vance Zemon

The spatial contrast sensitivity function (CSF) is a psychophysical measure of the minimum amount of contrast needed to detect the presence of spatial stimuli. It provides information about contrast perception over a range of spatial frequencies and is used as a measure of overall visual performance. In addition, it has become an important clinical tool for evaluation of pathological losses of visual function. The conventional method of measuring the CSF requires concentration and an active judgment by the observer and thus can yield unreliable results in patient populations. An objective measure that requires minimal cooperation from the patient would be indispensable. Primary among objective measurements of the CSF has been the visual evoked potential (VEP). However, a controversy exists over how well or poorly an evoked potential measure of contrast sensitivity in humans correlates with standard psychophysical measures. The purpose of this study was to quantitatively compare psychophysically derived contrast sensitivity functions with those derived from steady-state visual evoked potentials using a systems analysis approach.

Stimuli included vertical sinusoidal gratings of several spatial and temporal frequencies and contrasts. Gratings were temporally modulated sinusoidally in an appearance-disappearance manner. In the psychophysical experiments, the method of adjustment was used to collect two types of contrast detection thresholds. Observers

were instructed to adopt two separate criteria for setting contrast: 1) to adjust contrast until the spatial pattern was just visible, and 2) to adjust contrast until the temporal flicker was just visible. In this way, separate pattern and flicker thresholds were obtained. Visual evoked potentials were recorded to these same stimuli modulated at 6.27 Hz at ten contrast levels ranging from 0.01 to 0.48. Fourier analysis of the VEP yielded fundamental (F1) and second harmonic (F2) response components. Amplitude and phase of these response components were plotted as functions of contrast for each spatial frequency tested. Contrast sensitivities were derived from these VEP data according to several criteria and were then compared to the psychophysically determined sensitivities. VEP criterion measures derived from amplitude or phase data alone yielded CSFs similar to those derived from amplitude and phase data combined. For one observer, a CSF derived from the second harmonic (F2) response correlated highly ($r^2 = 0.99, p < 0.05$) with the psychophysical pattern CSF over the entire spatial frequency range. However, a consistent evoked potential correlate of the psychophysical functions was not observed across observers. For spatial frequencies above 3.6 cycles/degree, there was good agreement between VEP and psychophysical CSFs, regardless of the harmonic component used for the analysis. Results are discussed in terms of underlying cortical processing and clinical applications of VEP contrast sensitivity derivation techniques.

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INTRODUCTION

The response behavior of sensory systems as a function of stimulus intensity has been a fundamental concern of sensory physiology and psychophysics for more than a century. This is especially true of the visual system. In 1935, Graham and Hartline recorded action potentials from individual Limulus optic nerve fibers to different wavelengths of light. From these responses, they derived neural visibility (sensitivity) curves by plotting "energy" versus wavelength. This was one of the earliest experiments in which a criterion threshold response was derived from a stimulus intensity-response function. Any visual system may be thought of as having two goals; to determine the spatial layout of the visual world, and to identify objects in that world. To achieve these goals, the visual system must first encode low-level features of the image. These features include luminance, contrast, spatial frequency, orientation, motion, and color. The most important aspect of our visual experience is contrast. Without it, pattern vision is not possible. The encoding and perceptual experience of contrast has been a major focus of vision research for several decades. The goal of this study was to quantitatively characterize the sensitivity of the human visual system to contrast using the visual evoked potential.

Human Spatial Vision

Psychophysical determination of threshold

Psychophysics is the study of the relationship between the physical stimulus applied to a sensory system and the perceptual event that it elicits. G.T. Fechner, who first coined the term "psychophysics", devised its classical methods: all of which try to quantify the relationship between stimulus and sensation (Gescheider, 1976). The concept of threshold underlies classical psychophysics. The minimum quantity of a stimulus that can be perceived by a sensory system is its absolute threshold.

Spatial contrast sensitivity function

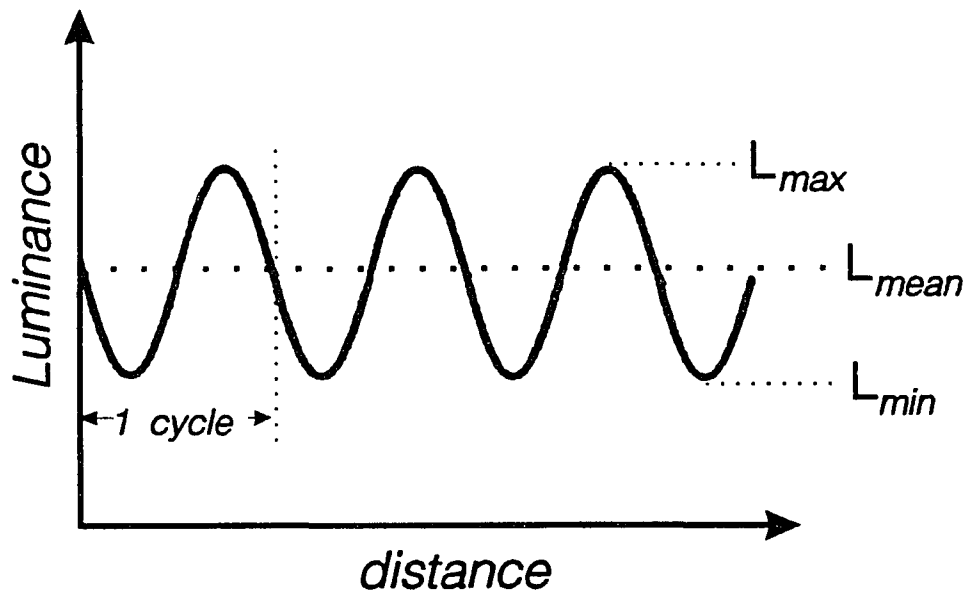
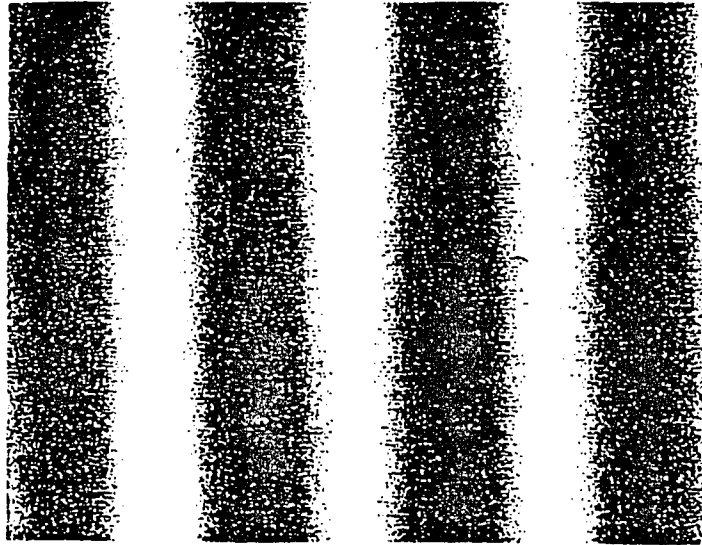
Schade (1956) measured the spatial contrast sensitivity of human observers to spatial sinusoidal gratings. He was the first to measure the spatial contrast sensitivity function in humans using a systems analysis approach. Sensitivity to sinusoidal luminance flicker was studied by De Lange (1958) and Kelly (1961). De Lange showed that sensitivity to luminance flicker has a bandpass temporal function which peaks at 10 Hz. Since that time, sinusoidal gratings have been widely used in basic and clinical vision research. They are considered one of the simplest forms of patterned visual stimuli, since they have only one spatial frequency at one orientation. Luminance of a grating is a one-dimensional function of distance and spatial frequency is defined as the number of cycles of the grating per degree of visual angle (cpd). An example of a sinusoidal grating with its luminance profile are shown in Figure 1.

Modulation transfer function

The modulation transfer function (MTF) has been used to describe how well an optical system performs. In optics, it can be derived from the wave properties of light. The way to derive an MTF psychophysically in humans is to measure contrast thresholds to sine wave gratings over a range of spatial frequencies. Psychophysical data have classically been presented in the form of a modulation transfer function. The reciprocal of the stimulus contrast required to reach threshold is plotted against spatial frequency. The threshold value is the minimum contrast necessary for an observer to just detect the presence of a grating emerging from a uniform field of equal mean luminance. Contrast sensitivity is defined as the inverse of the contrast required to attain threshold performance. When sensitivity is plotted as a function of spatial frequency on a log-log scale, an MTF is obtained. Figure 2 illustrates a general finding of mammalian visual systems; selective sensitivity to a range of spatial frequencies. Along the spatial frequency dimension, contrast sensitivity is highest to frequencies between 2 and 5 cycles/degree and progressively falls off at higher and lower spatial frequencies.

Figure 1.

Top: a sinusoidal grating. Middle: its luminance profile plotted as a function of distance perpendicular to the orientation of the bars. Bottom: spatial frequency and contrast equations. L_{\max} = maximum luminance, L_{\min} = minimum luminance, and L_{mean} = mean luminance.



$$\text{Spatial Frequency} = \frac{\text{number of cycles}}{\text{unit distance}}$$

$$\text{Contrast} = \frac{L_{max} - L_{min}}{L_{max} + L_{min}}$$

Figure 1.

Figure 2.

Example of spatial contrast sensitivity functions for pattern detection (filled symbols) and flicker detection (open symbols) at 3.5 Hz square-wave modulation. Mean luminance = 7 cd/m². Both spatial frequency and sensitivity are typically plotted on logarithmic scales. From Kulikowski & Tolhurst, 1973.

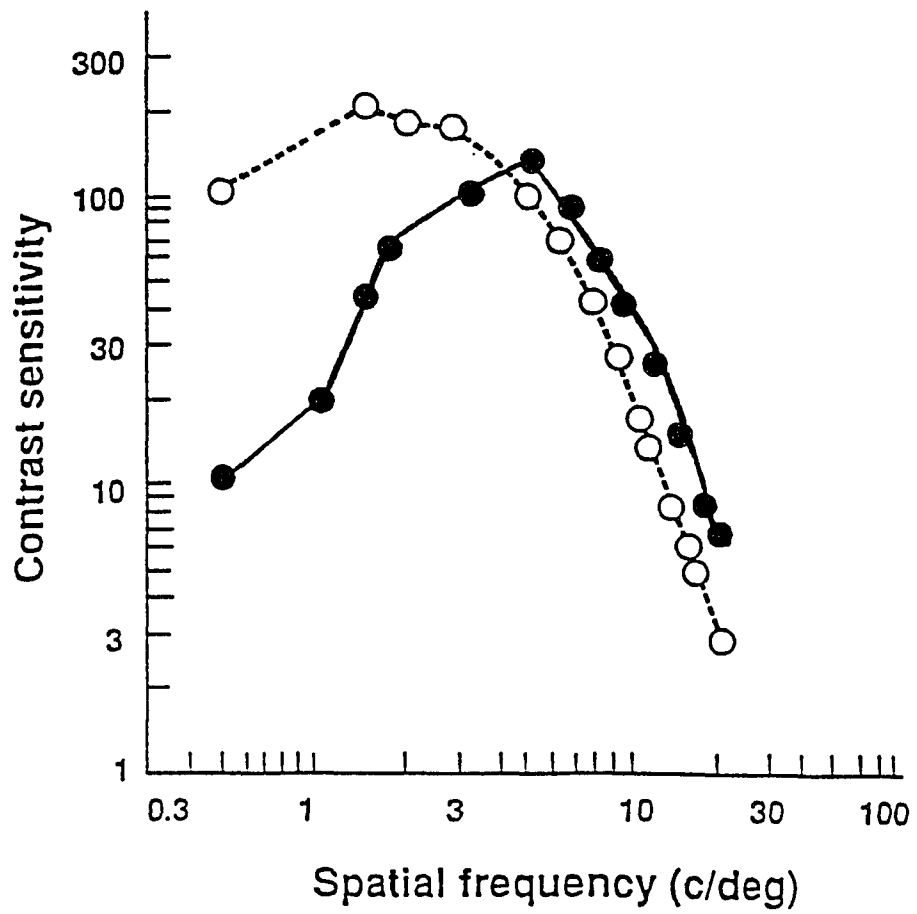


Figure 2.

Attenuation at high spatial frequencies derives from optical as well as neural factors (Campbell and Green, 1965; Graham, 1989). Attenuation at low spatial frequencies, however, represents a balance between antagonistic processes which have been modeled by the center-surround receptive field organization of retinal ganglion cells. Rodieck (1965) was the first to represent the receptive field of the cat's ganglion cell as overlapping center and surround mechanisms. Certain properties of the spatial sensitivity function can be understood in terms of Rodieck's model. The spatial resolution limit is due to the finite size of the center, and it is proportional to the reciprocal of the center's spread. The grating of the optimal spatial frequency is one to which the center is very sensitive but the surround is very insensitive. The loss of sensitivity seen at low spatial frequencies reflects the increasingly effective antagonism of the surround. Rodieck showed that his model accurately predicted the responses of cat ganglion cells to drifting bars of light. In 1966, Robson derived contrast thresholds for square-wave gratings sinusoidally modulated at several temporal frequencies. He concluded that the falloff in sensitivity to high spatial frequencies was independent of temporal frequency and that the falloff in sensitivity to low spatial frequencies occurs only when temporal frequency is low as well. Robson explained his results in terms of Rodieck's antagonistic center/surround model. He proposed that at high spatial and temporal frequencies, contrast thresholds are determined by the center region only and that any contribution to the response from the surround is negligible.

Psychophysical methods used to measure the contrast sensitivity function

Thresholds measured by various psychophysical procedures will not be identical, although for most experimental purposes they will be quite similar. One of the simplest and fastest ways to measure detection thresholds is the method of adjustment. The observer is simply instructed to adjust the contrast of the pattern until it is "just visible". Kelly and Savoie (1973) compared the method of adjustment with another commonly used psychophysical method, the forced-choice staircase procedure, for attaining contrast

sensitivity functions. They concluded that the method of adjustment was easier and ten times faster than forced-choice for obtaining psychophysical judgments when trained subjects are used. Near-threshold results did not seem to depend on psychophysical method. Both methods gave the same shaped functions, but forced-choice produced consistently higher sensitivities. In 1983, Ginsburg and Cannon compared the method of adjustment with the method of increasing contrast and the Bekesy tracking method. Contrast sensitivity functions (CSFs) for all three methods were identical in shape and standard deviations were comparable. The method of increasing contrast produced the lowest sensitivities while the Bekesy tracking method produced the highest sensitivities. The method of adjustment fell between these two.

Multiple Channel Hypotheses

Spatial frequency selectivity

There is a wealth of data and arguments for spatial frequency selective channels in the visual system. In 1965, Campbell and Green reported that the psychophysical contrast threshold differs for gratings of different spatial frequencies and that log contrast sensitivity falls off linearly with spatial frequency. Enroth-Cugell and Robson (1966) investigated the properties of cat retinal ganglion cells and found that individual units were sensitive to different ranges of spatial frequencies. In other words, each cell had a characteristic receptive field size. They found that the range of diameters of the receptive field centers was 0.5 to 4.4 degrees in the central retina. Campbell and Robson (1968) argued that the frequency components of a patterned stimulus are processed separately within the visual system and that detection occurs when one component exceeds its individual threshold. They hypothesized the existence of multiple channels within the visual system selectively tuned to different spatial frequencies. Campbell, Carpenter, and Levinson (1969) investigated cells in the cat visual cortex and, at this level too, found units selectively sensitive to a narrow range of spatial frequencies.

evidence was obtained psychophysically by Blakemore and Campbell (1969) who determined an increase in threshold over a range of spatial frequencies for a number of adapting frequencies. They concluded that the threshold elevation was maximal at the spatial frequency used for adaptation and extended over a limited range of frequencies on either side of the adapting frequency. They also found that spatial adaptation shows interocular transfer; adaptation of one eye caused threshold elevation through the other eye. They note that an advantage of a system based on frequency analysis is that it simplifies recognition of familiar objects presented at unfamiliar magnifications; objects do not have to be learned at every possible size. In 1970, Campbell and Maffei used the visual evoked potential (VEP) to study spatial frequency selectivity. They reasoned that when they stimulated with two spatial frequencies, and if these frequencies were far enough apart, two separate channels would be activated and the resulting VEP amplitude would be greater than the response to a single frequency. Their results concurred with their prediction. They also report that the effect of presenting two different frequencies was maximal when the frequencies were one octave apart.

Pattern and Flicker Detection

The perception of form and flicker are two different aspects of the visual sense. When we view a blank screen and luminance contrast of a temporally modulated spatial grating increases from zero, perception changes from that of a blank field to bars across the screen to the impression that the bars are flickering on the screen. However, when the stimulus is a low spatial frequency grating modulated at a high temporal frequency, the first impression is of indistinct blobs flickering. Then as contrast increases, the blobs become bars that extend across the field. It has been suggested that the existence of different contrast thresholds for pattern perception and flicker perception reflects the presence of two neural mechanisms. This hypothesis has been studied extensively (Robson, 1966; van Nes, Koenderink, Nas and Bouman, 1967; Tulunay-Keesey, 1972; Kulikowski and Tolhurst, 1973; Kelly, 1977). They all reported a difference in the

amount of contrast subjects needed to detect the presence of flicker or pattern in a visual field when asked to set thresholds using two qualitatively different criteria. Kulikowski and Tolhurst (1973) made the distinction between conventional stimulus detection threshold and flicker or pattern thresholds. With conventional threshold, the subject is instructed to decide whether or not the screen is uniform (spatially, temporally, or both). They used the method of adjustment to measure flicker detection and pattern recognition thresholds for 0.8 and 12 cpd sinusoidal gratings flickering sinusoidally at temporal frequencies from 0 to 15 Hz. The contrast sensitivity functions produced were very distinctive. Pattern thresholds as a function of temporal frequency were low-pass, and flicker thresholds, also as a function of temporal frequency, were band-pass. The thresholds were separated by a factor of two or three. On the basis of these two contrast sensitivity functions, they argued for the existence of two systems. van Nes, Koenderink, Nas, and Bouman (1967) suggested that the mechanism subserving the detection of a flickering grating does not encode pattern information. Burbeck (1981) challenged this idea when she found that pattern sensitivity and flicker sensitivity were equivalent under all conditions except for very low spatial frequencies. Observers who were setting flicker thresholds could also detect pattern. Her results cast doubt on the existence of a flicker threshold mechanism that carries no spatial information. This body of work in human psychophysics closely paralleled the conclusions drawn from animal experimentation during the 1960's and 1970's.

Sustained/Transient Dichotomy

Several authors proposed that the visual system of animals (Enroth-Cugell and Robson, 1966; Gouras, 1968; Cleland, Dubin, and Levick, 1971) and of humans (Kulikowski, 1971; Tulunay-Keesey, 1972; Tolhurst, 1973; Breitmeyer and Ganz, 1977) contains two independent detector mechanisms; a "transient" or movement-analyzer mechanism for perception of temporal change and a "sustained" or form-analyzer mechanism for mediation of pattern vision. Kulikowski (1971) compared sensitivity for

on-off and counterphase flickering gratings with the assumption that transient mechanisms would be twice as sensitive to the counterphase flicker. His findings supported this idea, but only for spatial frequencies below 3 cpd. Tulunay-Keesey (1972) measured pattern and flicker contrast sensitivity functions for stabilized and unstabilized retinal images. For temporal frequencies between 0.8 and 20 Hz, more contrast was required to detect the presence of a bar on the screen than to detect the flicker. She reported a maximum difference between flicker and pattern responses at low spatial frequencies when temporal frequency ranged from 3 to 10 Hz. Below 0.8 Hz modulation, there was no difference between pattern and flicker thresholds. Sensitivities were lower overall by a factor of 1.5 for stabilized images than for unstabilized. She concluded that the differences between flicker and pattern responses remain invariant regardless of retinal image movements. In order to optimize the separation of pattern mechanisms from flicker mechanisms, Kulikowski and Tolhurst (1973) recommended a temporal modulation of about 6 Hz. They noted that pattern sensitive channels responded equally to contrast reversal and appearance-disappearance modulation up to about 8 Hz. Breitmeyer and Ganz (1977) investigated the summation at threshold to two brief presentations of a grating as a function of stimulus onset interval between the two presentations. They interpreted their findings in terms of the differences between temporal properties of the "sustained" channels sensitive to high spatial frequencies and the "transient" channels sensitive to low spatial frequencies. Channels tuned to low spatial frequencies respond best to moderate temporal modulation. Whereas, channels tuned to higher spatial frequencies give sustained responses for the duration of the pattern and respond best to gradual temporal change. Furthermore, they suggested that the two types of channels have distinct functional roles - the "sustained" channels mediate pattern perception and the "transient" channels mediate flicker perception. Legge (1978), using a spatial frequency masking paradigm, concluded that the transient system mediates detection only for spatial frequencies below 4 cpd. Green (1981)

measured sensitivity to drifting gratings before and after adaptation to a uniform flickering field to test the validity of the sustained-transient model. He proposed that if the transient system mediates detection only at low spatial frequencies, then flicker adaptation should only impair sensitivity when low spatial frequencies are employed. This prediction was tested by determining thresholds with and without adaptation to 16 Hz uniform flicker for gratings ranging in spatial frequency from 0.5 to 16 cpd. The adaptation effect reduced sensitivities for spatial frequencies less than 3 - 4 cpd. His results supported that of Kulikowski (1971) and Legge (1978) of a transient system which operates for spatial frequencies $\leq 3 - 4$ cpd. Further, he concluded that motion in higher spatial frequencies is signaled by the sustained system.

Hypothesized neurophysiological correlates

Microelectrode recordings from cat and monkey have provided evidence for cell groups which appeared to be physiological correlates of the psychophysical channels studied in humans. The psychophysical findings were interpreted in terms of the functional properties of cortical areas (typically V1 and V2) and/or individual cell types. Using the terms "sustained" and "transient" to identify X and Y cells, respectively, Cleland, Dubin, and Levick (1971) showed that Y cells are able to respond to much higher velocities of a moving stimulus than are the X cells. Bodis-Wollner, Hendley, and Kulikowski (1972) and Tolhurst (1973) proposed that form-analyzers and movement-analyzers were analogous to X and Y cells respectively of the cat visual system (Enroth-Cugell and Robson, 1966; Fiorentini and Maffei, 1973). The Y cells responded transiently, while X cells gave sustained responses to prolonged stimulation and responded to higher spatial frequencies of a sinusoidal grating than did Y cells in the same part of the visual field. Victor and Shapley (1979) determined that X cells in the cat had a higher optimum spatial frequency than Y cells at the same retinal location and that these cells were tuned to different spatial frequency ranges. Movshon, Thompson, and Tolhurst (1978) derived contrast thresholds to sinusoidal gratings for 28 simple cells

in cat visual cortex. They speculated on the site of movement analysis in cat visual cortex and regarded the predominance of Y cell input to area 18 and X cell input to area 17 as reflecting a functional significance of these regions. By 1983, Murray, MacCana, and Kulikowski decided this idea was attractive but oversimplified. Regan (1989) summarized the sustained/transient literature by hypothesizing the existence of at least two spatiotemporal channels mediating human spatial vision; both of which are capable of carrying some pattern information.

Phasic versus Tonic or M versus P mechanisms

Visual information processing is done in parallel and begins at the retinal level. It has been proposed that the inferotemporal pathway is the continuation of the parvocellular pathway (P cell) and that the parietal pathway is the continuation of the magnocellular pathway (M cell). Parvocellular and magnocellular groups were defined anatomically on the basis of cell size in the monkey LGN; the larger magnocellular neurons constitute the bottom two of six layers. Gouras (1968) was the first to study the conduction velocities of macaque M and P ganglion cell axons. He called the P and M cells "tonic" and "phasic", respectively, because of their response properties to steps of illumination. He reported the P cells produce a prolonged change in impulse firing rate to an optimal stimulus (i.e., a green-on center cell has a prolonged increased firing rate to a step increase of mid-wavelength light). M cells change their impulse firing rate in a transient manner in response to step changes of white light. Hawken and Parker (1984) measured the contrast sensitivity function of layer IV of monkey striate cortex. They found that cells in layer IV α had higher contrast sensitivities than those in layer IV β . The different sensitivities are thought to reflect differences between the magnocellular afferents which project to IV α , and parvocellular afferents which project to layer IV β . They also reported that some single cortical neurons can respond to visual stimuli with a sensitivity that at least equals that of the entire system psychophysically. They caution, however, that many more cortical neurons must be analyzed before we can understand

how contrast is coded in their responses and how this forms the basis for psychophysical performance (Parker and Hawkin, 1985). From their work on X- and Y-like cells in magnocellular layers of the LGN, Kaplan and Shapley (1982) have proposed that M cells are the evolutionary homologues in the primate of the cat X and Y ganglion cells. They later found that the retina was responsible for the 8-fold difference in contrast gain recorded from magnocellular and parvocellular layers in the LGN (Kaplan and Shapley, 1986). Barlow, Kaushal, Hawken, and Parker (1987) compared contrast discrimination measurements from visual cortex of Old World monkeys with measurements of human performance. Purpura, Tranchina, Kaplan and Shapley (1990) presented results on ganglion cells, which to some extent, support Gouras' original findings. Their data suggest that the temporal properties of M and P cells are quantitatively rather than qualitatively different. At low temporal frequencies, the response of P cells was higher than M cells to achromatic modulation. Schiller and Logothetis (1990) measured contrast sensitivity to checkerboards in Old World monkeys and found little or no deficits following magnocellular lesions. Parvocellular lesions, however, produced large deficits in contrast sensitivity at high spatial frequencies and only small deficits at low spatial frequencies.

Visual Evoked Potentials

The visual evoked potential is a gross electrical signal in response to visual stimulation. It is recorded from electrodes attached to the scalp at the occipital region. Every evoked response waveform consists of two components: 1) that which is locked to the stimulus and therefore reinforced by signal averaging; and 2) that which is extraneous to the signal (i.e., noise). Evoked responses indicate the coordinated activity of neural populations and may provide a bridge between human psychophysical data and the properties of individual cortical neurons. As such, the VEP has been used extensively to investigate the importance of contrast in human vision. In 1963, Dustman and Beck

measured the test-retest reliability of evoked potentials recorded from ten observers over several weeks ($r^2 = 0.88$). Parker and Salzen (1977) addressed the usefulness of sine-wave gratings to VEP recordings and reported consistent response waveforms across subjects. According to Regan (1989) it is a technique for obtaining objective data from human subjects which compliments the psychophysical and single-cell techniques for studying visual functioning.

Electrogenesis of the VEP

Physiological studies suggest that the electroencephalogram (EEG) is the product of summation of a large number of graded postsynaptic potentials generated by cortical neurons (Eccles, 1951; Clare and Bishop, 1954). These postsynaptic potentials have been shown to be both excitatory and inhibitory in nature. Through direct electrical stimulation of the cerebral cortex in the cat, Creutzfeldt and Kuhnt (1973) concluded that the visual evoked response is generated by the apical dendrites of pyramidal cells. These cells are organized in parallel columns perpendicular to the cortical surface. Excitatory postsynaptic potentials occurring on these apical dendrites, generate a superficial current sink and a corresponding deep current source, thus producing surface negativity. Inhibitory postsynaptic potentials occurring at similar sites generate a superficial source and corresponding deep sink, producing surface positivity. An active extracellular current sink at the apical dendrites along with a passive extracellular current source at the cell bodies results in a current dipole. Dipole modeling localizes the center of large synchronously activated neuronal populations rather than complex interactions between smaller subpopulations. In an attempt to separate the contributions of excitatory and inhibitory postsynaptic potentials to the VEP, Zemon, Kaplan and Ratliff (1980) used a GABA antagonist, bicuculline, to block the GABAergic receptor sites in cat visual cortex. GABA (γ -aminobutyric acid) is known to be the primary inhibitory neurotransmitter in visual cortex. They demonstrated that the positive wave of the VEP was reduced by the application of bicuculline while the negative wave was greatly

enhanced. This suggests that GABA-mediated inhibition can play a major role in the genesis of the visual evoked potential.

VEPs in general

The VEP contains components driven by local luminance, local contrast, and more complex stimulus attributes, such as pattern. For the traditional contrast-reversal checkerboard stimulus, all of these components contribute to the steady-state VEP at the reversal frequency (second harmonic) and higher even harmonics. Spekreijse, van der Tweel, and Zuidema (1973) have proposed that for pattern appearance-disappearance modulation of checkerboards or gratings, contrast and pattern sensitive mechanisms contribute to the response at the stimulus frequency and its higher odd harmonics, while all types of mechanisms may contribute to the even harmonics. The visual evoked potential reflects the electrical activity of the central visual field. Projections from central retina are sent to the surface of occipital cortex while peripheral retina projects into the calcarine fissure. Therefore, scalp electrodes placed over visual cortex record primarily from cortical cells receiving central retinal input (Sokol, 1976).

Evoked potentials can be recorded as "transient" or "steady-state" responses. Transient responses are evoked by stimuli presented at a rate sufficiently slow that the response to one stimulus presentation is finished before the next stimulus occurs. When stimuli are presented at a rate sufficiently high to cause an overlap of responses to successive stimuli, VEPs are called steady-state responses (Regan, 1989). Steady-state responses, therefore, have a constant phase relation to the repeating stimulus and are evaluated using signal averaging or frequency based techniques such as Fourier analysis. In order to quantify the evoked potential, we convert the components of the EEG signal from the time domain (which describes the response in terms of amplitude vs. time) to the frequency domain (amplitude and phase vs. frequency). The most common way to convert from the time to the frequency domain is known as the Fourier transform.

Fourier's theorem states that any waveform or distribution can be generated by summing the appropriate sine waves, and, any distribution can be completely described by specifying some particular set of sine waves (that set which, when added together, will reproduce the given distribution). The procedure for finding the particular set of sine waves that must be added in order to obtain a given waveform is called Fourier analysis, and the sine wave components obtained are called Fourier components of that waveform (Cornsweet, 1970).

Systems Analysis Approach

The study of spatial vision has been strongly influenced by linear systems theory. Schade (1956) was one of the first to apply this approach to the study of the human visual system. Systems analysis involves determining the relation between the input signals applied to a system and the corresponding responses measured at the output (Oppenheim, Willsky and Young, 1983). Individual neurons are viewed as filters of visual signals. When we characterize a system by its input-output relations we are taking a systems analysis approach. In practice, an ensemble of test stimuli are chosen such that the responses they generate will specify or distinguish the system under study. A linear system obeys the principle of superposition; as described by the following examples: $S_1 \Rightarrow R_1$, $S_2 \Rightarrow R_2$, $S_1 + S_2 \Rightarrow R_1 + R_2$ where S_1 = stimulus 1, S_2 = stimulus 2, R_1 = response 1, and R_2 = response 2. The principle states that if S_1 elicits R_1 and S_2 elicits R_2 , then the sum of S_1 and S_2 will produce $R_1 + R_2$. Furthermore, if the stimulus is multiplied by a constant then the response will be scaled by the same amount. Therefore, if a sinusoidal stimulus is applied to a linear system, then the response will also be sinusoidal and at the same frequency as the stimulus. A nonlinear system cannot be described in this manner. Nonlinearities can generate response components at frequencies which are multiples (harmonics) of the original frequency (fundamental) and combinations of these frequencies. There is considerable evidence that the sensitivity of the visual system is achieved by nonlinear processing (Regan, 1989). Several kinds of

nonlinearities are found in the mammalian visual system including hysteresis, nonlinear inhibition and facilitation, logarithmic compression, and rectification. Rectification is one of the most common types of nonlinearities posited to explain neuronal behavior. For example, Spitzer and Hochstein (1985) demonstrated that cortical simple cells and some complex cells in the cat exhibited "rectifier-like" nonlinear responses to contrast-reversal stimulation of a grating. They proposed that half-wave rectification of the input signal by simple cells produced the even and odd harmonic components present in the response. A full-wave rectifier on the other hand, would have produced a strong second harmonic and higher harmonics, but no fundamental response component.

Comparisons between Psychophysics and Electrophysiology

In many studies, VEP and psychophysical measures have yielded similar results. One of the earliest ways of deriving a threshold measure from VEP data includes the extrapolation method. Threshold is taken as the "zero" amplitude intercept of a linear extrapolation of VEP signal measured in a suprathreshold region, and where the signal-to-noise ratio is greater than 1. This method assumes a linear relationship between stimulus intensity and response magnitude into the threshold range. Campbell and Maffei (1970) who first used this method, reported a strong correlation between the contrast intercept at an electrophysiological "zero" voltage and psychophysical threshold to spatial frequencies above 3 cpd modulated by a square-wave temporal signal. They derived contrast sensitivity from a suprathreshold contrast versus VEP response function and compared their results to behavioral results in both humans and cats (Maffei and Campbell, 1970; Campbell, Maffei, and Piccolino, 1973). The concept of a direct relationship between spatial contrast sensitivity determined psychophysically and from VEP data was further strengthened in subsequent papers by Bodis-Wollner, Hendley, and Kulikowski (1972) and Campbell and Kulikowski (1972), where responses to single spatial frequencies were studied in detail. Bobak, Bodis-Wollner, Harnois, and Thornton

(1984) used pattern-appearance modulation at 7.5 Hz and derived contrast response functions from fundamental and second harmonic Fourier components of the VEP. Using the Campbell and Maffei method, and only one spatial frequency (6 cpd), they concluded that the fundamental Fourier component was responsible for pattern detection, and that the second harmonic was responsible for flicker detection. The "extrapolation to zero" voltage method has been used in a variety of other experimental paradigms as well with comparable results (Fiorentini and Maffei, 1973; Allen, Norcia, and Tyler, 1986; Bonds, Casagrande, Norton, and DeBruyn, 1987; Chen, Wu, and Wu, 1990).

Other methods have also been used to compare psychophysical and VEP contrast sensitivity functions. For example, Cannon (1983a) presumed that regardless of the underlying mechanism responsible, the choice of the most sensitive response component to determine threshold would give a high correlation between VEP and psychophysical contrast sensitivity functions. Therefore, he chose the Fourier response component (fundamental or second harmonic) which first exceeded a criterion signal-to-noise ratio of 1.25. Like other investigators, Cannon's estimate of noise was taken as the average of the EEG signal at frequencies adjacent to the stimulus frequency within a specified bandwidth. He reported good agreement between the VEP fundamental response component and pattern detection sensitivities ($r^2 = 0.94$) using pattern-appearance modulation.

All of the authors mentioned above point out similarities between psychophysics and the VEP. Assessment of visual functioning in certain patient populations would improve greatly, if reliable, objective measures can be derived from the VEP. However, not all investigators concurred with Campbell and Maffei's initial findings. Tyler, Apkarian, and Nakayama (1978) using high contrast gratings demonstrated functions of VEP amplitude versus spatial frequency that did not resemble contrast sensitivity functions. In fact, for a variety of temporal frequencies, they found that the VEP response demonstrated a narrow spatial frequency tuning similar to the tuning of cortical

cells (Nakayama and Mackeben, 1982). This is in contrast to the broad tuning of the psychophysical spatial frequency function. They concluded that some spatial frequencies, though highly visible, elicit little response from the cortex. They also reported that multiple peak responses occur at different spatial and temporal frequencies for different observers. In other words, extensive between-subject variability was found. Within-subject variability was very low, however, and replications of spatial frequency functions were obtained from the same observers over several months. They cautioned that mismatches of VEP to psychophysical data may be due to a narrow tuning of the VEP. A careful examination of Cannon's (1983a) data shows that VEP correlates to CSF flicker detection ($r^2 = 0.55$) were much weaker than to pattern detection. Seiple, Kupersmith, Nelson and Carr (1984), using a swept-contrast technique, found that the VEP contrast sensitivity was on the average two to three times less than that obtained using psychophysical methods. They did not extrapolate to zero voltage, but instead defined threshold as the contrast at which the VEP signal exceeded the resting voltage level of the background EEG.

Rationale for Proposed Research

From the literature presented above, we see that any description of human spatial vision must include temporal as well as spatial characteristics. When we compare VEP derived contrast sensitivity functions with those obtained psychophysically, we assume that the VEP reflects the underlying neural mechanisms responsible for luminance contrast detection. It seems clear that we must first ask if we can measure a VEP at sensory threshold? Given that this was plausible, this research was designed to determine the extent to which individual Fourier components of the VEP compare to contrast detection for a range of spatial frequencies. Methodological differences may have accounted for the discrepancies in this literature. For example, how do the variety of VEP threshold derivation techniques (i.e., extrapolation method, signal-to-noise criteria,

phase coherence) influence the VEP/psychophysical comparisons? Interpretation of the results may be the other contributor to this dilemma. By looking at a range of spatial frequencies and not just single frequencies, we hoped to present a more complete picture of this spatiotemporal behavior. The specific questions are presented below:

1. Will either/or both of the psychophysical contrast sensitivity functions be better fit by either/or both of the VEP response components ?
2. Which if any of the VEP derived measures yields contrast sensitivity functions that most resemble the psychophysical functions ?

A possible experimental outcome was that the fundamental (F1) would match the pattern detection threshold and the second harmonic (F2), would match the flicker threshold (Bodis-Wollner and Hendley, 1979; Bobak, Bodis-Wollner, Harnois, and Thornton, 1984). Cannon's (1983a) findings predicted a different outcome. His results showed that the second harmonic (F2) mediates threshold at low spatial frequencies while the fundamental (F1) determines threshold at intermediate-to-high spatial frequencies. He concluded that the combination of these two response components accounted for the psychophysical pattern detection curve.

METHODS

Subjects

The observers included three healthy adult volunteers; two males (ages 22 and 34), and one female (age 25). All had normal or corrected-to-normal visual acuity and no neuro-ophthalmologic disease.

Stimuli

The stimuli consisted of sinusoidal gratings ranging in spatial frequency from 0.9 to 7.3 cycles per degree. Mean luminance of the oscilloscope display was held constant

at 150 cd/m². Gratings were vertically oriented, and sinusoidally temporally modulated in an appearance-disappearance manner. The modulation was such that the grating appeared (contrast increases to its maximal or peak value) and then disappeared (contrast decreases to its minimum value or background mean luminance) without changing spatial phase. It is well established that the type of stimulus modulation used determines the Fourier components present in the response (Spekreijse et al., 1973; Sokol, 1976). A response to contrast-reversal modulation of a grating or a checkerboard, for example, will contain only even harmonic components of the stimulus frequency. With appearance-disappearance modulation, the VEP response consists of both odd and even harmonics of the stimulus frequency. For the purpose of this study, the fundamental (F1) and second harmonic (F2) Fourier components were examined.

Apparatus

Stimuli were generated on a Tektronix 608 oscilloscope (P31 phosphor) controlled by specialized electronics (Milkman, Schick, Rossetto, Ratliff, Shapley, and Victor, 1980) interfaced to a Digital PDP 11 computer. This apparatus produces a 256 x 256 pixel raster display with a frame rate of 270.3 Hz. The display subtends a visual angle of 8.8 degrees at a viewing distance of 57 cm. Stimulus contrast is defined in terms of luminance (L) by the following equation:

$$\text{Contrast} = (L_{\text{max}} - L_{\text{min}}) / (L_{\text{max}} + L_{\text{min}}) \quad (\text{see Figure 1.})$$

The Tektronix 608 monitor was modified by the addition of linearization circuitry and calibrated using a specially designed photometer. For all experiments described below, stimulus contrast ranged from 0.01 to 0.48. Luminance was determined to be a linear function over this range of contrast (see Appendix A). Significant deviations from linearity do not appear until contrasts rise above 0.90.

Procedure

General

During experimental sessions, the observer was seated in the darkened room for five to ten minutes prior to the beginning of data collection. Each observer was instructed to fixate on a blackened point in the center of the display. Viewing was monocular and an eye patch occluded the unused eye. A block diagram of the experimental procedure is shown in Figure 3.

Experiment I - Psychophysical threshold determination

Detection thresholds were obtained for sinusoidal gratings of five spatial frequencies (0.9, 1.8, 3.6, 5.0, and 7.3 c/deg) presented at five temporal frequencies (2.08, 4.22, 6.27, 8.44, and 12.45 Hz). Subjects used a keypad interfaced to the computer to adjust contrast of the display according to one of two criteria; until the spatial pattern was just visible regardless of flicker, or until the temporal flicker was just visible regardless of pattern. See Figure 3 (inset) of keypad. Pattern and flicker detection judgments were made separately in alternating experimental blocks and counterbalanced across observers. Each block consisted of 25 randomized trials; five spatial frequencies presented at five temporal frequencies. Ten threshold responses were obtained for each condition. Two experimental sessions, each one-hour in duration, were required to obtain the psychophysical data from each subject. An additional session was required from observer JC to obtain thresholds for two higher spatial frequencies (10.0 and 14.6 c/deg). Mean sensitivities, standard errors, and the individual trials for each subject are shown in Appendix B.

Experiment II - Evoked Potential Recordings

A block diagram of the experimental apparatus for all VEP experiments is shown in Figure 4. Visual evoked potentials were recorded with Grass EEG gold cup electrodes attached to the observer's scalp. Electrode placement was Oz - Cz with a ground at Pz according to the 10-20 Electrode System of the International Federation (Jasper, 1958).

Figure 4 (inset) shows electrode placement. Responses were amplified (gain = 10,000), filtered (bandwidth: 0.03 - 100 Hz), and digitized by a Digital PDP-11/23 computer. The EEG was sampled at a rate of 270.3 Hz (time-locked to the modulation rate of the stimulus), and two 30 second epochs were averaged during each one-minute trial. Gratings were presented for one-minute trials in ten steps of ascending peak contrasts ranging from 0.01 to 0.48. Temporal modulation was sinusoidal at 6.27 Hz. Spatial frequencies were presented in random order in each session. A single experimental session consisted of 50 one-minute trials with breaks and required approximately 1.5 hours of recording time. VEP data collection for each observer required three sessions. Additional recording sessions were obtained from observer JC for the temporal tuning and field size experiments described below.

Analysis

General

VEP data obtained from multiple recording sessions were vector averaged for each condition. The EEG record was Fourier analyzed on-line and yielded amplitudes and phases of the fundamental (F1) and second harmonic (F2) response components. Response amplitude is measured in microvolts and phase is measured in degrees relative to the sine phase of the stimulus. At the end of each one-minute trial, response components were printed to hard copy and saved to disk for subsequent analysis.

Contrast Threshold Estimation from Evoked Potential Responses

In order to derive contrast sensitivity measures from evoked potential data, the amount of contrast needed to produce a criterion response was determined. A VEP "threshold" is defined here as the stimulus intensity which evoked a response significantly different from what would be expected if there were only EEG noise in the recording. Typically, derivations are made from amplitude data (Cannon, 1983a; Zemon, Gutowski, and Horton, 1983; Bobak et al., 1984), or phase data (Nakayama and

Mackablen, 1982; Picton, Vajsar, Rodriguez, and Campbell, 1987; Dobie and Wilson, 1993). The derivations described below were made using amplitude, phase, signal-to-noise ratios, and contrast gain.

From the amplitude data, a 0.75 μV criterion response was applied to each contrast response function. This criterion value was chosen because it was above the average noise level for all three subjects. The contrast at which the VEP signal first exceeded and remained above this value for two successive contrast levels was used. An example is shown in Figure 5. Additionally, the amplitude versus contrast functions were fitted by a least-squares criterion. The parameters of the fitted functions and the smooth curves through the amplitude data are given in Appendix C. The smooth curves were derived from the Michaelis-Menten equation:

$$Y = aX / (b + X),$$

where $a \equiv$ maximum response value, $b \equiv$ the contrast at which Y reaches half of its maximal value (also known as the semi-saturation constant), and $X \equiv$ stimulus contrast. The slope (a/b) of this function at low contrast is a measure of contrast gain. Gain is defined as the change in the response per unit change in contrast. For this measure, contrast sensitivity is proportional to contrast gain. This measure of contrast gain (responsivity) for each spatial frequency, was compared directly with the psychophysically derived sensitivities. Quantitative descriptions of contrast response functions obtained electrophysiologically in animals have included least-squares functional fits to the data. Albrecht and Hamilton (1982) showed that for simple and complex cortical cells in both cat and monkey, a hyperbolic ratio function such as the Michaelis-Menten, fit 70% of the contrast response functions obtained. Kaplan and Shapley (1982), and Croner and Kaplan (1995) used this function to fit macaque LGN and retinal ganglion cells, respectively. Inspection of the fitted amplitude data in Appendix C shows the applicability of this function to VEP data as well. The amount of variance explained by this function ranged from 0.80 to 0.99.

Consistency of steady-state evoked potential data can be expressed in terms of phase coherence (Mardia, 1972). Probability of the VEP phase being randomly distributed between 0 and 360 degrees was assessed by the Rayleigh statistic (R). Phase coherence was calculated according to the formula:

$$R = \sqrt{(\sum \sin \theta_i)^2 + (\sum \cos \theta_i)^2} / N$$

where θ_i is the phase of each measurement and N is the number of measurements. When phase is randomly distributed, R has a value near 0.0. When the phase is constant, or changes very little, R has a value near 1.0. This has been used to measure response variance of auditory (Picton et al., 1987; Stapells, Makeig, and Galambos, 1987) as well as visual evoked potentials (Victor and Mast, 1991; Tang and Norcia, 1993). VEP threshold is taken as lowest contrast at which the phase response is significantly ($p < 0.05$) different from background. An example of this derivation is shown in Figure 6. The dashed line labeled 0.69 in this Figure indicates the value of R needed to exceed the 0.05 level of significance.

Signal-to-noise (S/N) ratios of 1 and 2 were determined from the T_{circ}^2 estimates of error about an averaged response. This statistic was used to determine whether the responses were significantly different from background noise and to determine the 95% confidence limits of the amplitude and phase for each harmonic. T_{circ}^2 is a normalized F statistic specifically designed to analyze the variability of Fourier response components (Victor and Mast, 1991). Previous methods used to assess the variability of Fourier components ignored one or more features of the data, such as the phase information. T_{circ}^2 uses both amplitude and phase information. It calculates a 2-dimensional confidence circle for the averaged response vectors for each Fourier component specified. Victor and Mast (1991) have shown that with an assumption of equal variances for the real and imaginary components of the response vectors, their circular T^2

Figure 3.

Block diagram of experimental apparatus for Exp. I. Inset: Diagram of keypad used in Experiment I. Three scale keys allow subjects to adjust contrast in steps of 0.25, 1.0, and 2.0 percent. The increase and decrease keys allow the subject to bracket their threshold. When a decision is reached, the subject presses the return to terminal key. This records the response and initiates the next trial. All blank keys are inoperable.

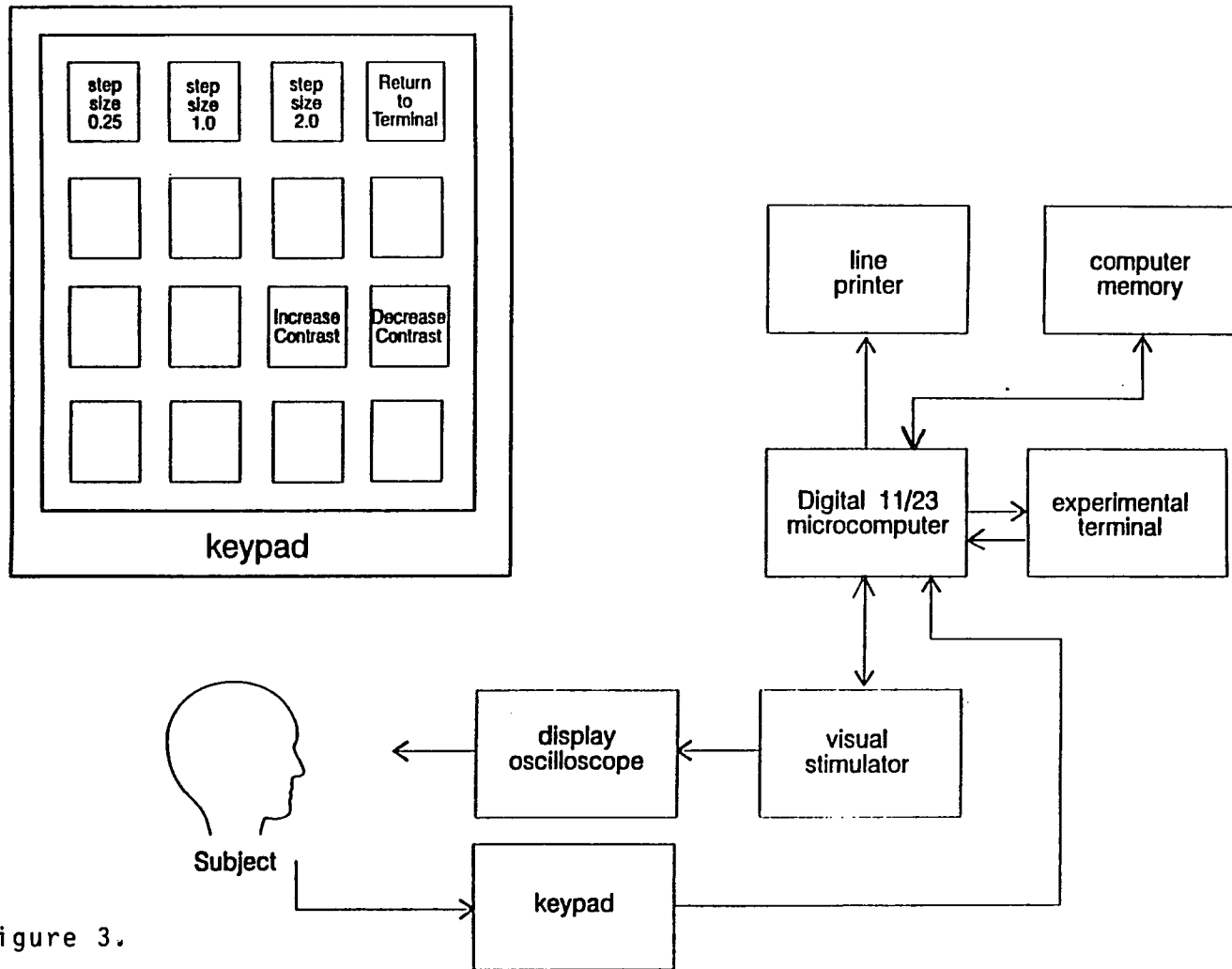


Figure 3.

Figure 4.

Block diagram of experimental apparatus for Exp. II. Inset: Placement of electrodes along the midline of the subject's head. The active electrode, designated Oz, is placed over the occipital region, 10 % of the distance frominion to nasion. It is referenced to a second electrode, Cz, located at 50 % of the distance frominion to nasion. The ground electrode, Pz, is placed midway between these two.

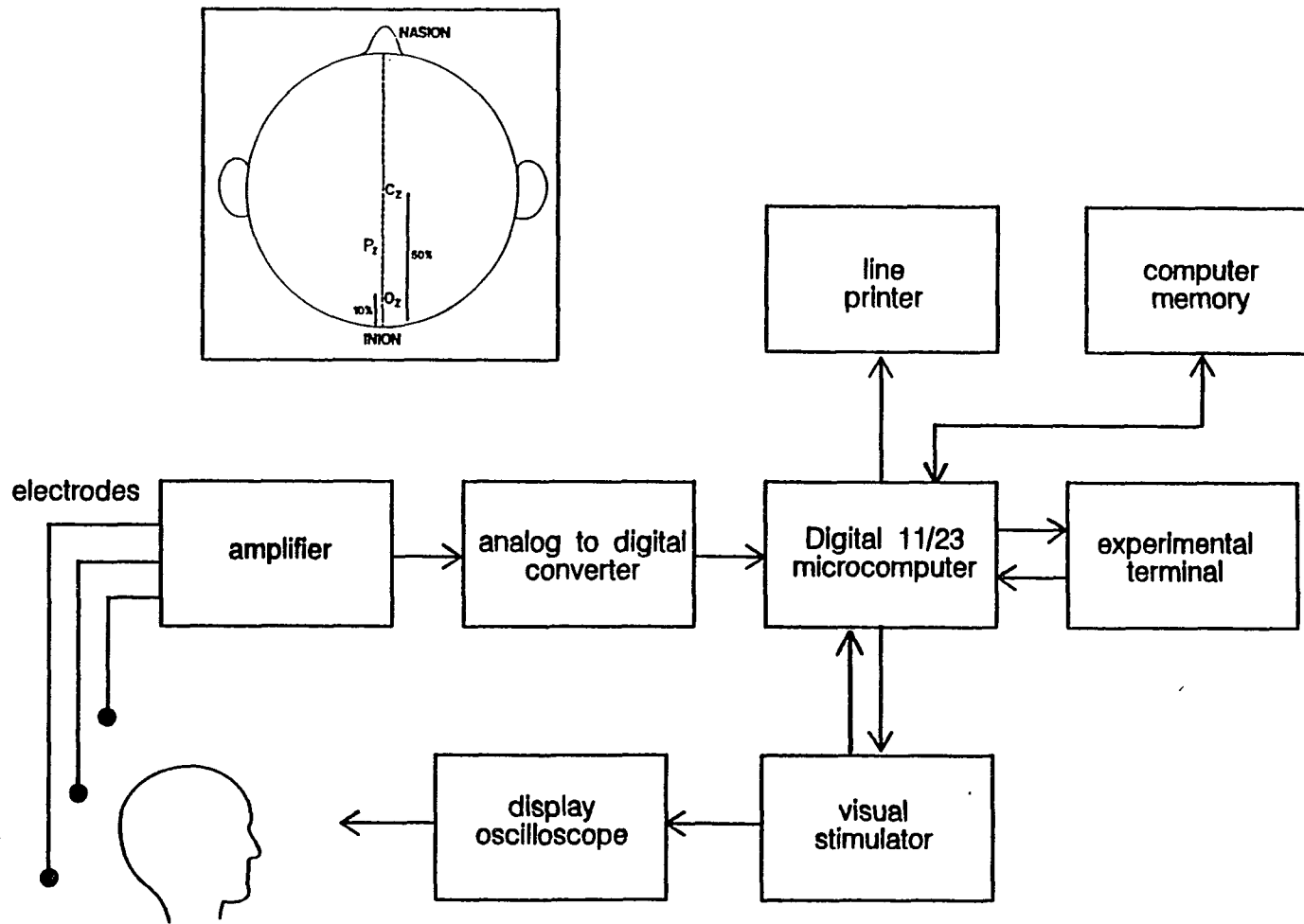


Figure 4. Subject

Figure 5.

Example of VEP criterion contrast response derivation using response amplitude. The arrow indicates the contrast at which the VEP exceeds $0.75 \mu\text{V}$ (dotted line). Subject: MC, spatial frequency = 0.9 cpd, second harmonic (F2) component.

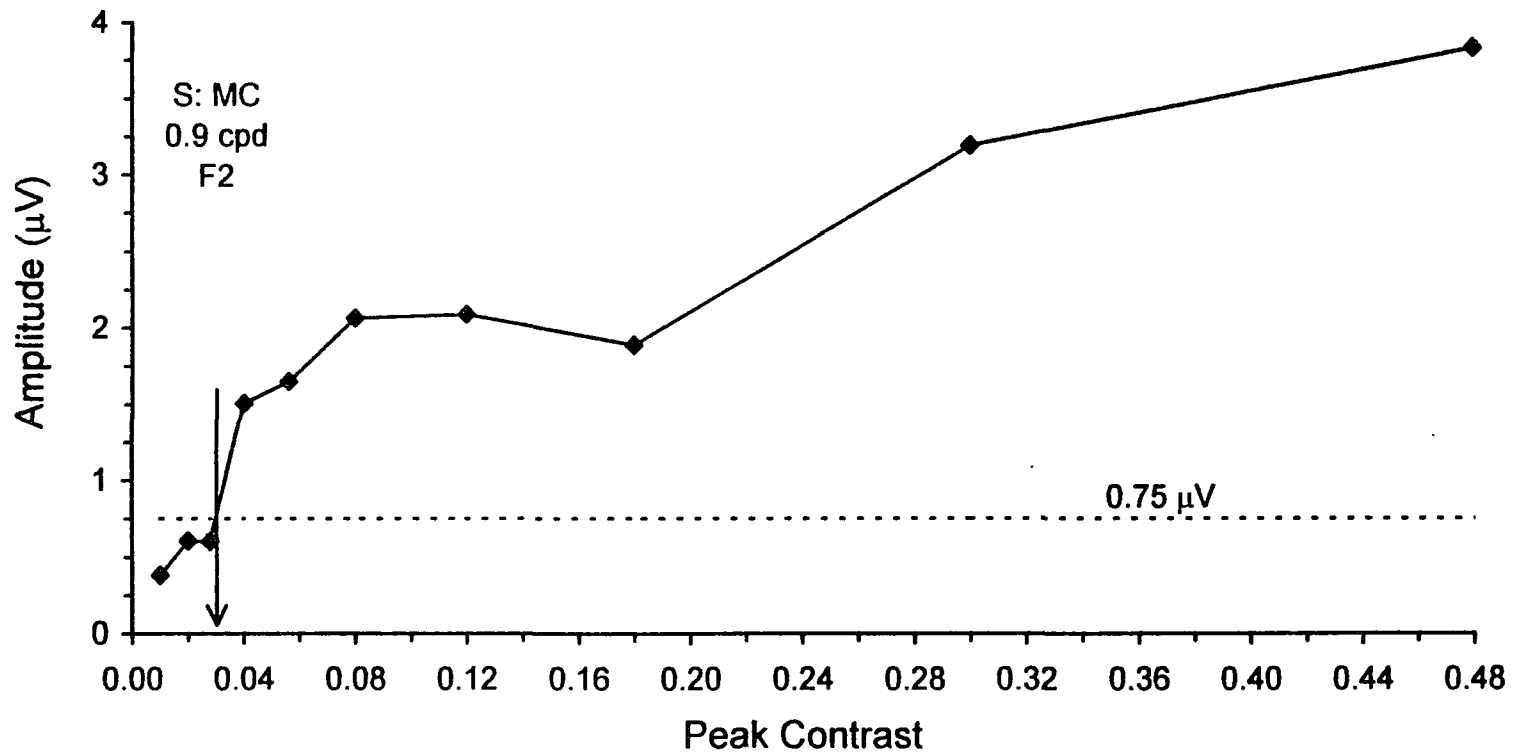


Figure 5.

Figure 6.

Example of VEP criterion contrast response derivation using Rayleigh phase coherence. The arrow indicates the contrast level at which response phase is coherent. The dotted line (Rayleigh coefficient = 0.69) represents the $p < 0.05$ level of significance for three trials. Subject: MC, spatial frequency = 1.8 cpd, second harmonic (F2) component.

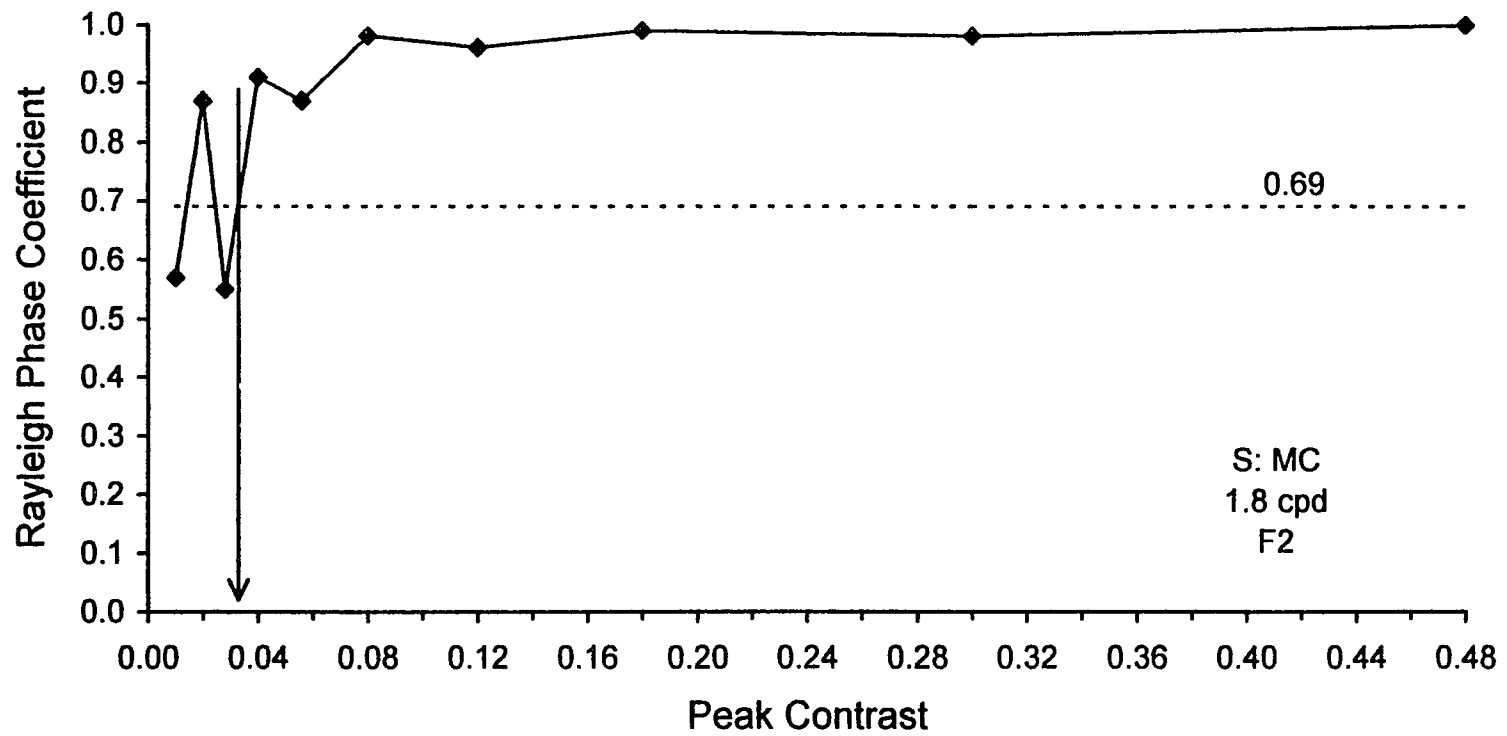


Figure 6.

Figure 7.

Example of VEP criterion contrast response derivation using a Signal-to-Noise ratio. The arrow to the left indicates the contrast at which the response exceeds a S/N ratio = 1. The arrow to the right indicates the contrast at which the response exceeds a S/N ratio = 2. Subject: JC, spatial frequency = 0.9 cpd, second harmonic (F2) component.

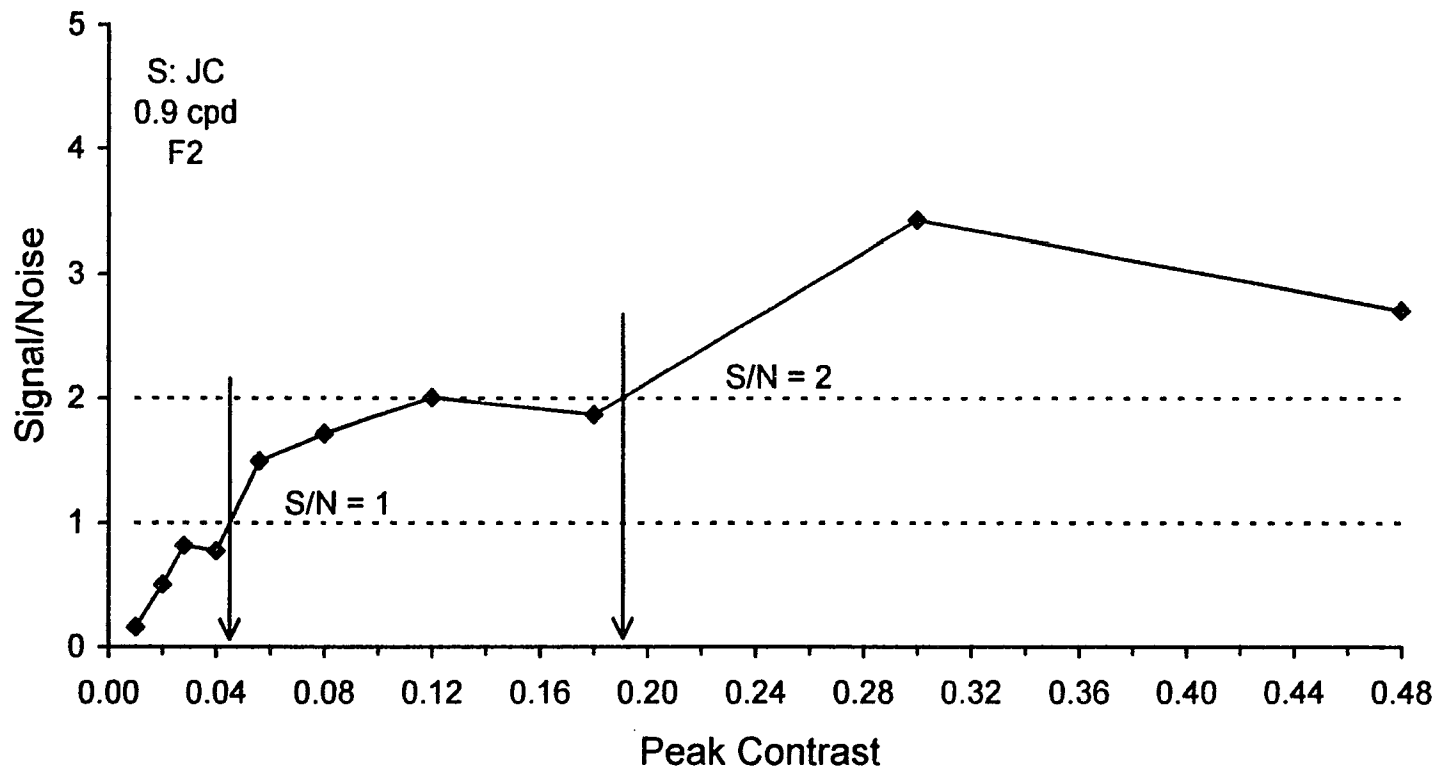


Figure 7.

is more powerful than the Hotelling T^2 in determining when a signal is present in the EEG record. As with the derivations from either amplitude or phase alone, threshold was taken as the contrast at which the response exceeded and remained above the signal-to-noise ratios for two or more successive contrast levels. See Figure 7 for an example of this derivation.

In summary, contrast sensitivities were derived from the VEP data in four ways by meeting specific criteria; criterion amplitude response, phase consistency or coherence, and S/N ratios of 1 and 2. Contrast sensitivities are the reciprocals of these criterion contrast values for all but the Michaelis-Menten measure. Calculation of the slope of the Michaelis-Menten fits to the amplitude data gave us a measure of contrast gain which serves as our fifth measure of VEP contrast sensitivity. Gain was then compared directly to the contrast sensitivities derived psychophysically.

RESULTS

Experiment 1 - Psychophysical Contrast Sensitivity Functions

In Figures 8a, b, and c we see that observers were able to set separate thresholds for the perception of flicker and pattern, and that there is good agreement between data from the three observers. All data points are based on the mean of ten threshold measurements and the vertical bars represent ± 1 standard error of the mean. In several instances, the standard errors were smaller than the data points and are not seen in the figures. The individual data trials and summary tables are shown in Appendix B. Filled symbols are sensitivities when pattern detection was the criterion and open symbols are sensitivities when flicker detection was the criterion. The CSF for pattern detection, regardless of temporal frequency, has a band-pass shape for all observers. Flicker detection criterion produces a low-pass function, again regardless of temporal frequency used. The effect of temporal modulation is seen here as an increase in sensitivity to the

low spatial frequencies. For MC and JC, this is evident for only the lowest spatial frequency of 0.9 cpd. This crossover at 0.9 cpd is not evident for DS, however. Examination of the individual trial data in Appendix B shows greater variability in this observer's judgments. It should be noted that DS was a naive psychophysical observer and may have been more susceptible to criterion shifts while making threshold judgments. Figures 9 and 10 demonstrate the consistency of these functions across observers and temporal frequency. Figure 9 illustrates that there is the greatest between-subject variability at the lowest spatial frequency, while in Figure 10 we see greater between-subject variability at the highest spatial frequency. Log sensitivities as a function of temporal frequency are plotted in Figures 11 and 12. Here again, we see that the contrast sensitivity functions are independent of temporal frequency over a range of 2 to 12 Hz. In Figure 11, the lowest sensitivities are to the lowest (0.9 cpd) and highest (7.3 cpd) spatial frequencies. The highest sensitivity is to the middle spatial frequency (3.6 cpd). Hence, band-pass functions similar to Figure 9 are obtained. In Figure 12, sensitivity decreases as spatial frequency increases to produce low-pass functions similar to Figure 10. Figure 13 shows how invariant the pattern detection function is to temporal modulation. Flicker detection functions in Figure 14 are low-pass with slightly lower sensitivities to 12 Hz. A comparison with results from Kelly and Savoie (1973), who used both the method of adjustment and a forced-choice staircase procedure, tells us that we are within 1/10 of a log unit to their highest log sensitivities. These results were consistent with those previously reported in the literature and form the basis against which the visual evoked potential data were compared.

In order to make a more direct comparison to the psychophysical literature, we attempted to extend our spatial frequency range. However, because of the low spatial resolution of the display raster, it was not possible to produce sine-wave gratings of spatial frequencies greater than about 8 cpd at the 57 cm. viewing distance. To obtain these additional data, observer JC, therefore, was seated at twice the viewing distance.

Figure 8.

Log sensitivity plotted as a function of log spatial frequency. Contrast sensitivities were derived separately for the detection of pattern (filled symbols) and flicker (open symbols) at five temporal frequencies. Temporal frequencies ranged from 2.08 to 12.44 Hz. Each data point is the mean of ten measurements. Error bars indicate ± 1 standard error of the mean. 8a. MC, 8b. JC, 8c. DS.

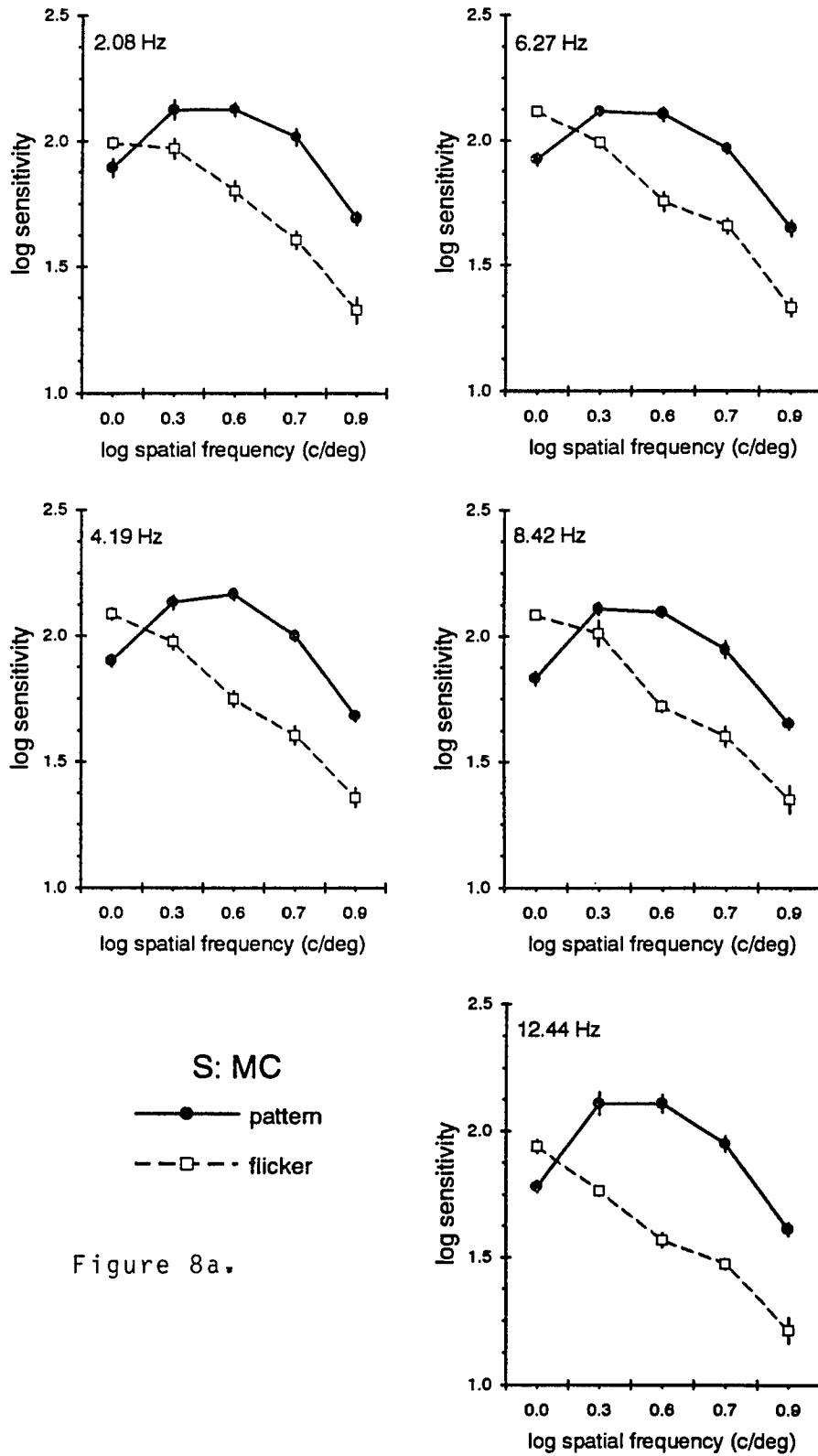
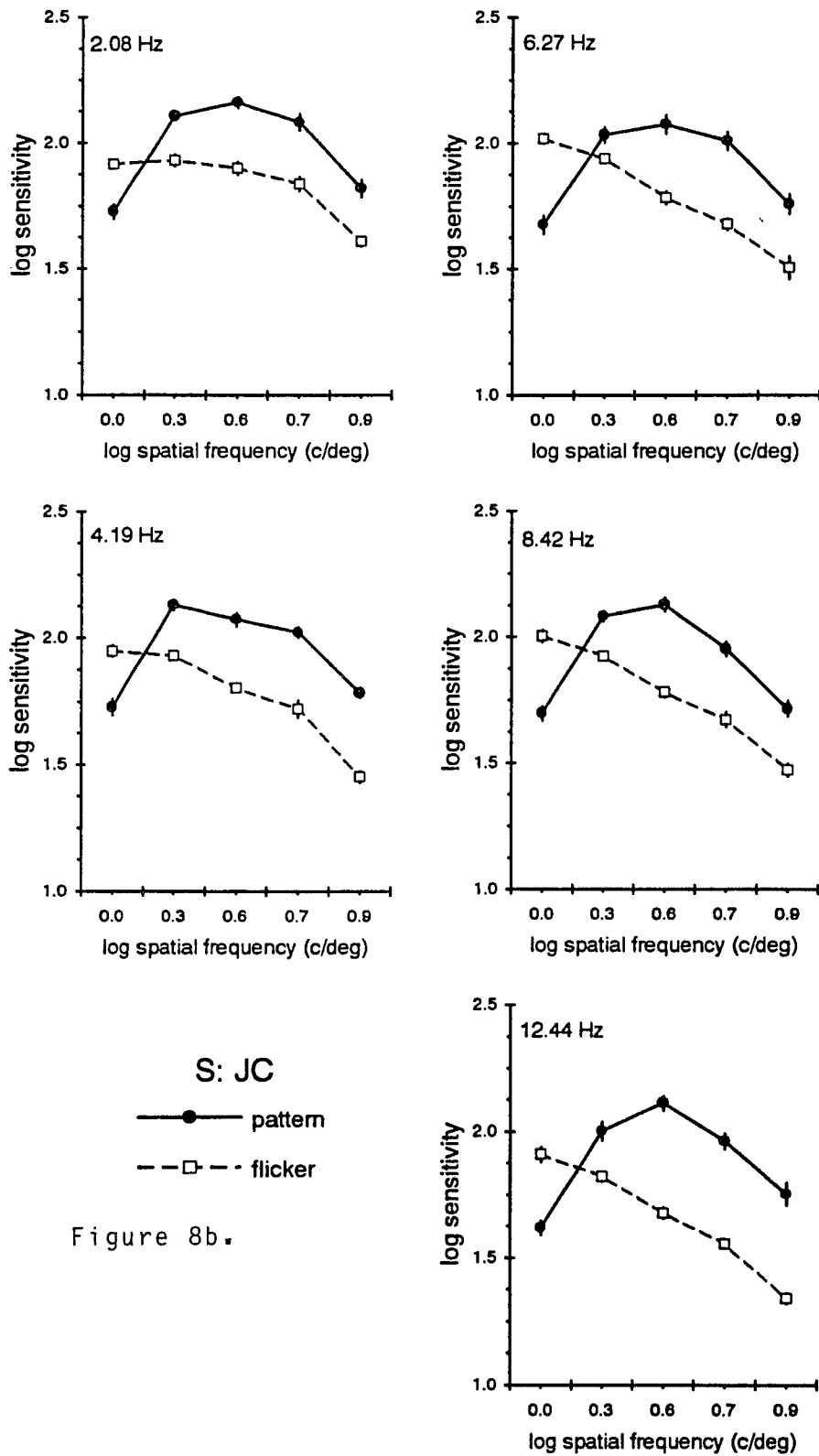


Figure 8a.



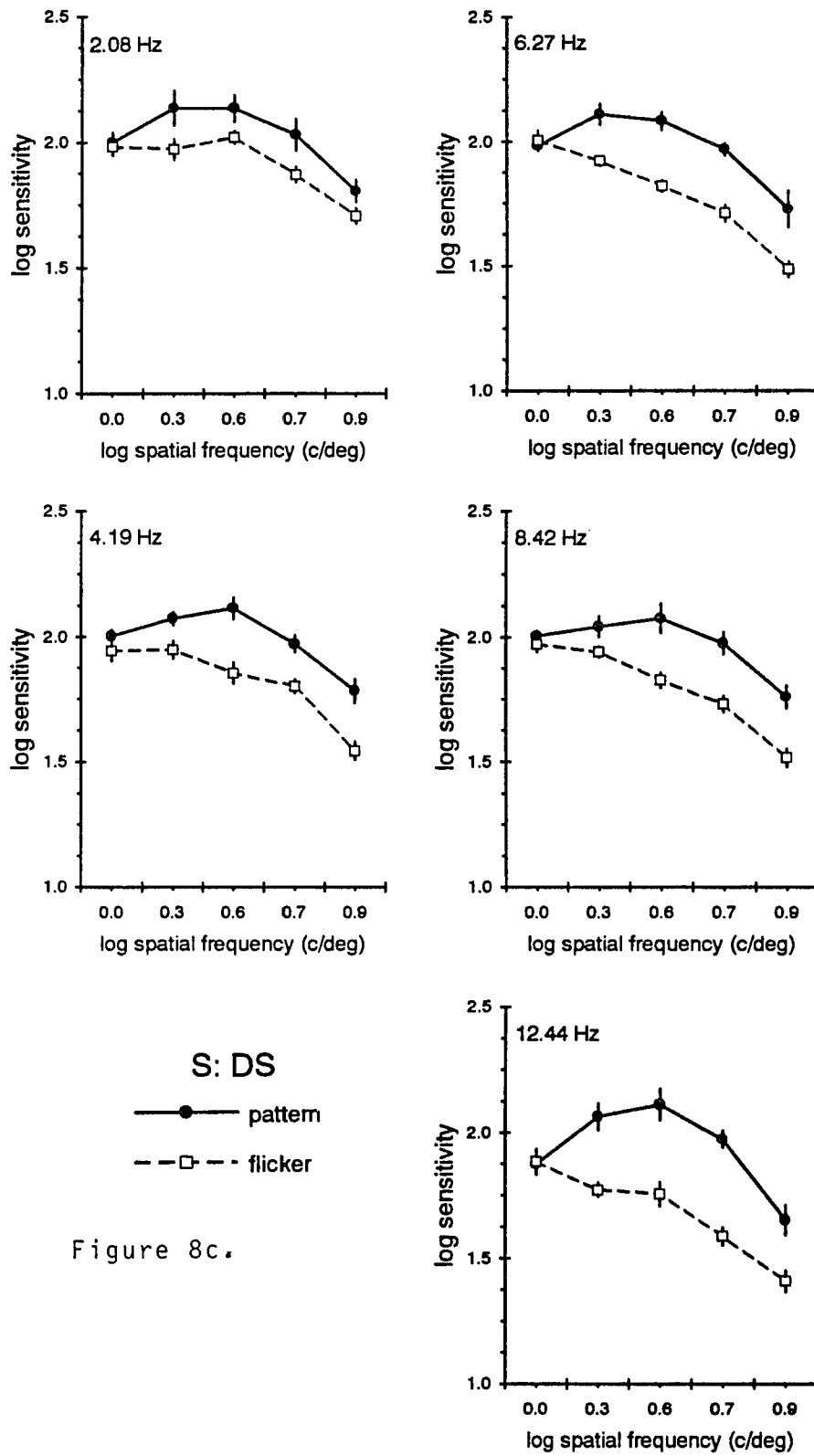


Figure 8c.

Figure 9.

Log sensitivity plotted as a function of log spatial frequency for pattern detection at five temporal frequencies. Temporal frequency: 2.08 - 12.44 Hz. Subjects: MC, JC, DS.

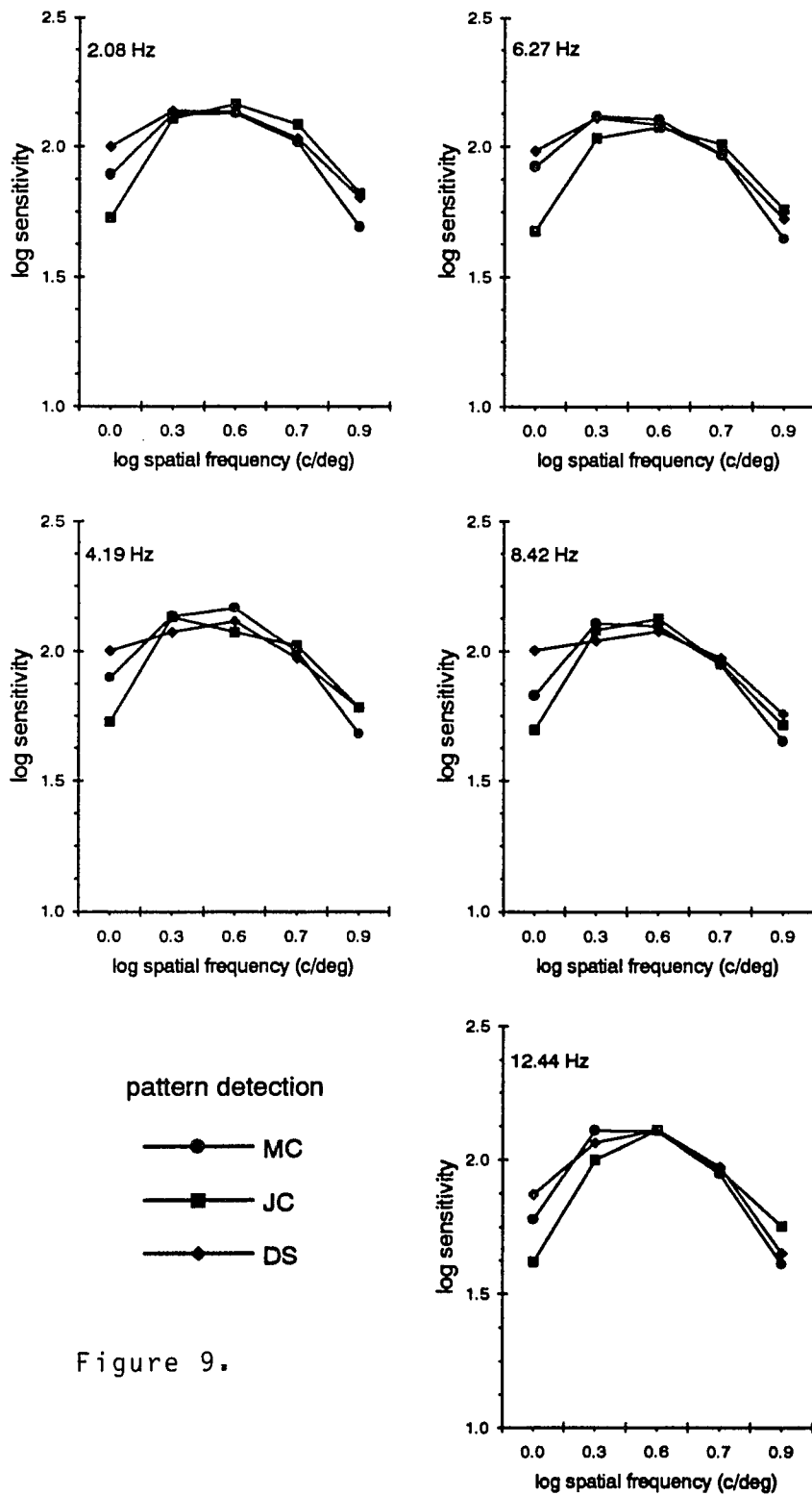


Figure 10.

Log sensitivity plotted as a function of log spatial frequency for flicker detection at five temporal frequencies. Temporal frequency: 2.08 - 12.44 Hz. Subjects: MC, JC, DS.

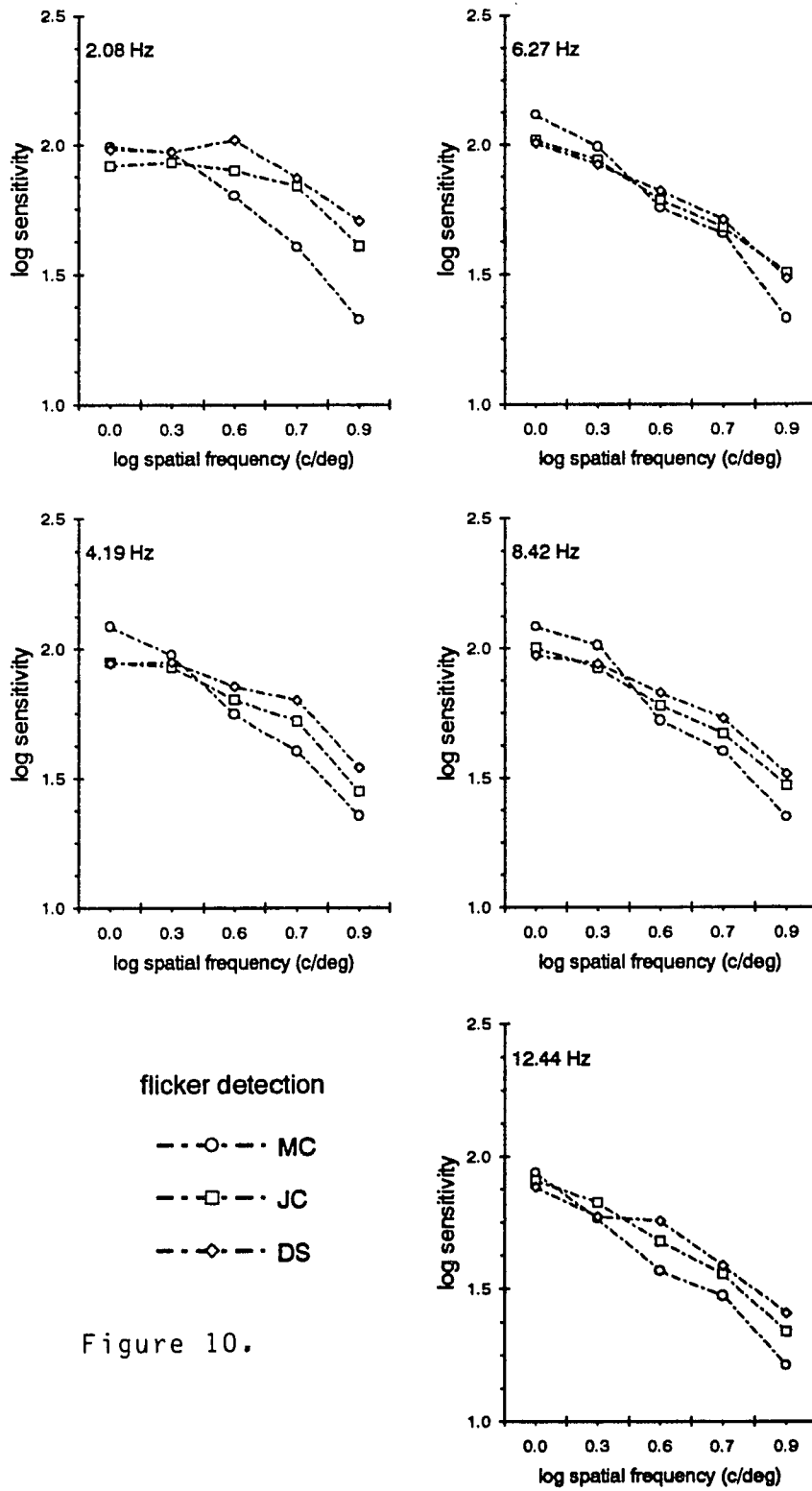


Figure 10.

Figure 11.

Log sensitivity plotted as a function of temporal frequency for pattern detection at five spatial frequencies. Spatial frequency: 0.9 - 7.3 c/deg. Subjects: MC, JC, DS.

pattern detection

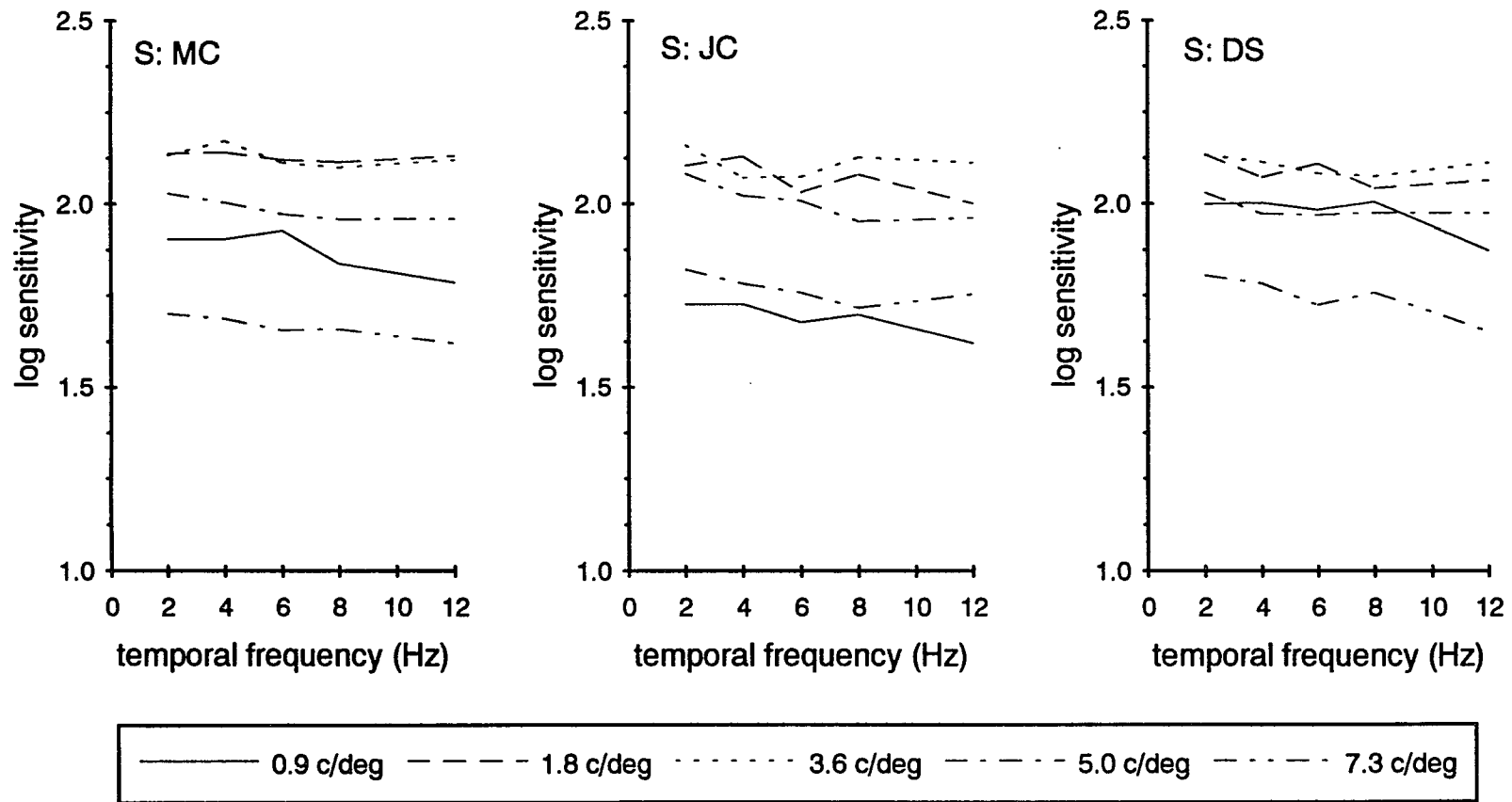


Figure 11.

Figure 12.

Log sensitivity plotted as a function of temporal frequency for flicker detection at five spatial frequencies. Spatial frequency: 0.9 - 7.3 c/deg. Subjects: MC, JC, DS.

flicker detection

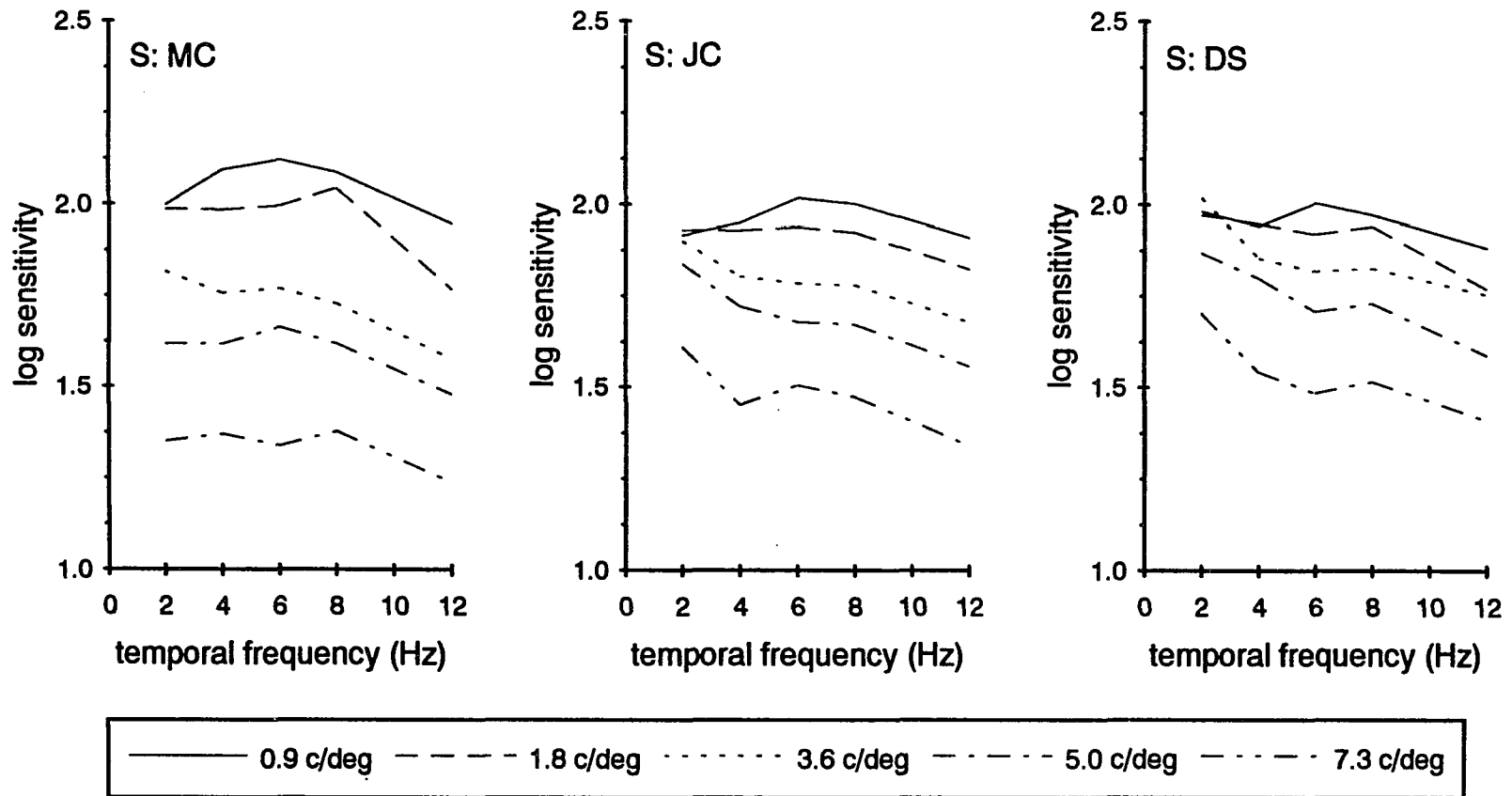


Figure 12.

Figure 13.

Log sensitivity plotted as a function of log spatial frequency for pattern detection at five temporal frequencies. Temporal frequency: 2.08 - 12.44 Hz. Subjects: MC, JC, DS.

pattern detection

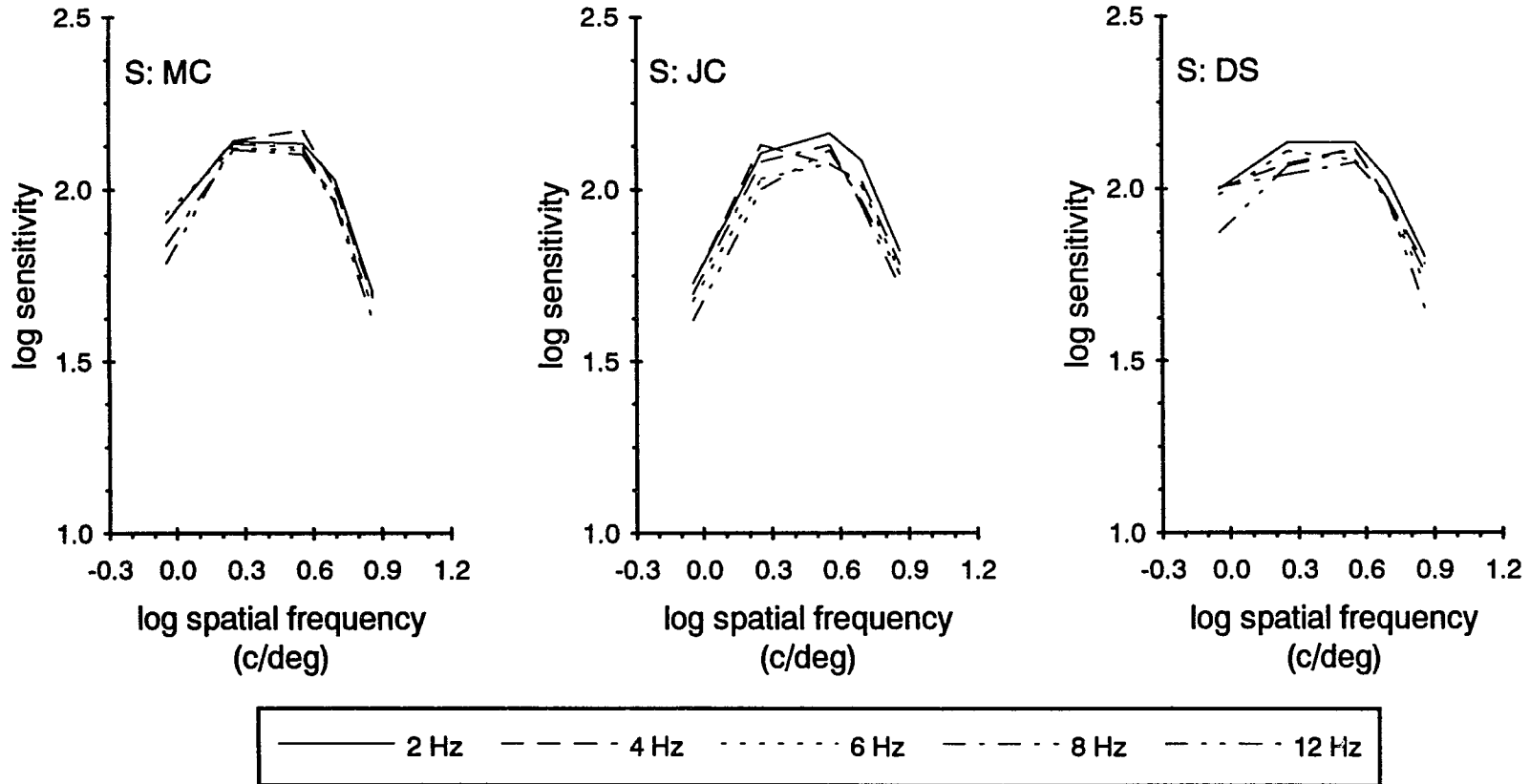


Figure 13.

Figure 14.

Log sensitivity plotted as a function of log spatial frequency for flicker detection at five temporal frequencies. Temporal frequency: 2.08 - 12.44 Hz. Subjects: MC, JC, DS.

flicker detection

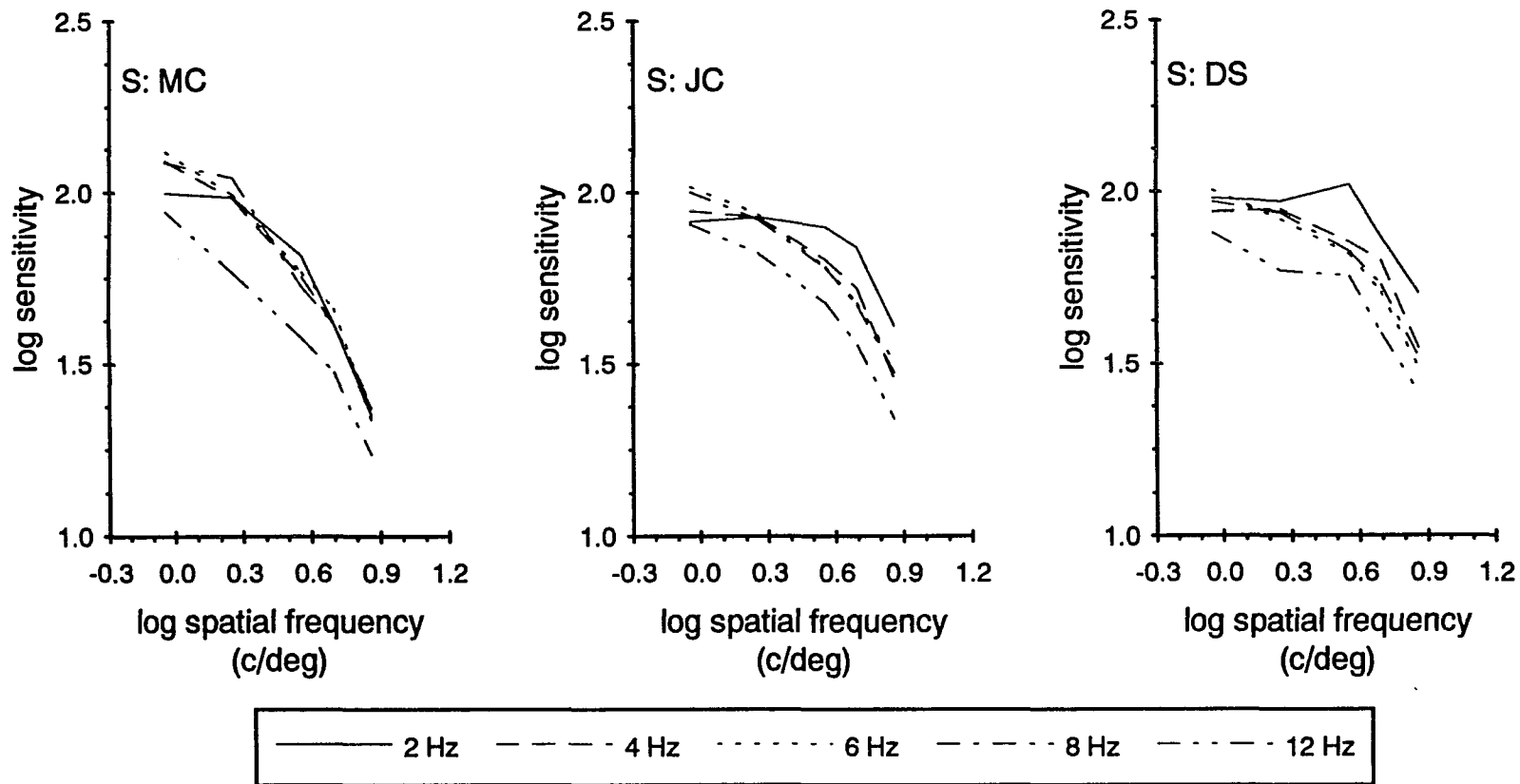


Figure 14.

Figure 15.

Pattern and flicker sensitivity functions to 6.27 Hz stimulation replotted from Figure 8b. Three additional spatial frequency (7.3, 10.0 and 14.6 cpd) points are shown. Each data point is the mean of ten judgments. Data were collected at two viewing distances: 57 cm. (solid lines) and 114 cm. (dashed lines). Subject: JC.

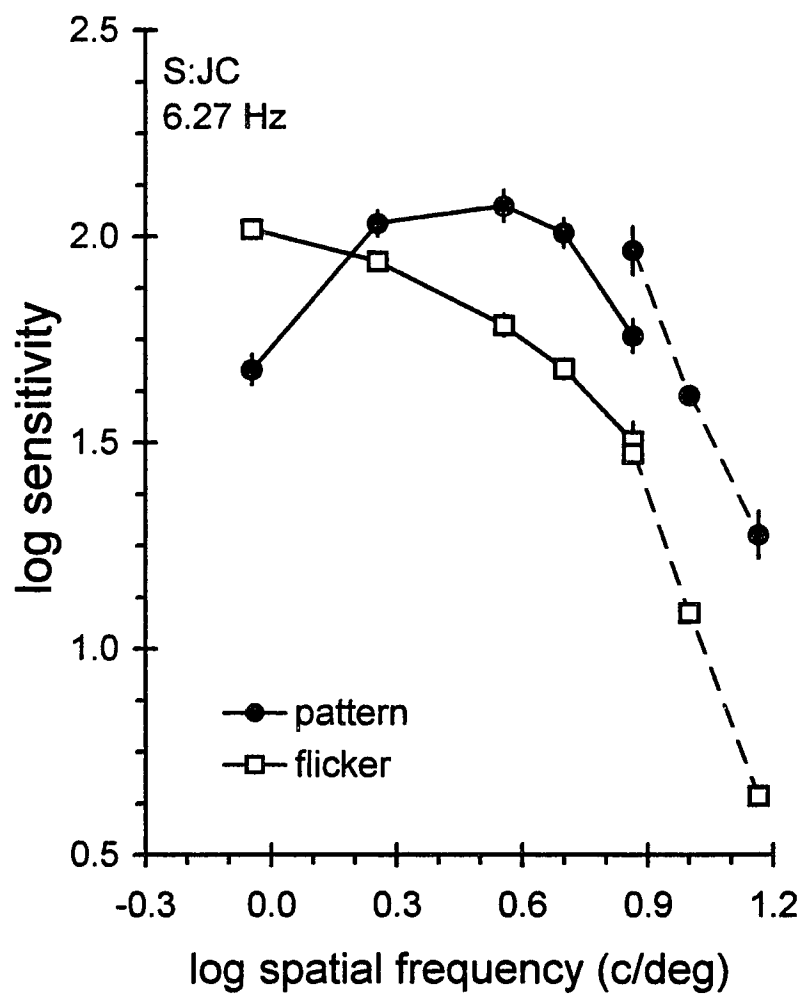


Figure 15.

This halved the field size from 8.8 deg to 4.4 deg. Both psychophysical and VEP data show that small field sizes reduce the sensitivity to low spatial frequencies much more than the sensitivity to high spatial frequencies (Cannon, 1983b). JC's pattern and flicker functions at 6.27 Hz are replotted in Figure 15. Data collected at the 114 cm. viewing distance were added and are indicated by the dashed lines. The additional spatial frequencies were 7.3, 10.0, and 14.6 cpd. Unexpectedly, sensitivity to 7.3 cpd for pattern criteria was greater at 114 cm. than at 57 cm. A possible explanation is response variability over time. Between-session variability is almost always greater than within-session variability (Graham, 1989). Thresholds at the 114 cm. distance were collected three months after the initial data collection period. Otherwise, data for 10.0 and 14.6 cpd complete the pattern and flicker functions quite well.

Experiment IIa - VEP Contrast Response Functions

Amplitude, phase, and signal-to-noise ratios of the fundamental (F1) and second harmonic (F2) VEP response components, plotted as functions of peak contrast for each spatial frequency are shown in Figures 16 through 20. Each data point represents three minutes of VEP recording time. The fundamental response is plotted on the left half and the second harmonic is plotted on the right half of each figure. Missing phase points indicate responses that are not above the noise level as stipulated by the 95% confidence region. Amplitude variability, as reflected by the size of the error bars, does not decrease as signal increases. This is a general finding in the visual evoked potential literature (Regan, 1989). Typically, responses to stimuli at the lowest peak contrast (0.01) were indistinguishable from the background EEG noise. The exact form of the contrast response function tends to vary with observer and spatial frequency. Yet the data presented here are remarkably similar. Generally, VEP response amplitude increases as stimulus contrast increases and then flattens or saturates (Spekreijse, Estevez, and Reits, 1977). When we look at the F1 amplitudes, we see a function which rises steeply at low contrasts and then saturates or decreases at the highest contrast (0.48). The shape of this

function suggests a compressive nonlinearity which behaves approximately linearly at low contrasts (Regan, 1989). The F2 responses generally do not saturate, but increase over the entire contrast range with much shallower slopes than the F1 functions. This effect is most dramatic at 7.3 cpd (Figure 20a, b, c). For this spatial frequency, the F1 response saturates at about 0.08 peak contrast, while the F2 is much less sensitive to contrast and increases gradually. Bobak, Bodis-Wollner and Marx (1988), who also used appearance-disappearance modulation, reported that the amplitude of the F1 component saturates at a lower contrast than does the F2 component to the same stimulus.

The signal-to-noise functions parallel the amplitude data in shape and overall size. With respect to amplitude, there was greater between-subject variability than within. The smallest responses were recorded from DS; the largest responses from JC. For observer JC, the F1 component was larger than the F2 component for all spatial frequencies. For MC and DS, F2 is the larger response component at low spatial frequencies (0.9 and 1.8 cpd), but this effect reverses itself by 3.6 cpd. Cannon (1983b) reported that this effect was present for modulation rates up to 20 Hz and concluded that this was a low spatial frequency phenomenon and not temporally dependent. If one expected an optimum spatial frequency to elicit the highest contrast sensitivity psychophysically, one could then expect that same spatial frequency to elicit the largest evoked response (Parker and Salzen, 1977). If this one-to-one analogy were true, then the largest amplitude (F1 or F2) would be to the spatial frequency which corresponds to the peak of the contrast sensitivity function. However, this proves not to be the case. The peak of the psychophysical CSF's for all three observers is approximately 3 cpd. The VEP-F1 responses to 5.0 and 7.3 cpd are clearly the largest for all observers. These results illustrate that response amplitude was strongly dependent on spatial frequency. In addition to the amplitude differences between the response components, there are phase differences as well. Response phase shows less dependence on contrast than the amplitude data. Within the suprathreshold range a phase advance with increasing

contrast was expected (Parker and Salzen, 1977; Vassilev, Manahilov, and Mitov, 1983). There is a slight phase advance for F1 and F2 (approximately 10 - 20 deg) at low contrasts (≤ 0.04). The F1 amplitude functions are rising rapidly at these near threshold contrasts. There is a more dramatic F2 phase shift (approximately 90 - 100 deg) at or above a contrast of 0.08. Figure 18c is an example of this phenomenon. A phase shift of this magnitude at higher contrasts has been hypothesized to reflect a shift in the balance between the excitatory and inhibitory inputs to the VEP (Zemon et al., 1983).

The contrast response functions to 7.3, 10.0, and 14.6 cpd for observer JC are shown in Figure 21a, b, c, respectively. These data were collected to compare to the psychophysical data obtained at the 114 cm. viewing distance (see Figure 15). There is a striking difference between the responses to 7.3 cpd collected at 57 (Figure 20b) versus 114 cm. (Figure 21a). The effect of halving the field size was substantially greater (a 50% drop in overall response size) for the VEP than it was for the psychophysics. At this further distance the retinal area that maps the stimulus field is one-quarter of the size of the area that maps the field at the 57 cm. distance. Spekreijse et al., (1977) estimated a 30% reduction of the VEP for an equivalent reduction in field size. A similar decrease in sensitivity was not evident in the psychophysics. These data were also more variable as evidenced by the size of the error bars. The second harmonic responses are even smaller for JC given the size of his responses at the 57 cm. viewing distance. Consequently, it was not possible to derive criterion measures from much of these second harmonic data because of the size of the responses. This accounts for the missing data points in Figure 24b. Despite the missing phase points for most of these data, there is a subtle phase lag at higher contrasts (from 0.30 to 0.48) for both the F1 (Figure 21c) and F2 (Figure 21b) components.

Experiment IIb - VEP Temporal Response Functions

As mentioned above, Kulikowski and Tolhurst (1973) recommended a temporal modulation of about 6 Hz to maximize the separation between pattern and flicker

mechanisms psychophysically. Previous evoked potential studies have reported robust fundamental and second harmonic responses to modulation frequencies between 4 and 8 Hz (Bodis-Wollner, Hendley, and Kulikowski, 1972; Srebro, Sokol, and Wright, 1981). Because of the time required for data collection, therefore, VEPs were elicited to only one temporal frequency, 6.27 Hz. Nevertheless, the overall size of the second harmonic (F2) responses obtained in Experiment II prompted an additional experiment to determine if 6.27 Hz was an optimum modulation frequency for this harmonic component. Temporal response functions were obtained at a suprathreshold contrast of 0.15 for one observer, JC. Temporal frequencies ranged from 4.26 to 8.74 Hz in steps of 0.75 Hz. Results are shown in Figure 22. F1 and F2 response amplitudes are plotted as functions of stimulus frequency. The data suggest that there is temporal frequency tuning, and that tuning depends on spatial frequency. At 1.8 cpd, for example, a large F1 peak at 4.26 Hz drops to one-quarter its size at 5 Hz. Narrow temporal tuning such as this, implies that information about the evoked potential is lost when only one temporal frequency is used for analysis (Tyler et al., 1978). It also implies that there are certain spatial frequencies which are highly visible and yet produce little response from the cortex. We see that stimulus frequencies above 5 Hz favored the F1 component, except at the two lowest spatial frequencies where 4.26 Hz elicits sizable responses. F2 responses, for the range of spatial frequencies used, however, were larger at 4.26 Hz than to frequencies around 6 Hz. We concluded that, for observer JC at 6.27 Hz, the appearance-disappearance VEP to sinusoidal gratings is dominated by the F1 component. A stimulus frequency of 4 Hz, rather than the 6.27 Hz used here, may have yielded larger F2 responses over the range of contrast studied. Future studies which attempt to compare VEPs to psychophysical sensitivity should consider the temporal tuning of the evoked response.

Psychophysics and VEPs Compared

In Figures 23 and 24, we see the comparisons between the psychophysical data (Exp. I) and the VEP derived sensitivities (Exp. IIa). Missing VEP sensitivity data points indicate that amplitude, or phase, or signal-to-noise criteria were not met. In total, there were 15 instances when a sensitivity estimate was not obtained from the evoked potential data. As one might guess, this occurred when the individual response components were too small or variable. For observer DS, for example, there are no VEP-F1 derivations to 0.9 cpd except the derivation from Michaelis-Menten gain which uses the entire contrast response function to calculate the slope. In general, the largest discrepancies between the VEP and psychophysical sensitivities occurred at the lowest spatial frequencies, particularly for the flicker detection condition.

In Figure 23, the five derivations from the VEP-F1 component are compared with both pattern and flicker detection curves. For MC (Figure 23a.), the five derivations from the F1 response produced remarkably similar functions. Derivations from the 0.75 μV criterion (.75 Amp), Rayleigh phase (Rayl), S/N = 1, and Michaelis-Menten contrast gain (MM gain) did equally well in matching pattern and flicker detection at 5.0 and 7.3 cpd. The VEP function derived from the S/N = 2 criterion was not sharply peaked at 5.0 cpd as were the others, and gave the poorest fit to the psychophysics. All five VEP-F1 CSFs fell dramatically short of matching the psychophysical data at 0.9, 1.8, and 3.6 cpd. This narrow tuning of the VEP (approximately two octaves) with a more broadly tuned psychophysical function (three octaves) is directly comparable to data described by Tyler, et al. (1978) and discussed above.

Figure 16.

The VEP contrast response function versus peak contrast (0.01 - 0.48).
Spatial frequency: 0.9 cpd. Temporal frequency: 6.27 Hz. Electrode placement: Oz-Cz.
Test distance: 57cm. Left: Fundamental (F1) component, Right: 2nd Harmonic (F2)
component. Top: Amplitude, middle: Phase, bottom: Signal-to-Noise. The dashed line
on the signal-to-noise plot indicates a S/N ratio = 1. Each data point is the vector average
of three trials. Error bars indicate two standard errors of the mean. 16a. MC, 16b. JC,
16c. DS.

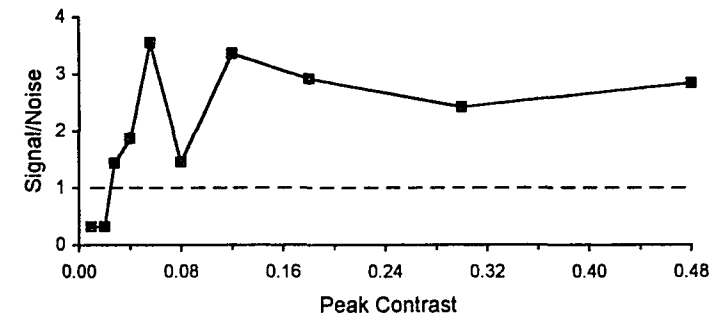
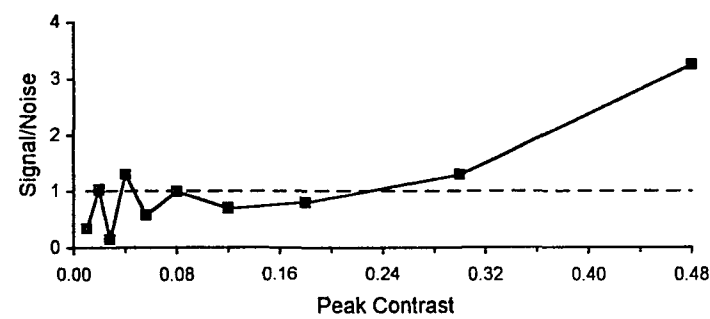
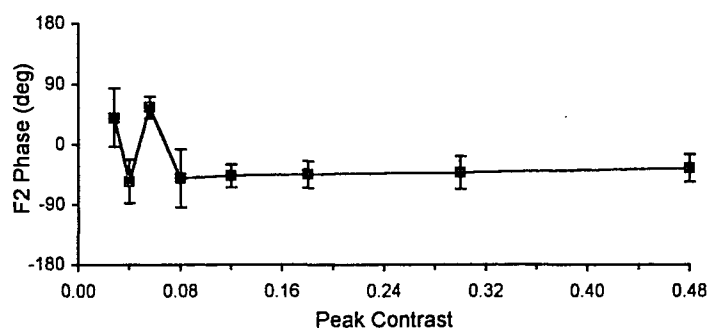
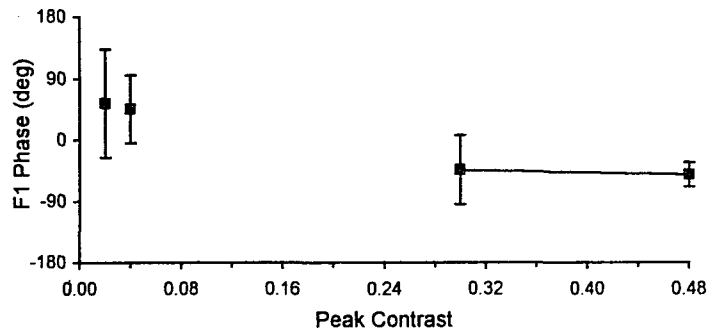
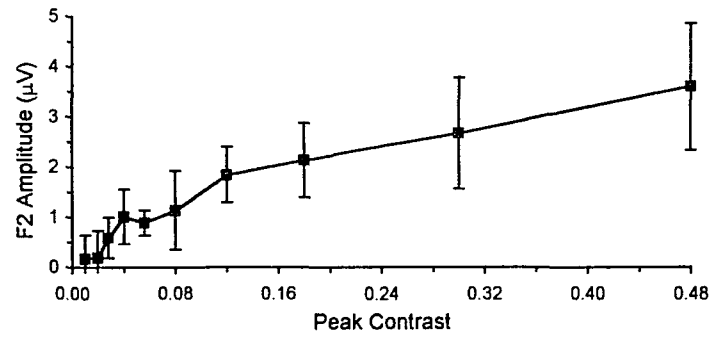
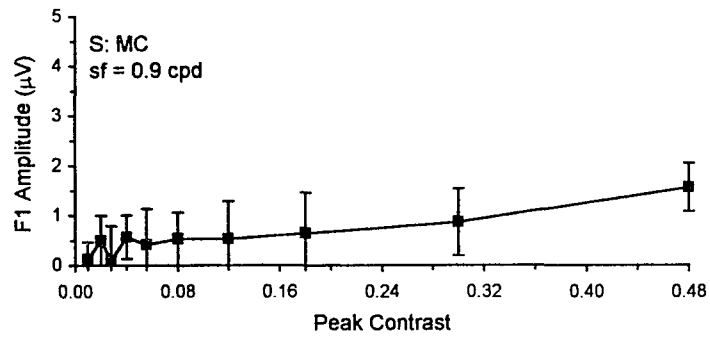


Figure 16a.

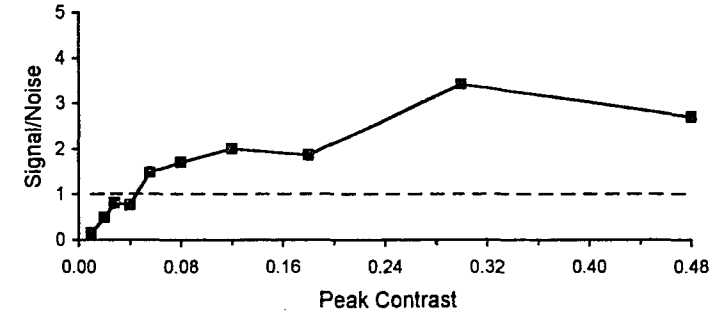
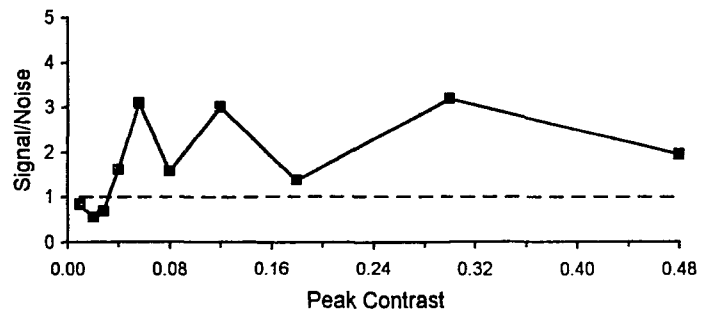
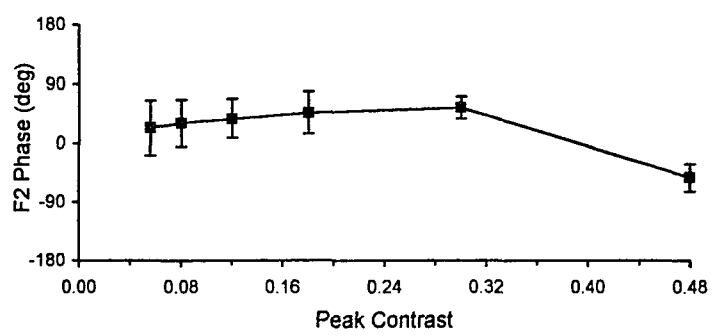
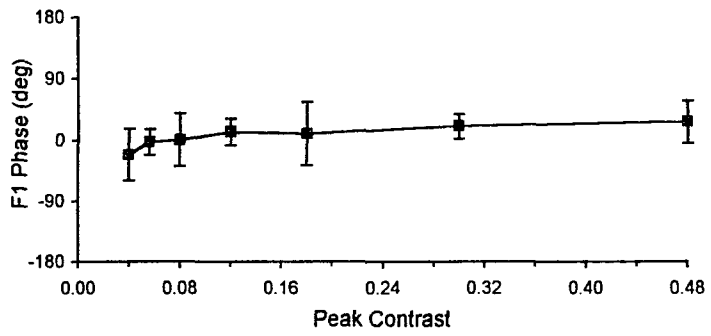
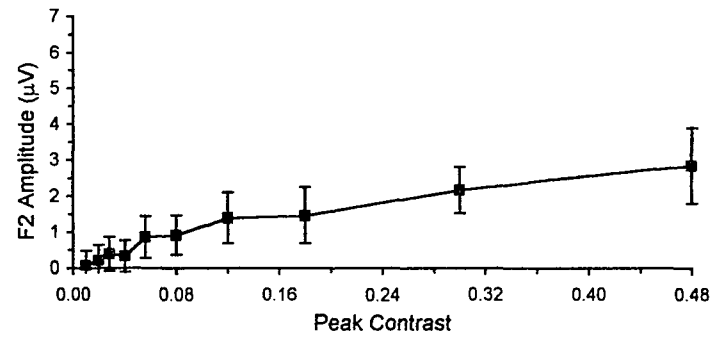
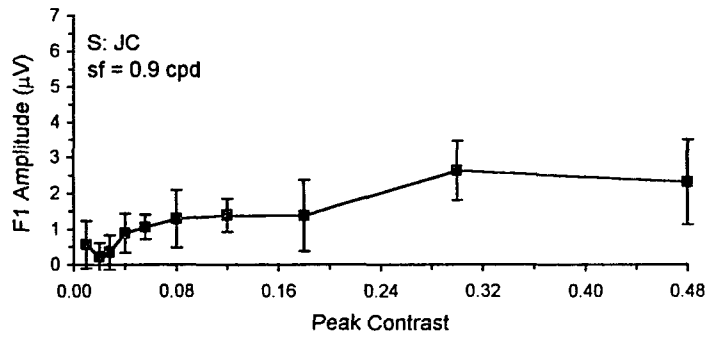


Figure 16b.

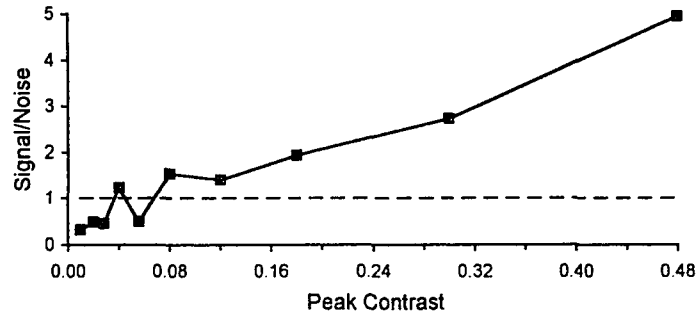
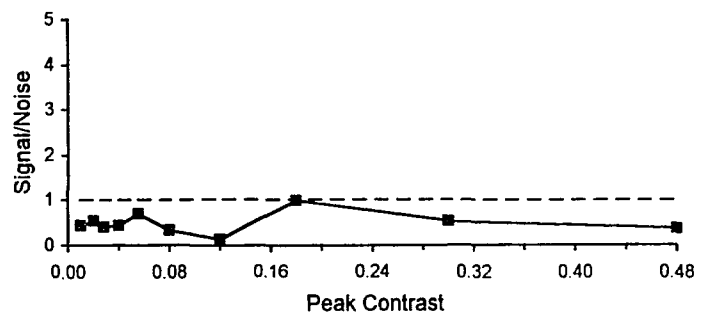
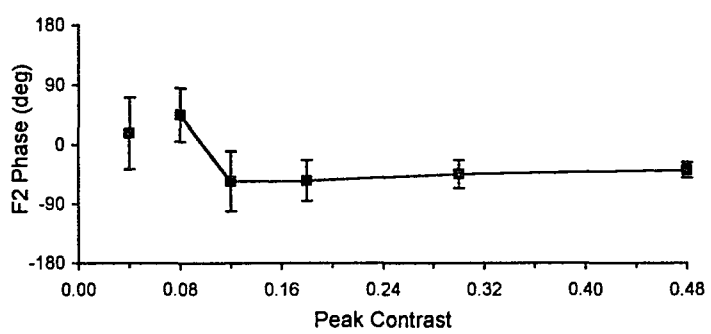
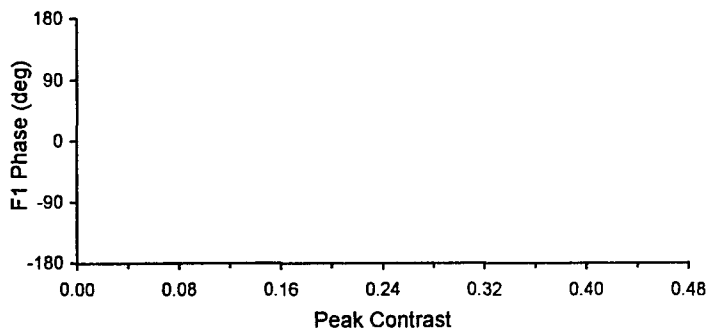
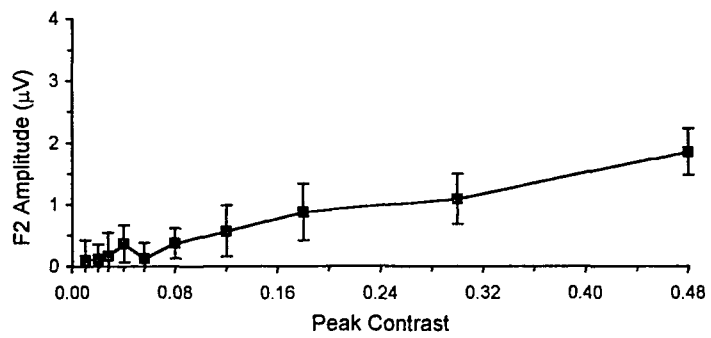
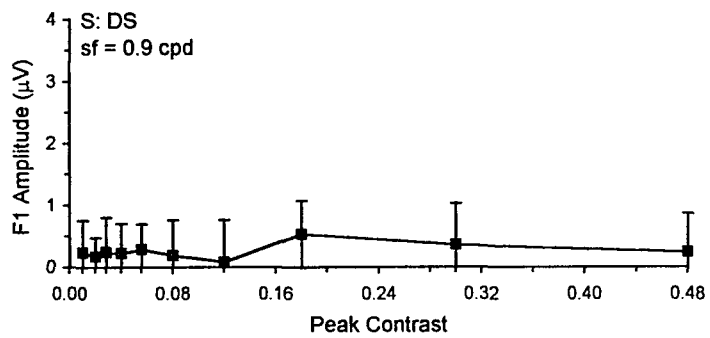


Figure 16c.

Figure 17.

The VEP contrast response function versus peak contrast (0.01 - 0.48).
Spatial frequency = 1.8 cpd. Temporal frequency = 6.27 Hz. Electrode placement: Oz-Cz.
Test distance: 57cm. Symbols and lines are used as in Figure 16. 17a. MC, 17b. JC, 17c.
DS.

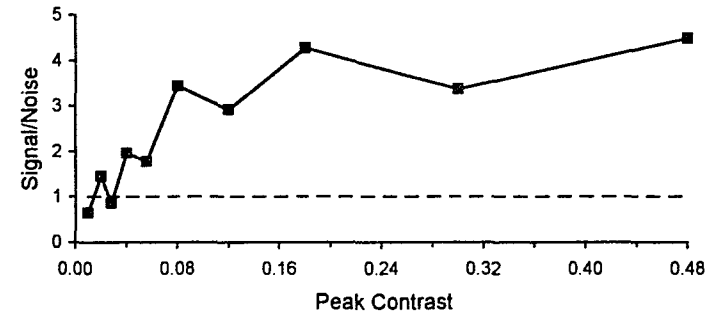
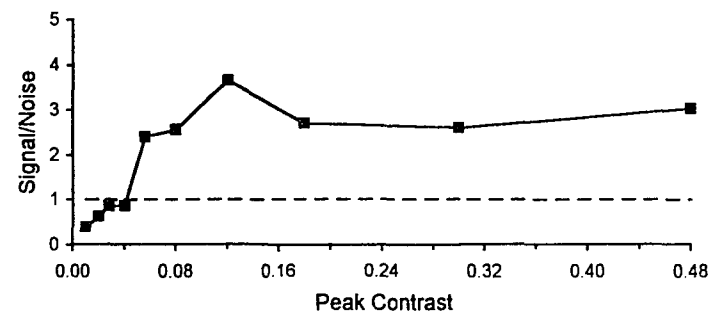
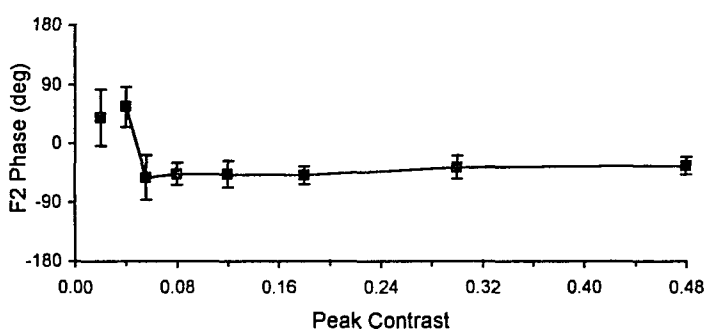
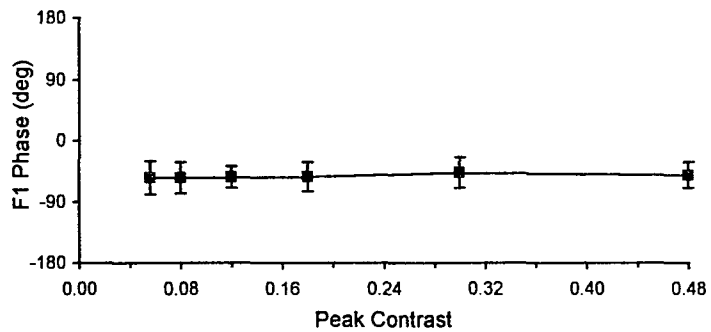
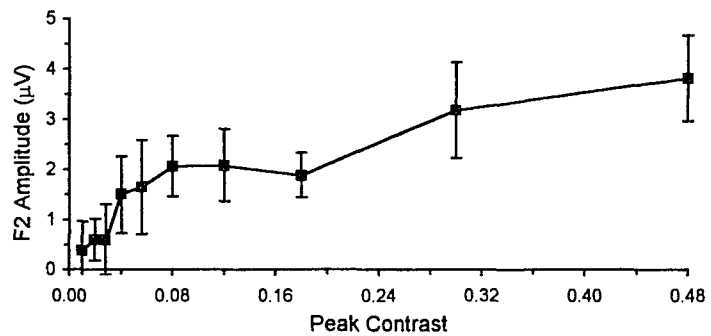
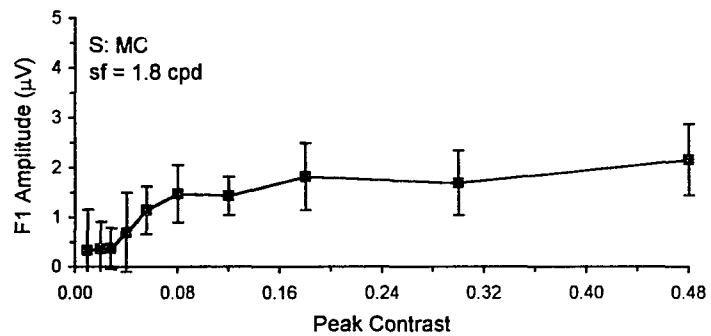


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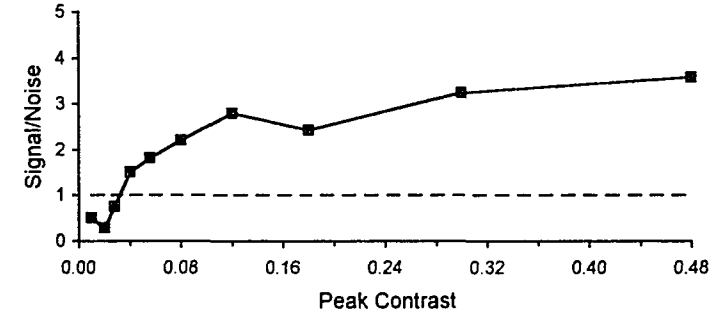
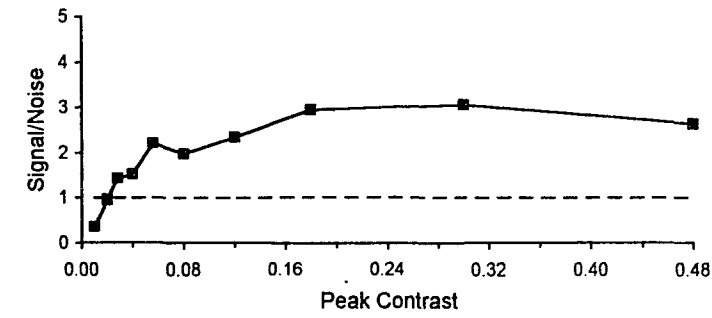
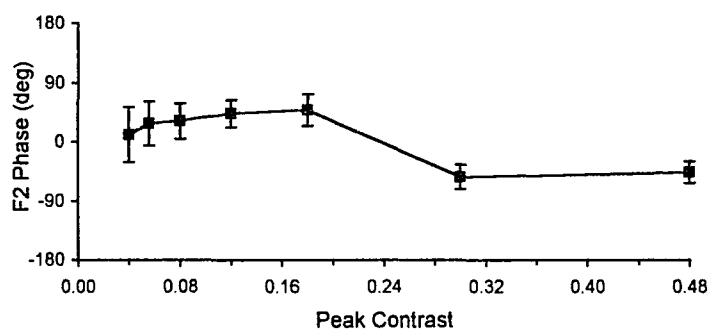
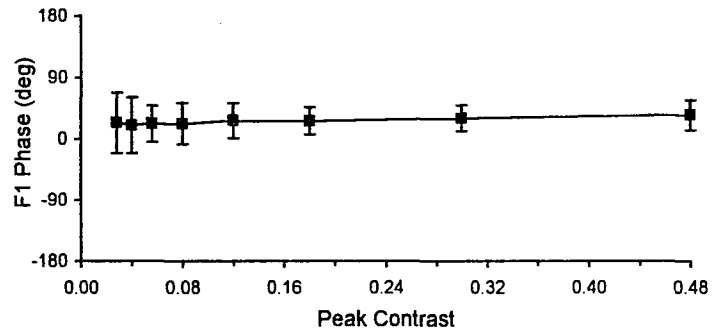
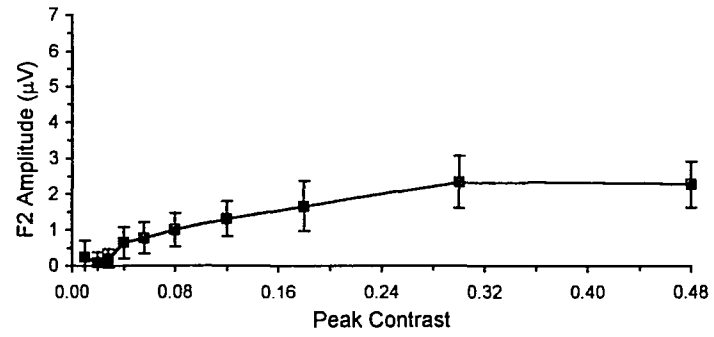
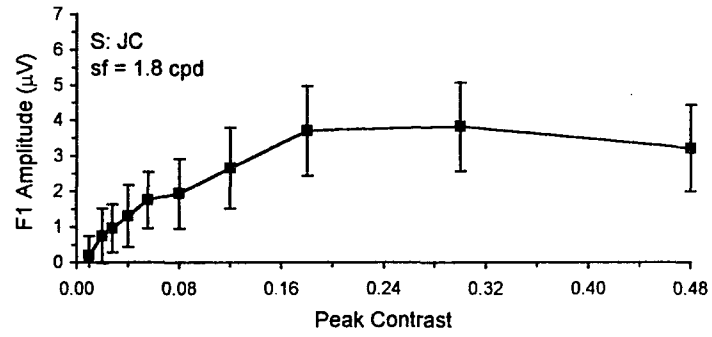


Figure 17b.

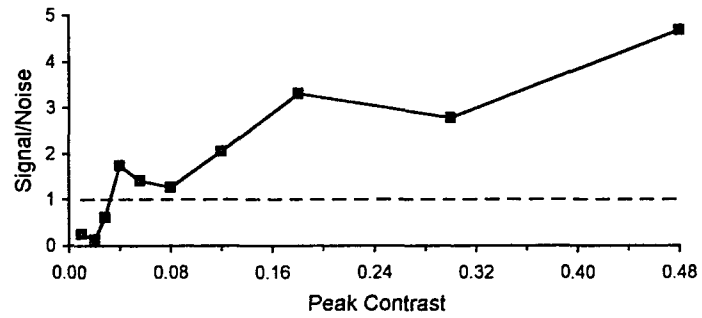
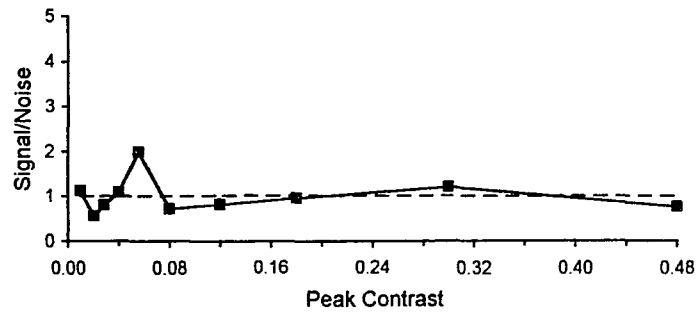
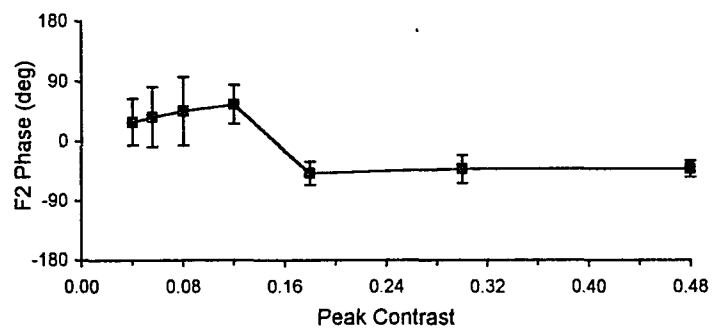
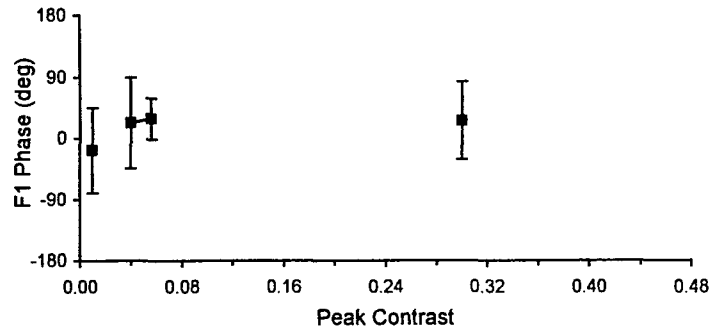
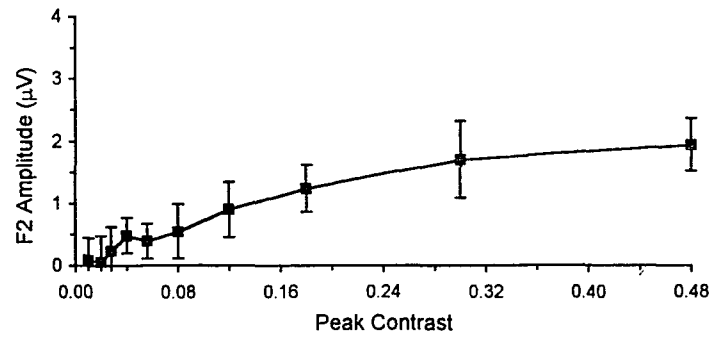
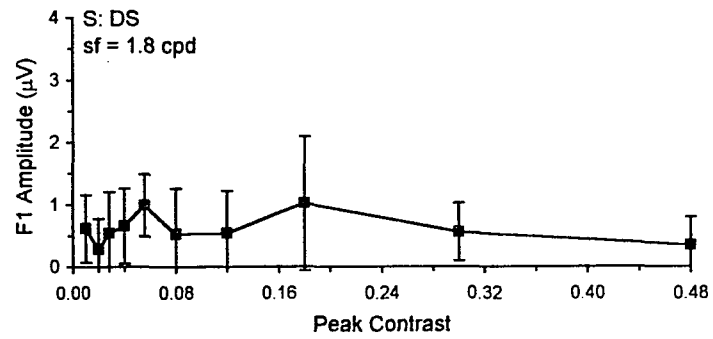


Figure 17c.

Figure 18.

The VEP contrast response function versus peak contrast (0.01 - 0.48).
Spatial frequency = 3.6 cpd. Temporal frequency = 6.27 Hz. Electrode placement: Oz-Cz.
Test distance: 57cm. Symbols and lines are used as in Figure 16. 18a. MC, 18b. JC, 18c.
DS.

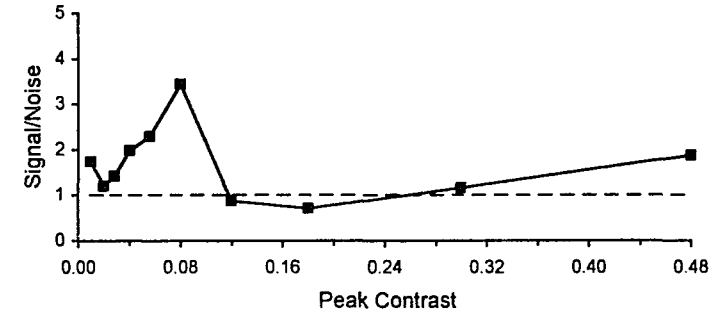
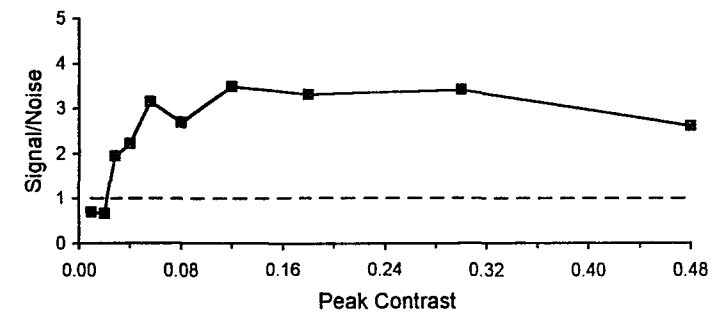
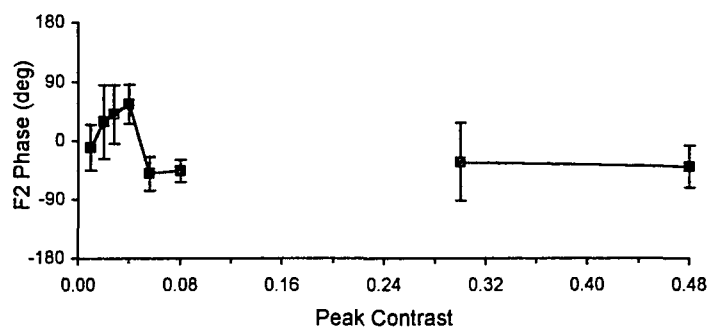
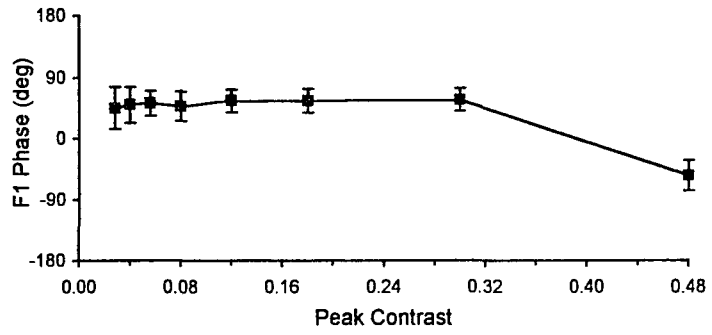
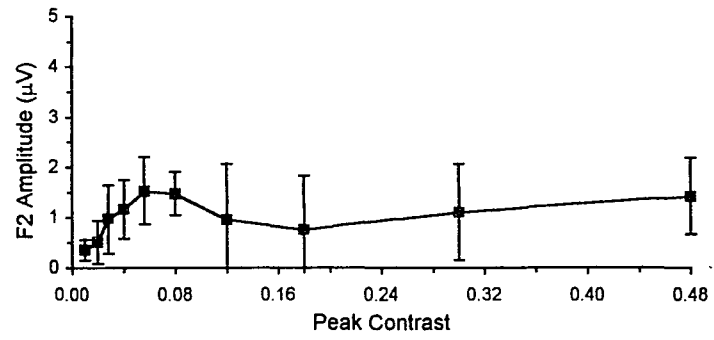
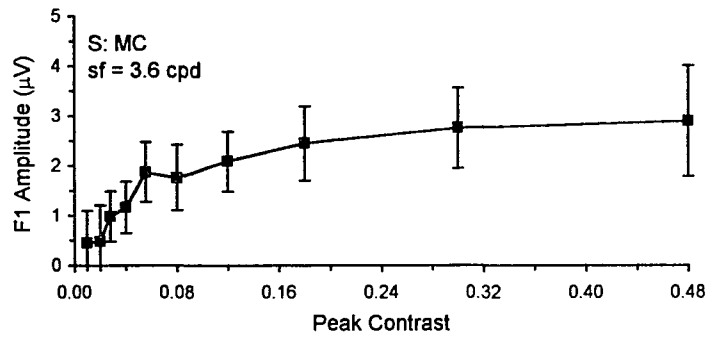


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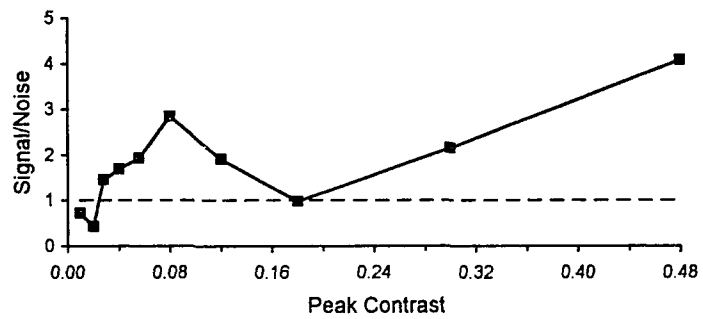
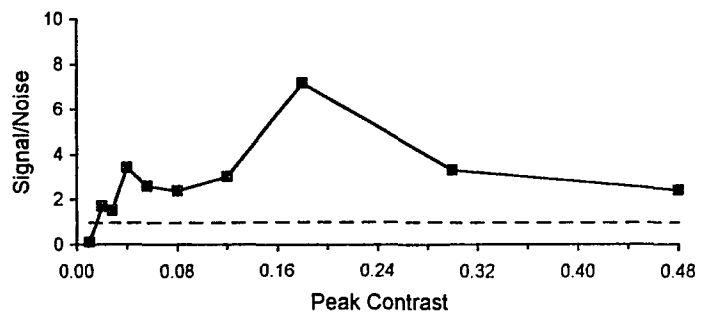
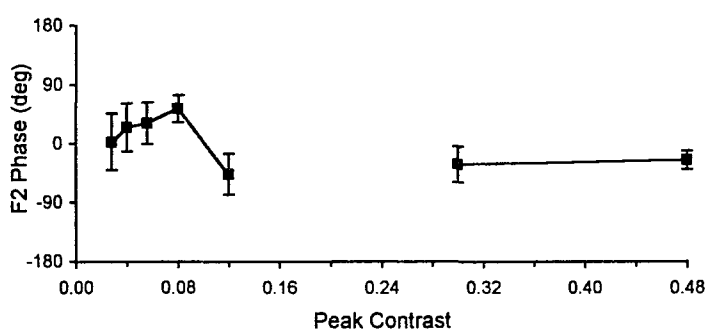
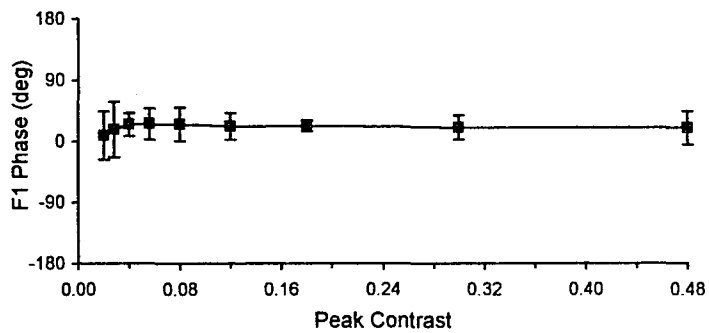
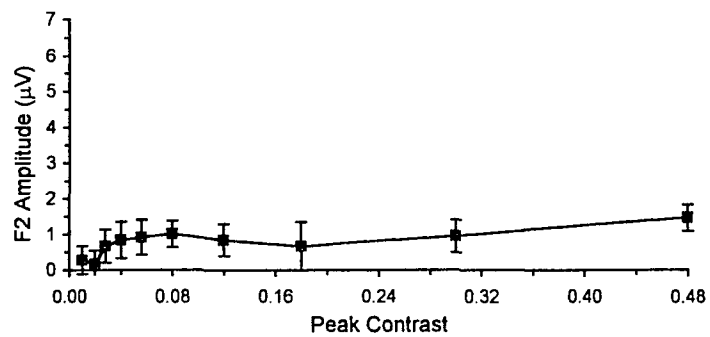
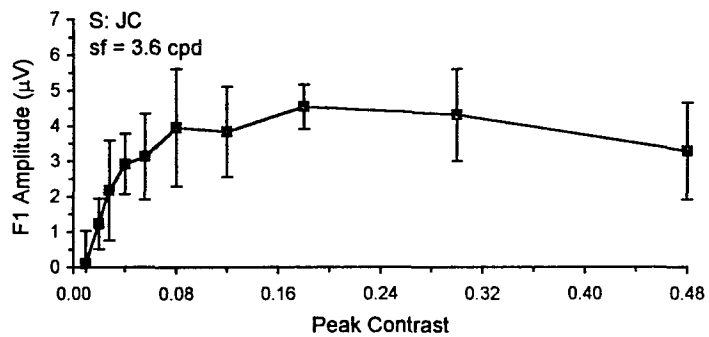


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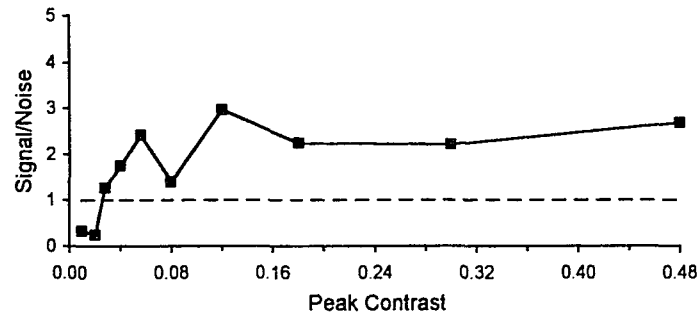
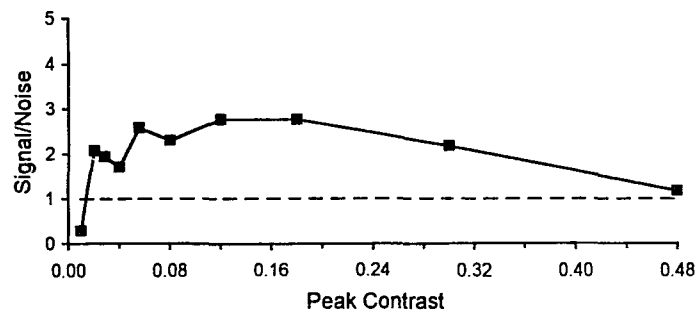
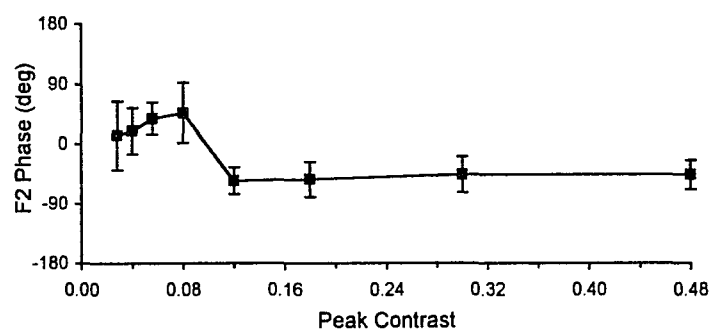
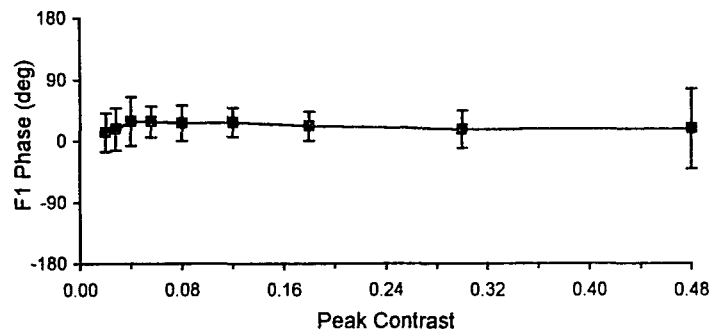
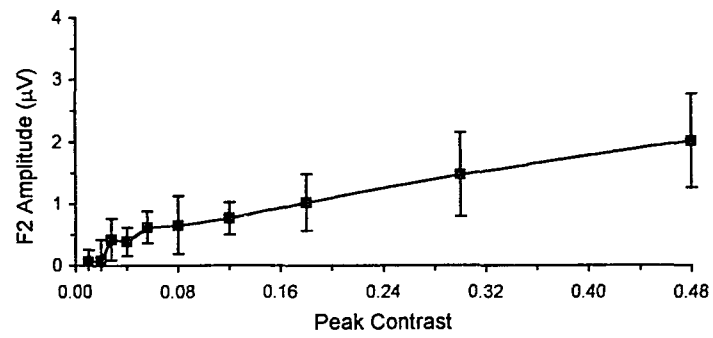
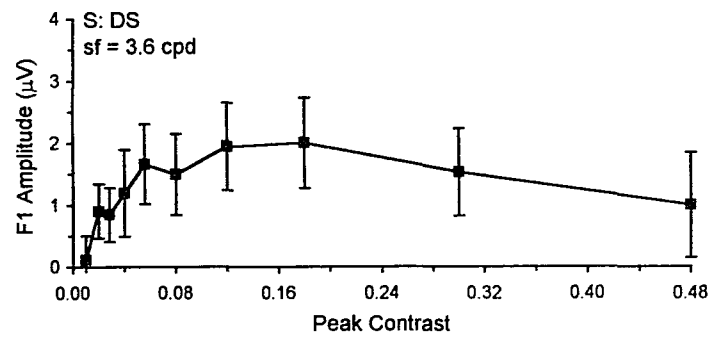


Figure 18c.

Figure 19.

The VEP contrast response function versus peak contrast (0.01 - 0.48).
Spatial frequency = 5.0 cpd. Temporal frequency = 6.27 Hz. Electrode placement: Oz-Cz.
Test distance: 57cm. Symbols and lines are used as in Figure 16. 19a. MC, 19b. JC, 19c.
DS.

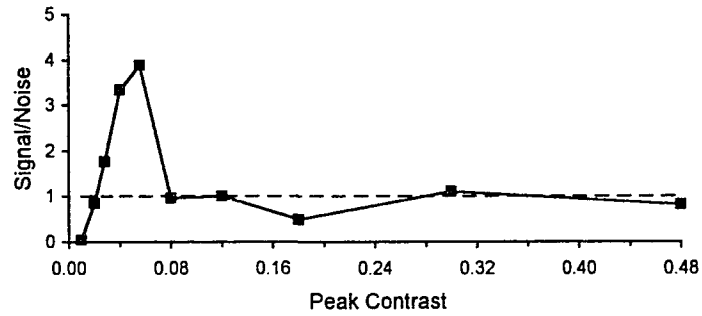
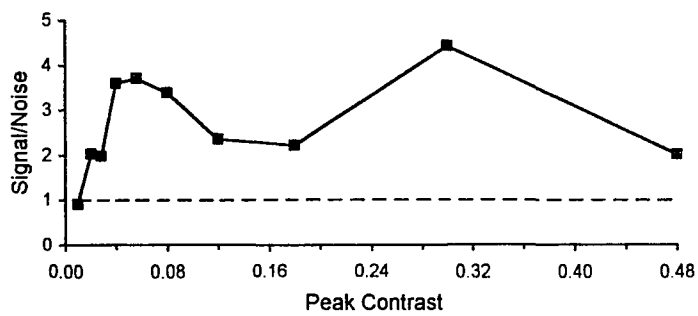
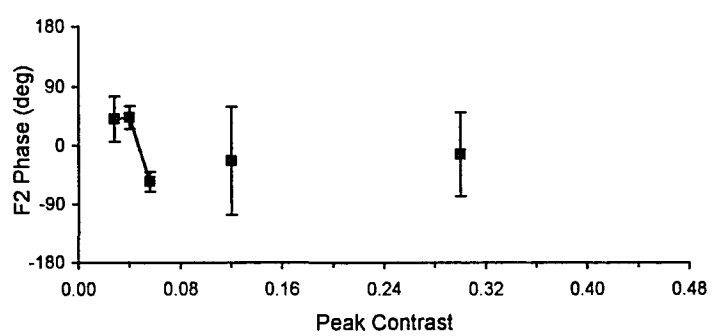
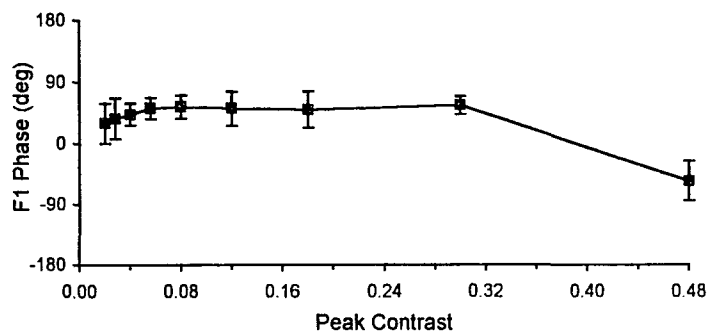
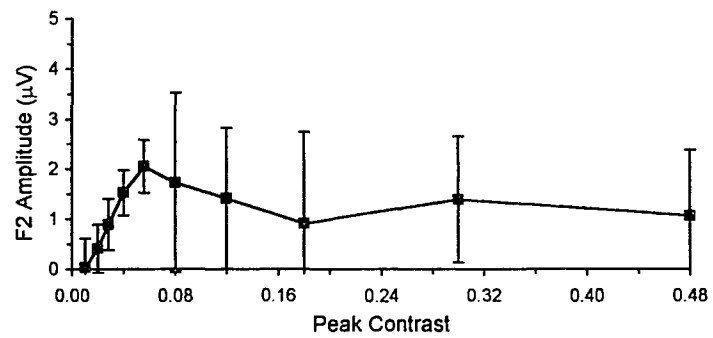
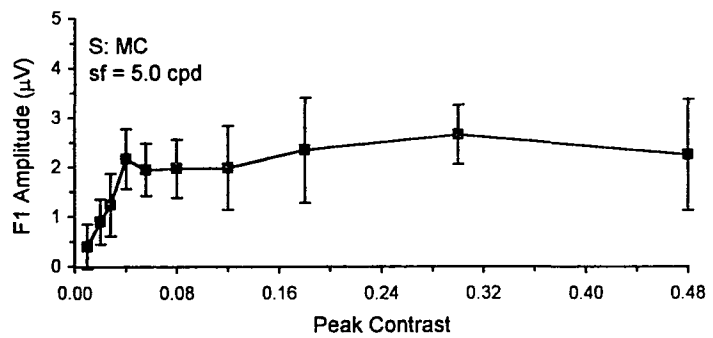


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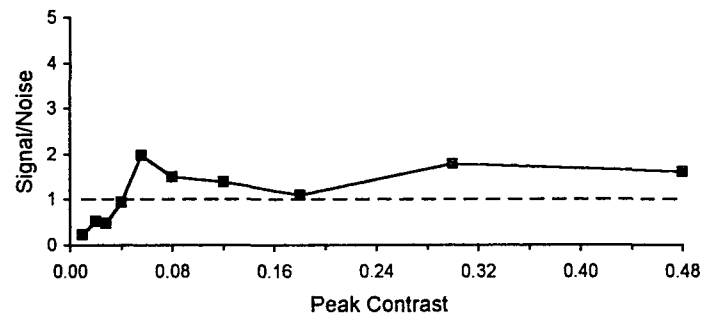
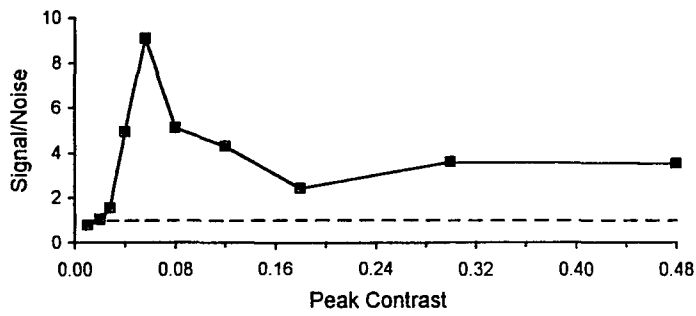
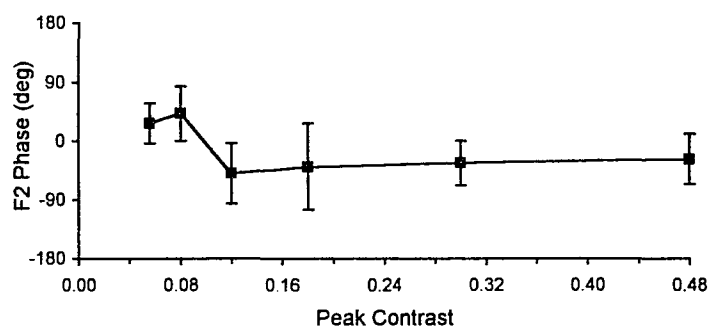
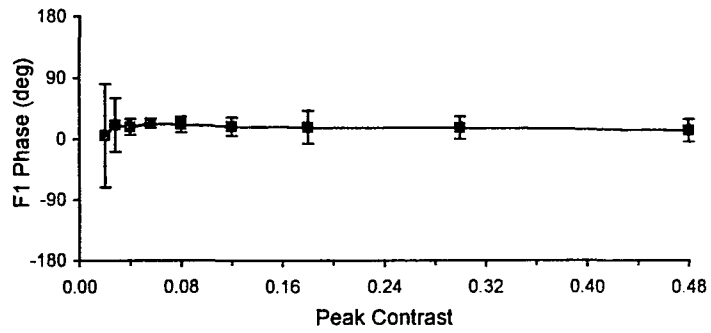
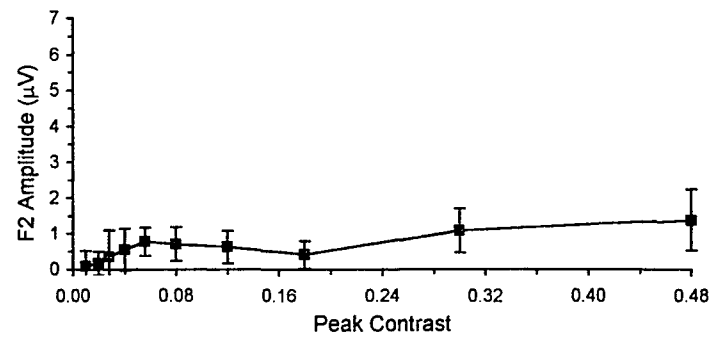
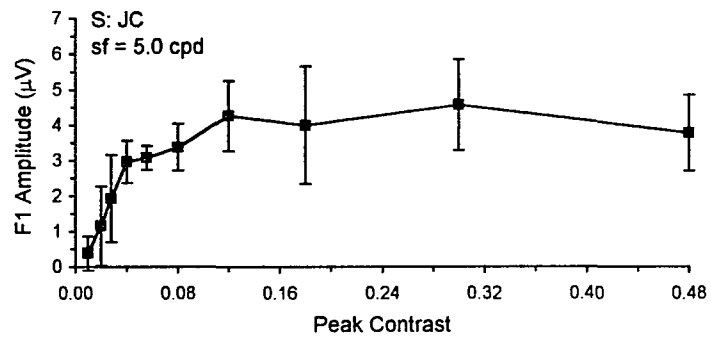


Figure 19b.

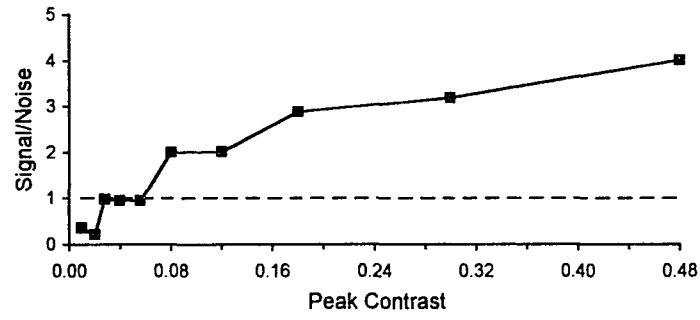
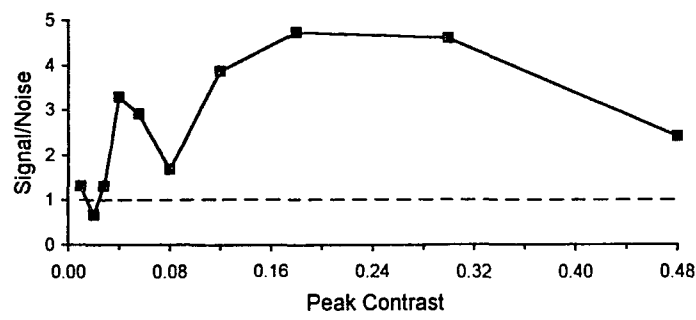
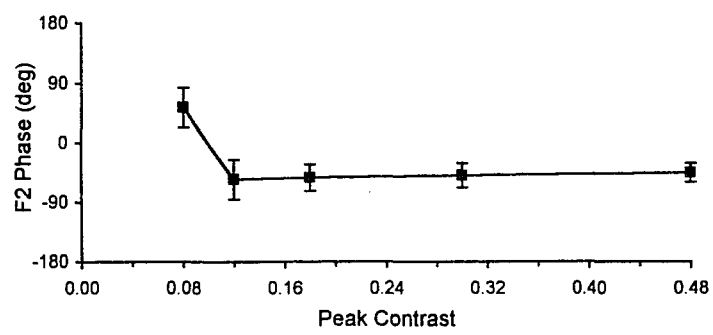
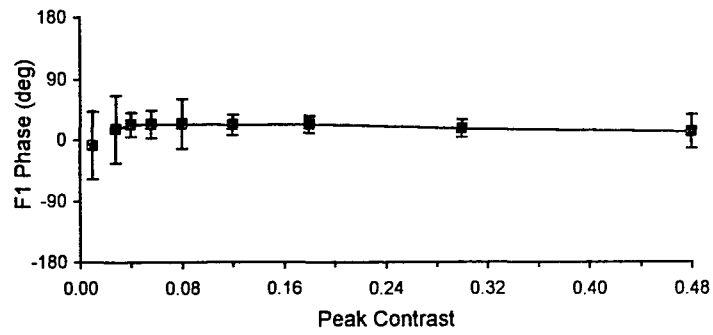
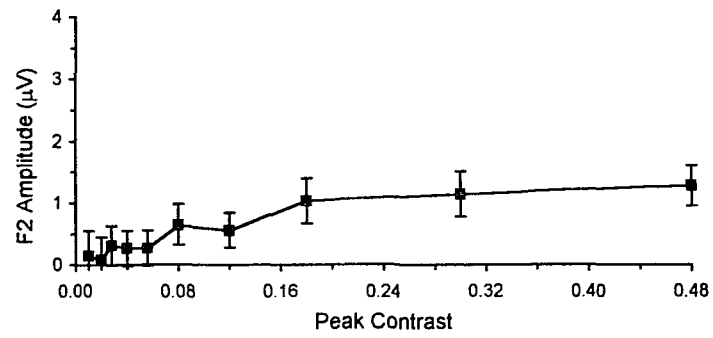
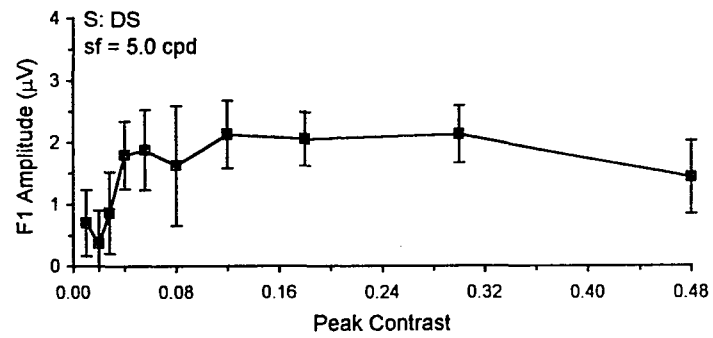


Figure 19c.

Figure 20.

The VEP contrast response function versus peak contrast (0.01 - 0.48).
Spatial frequency = 7.3 cpd. Temporal frequency = 6.27 Hz. Electrode placement: Oz-Cz.
Test distance: 57cm. Symbols and lines are used as in Figure 16. 20a. MC, 20b. JC, 20c.
DS.

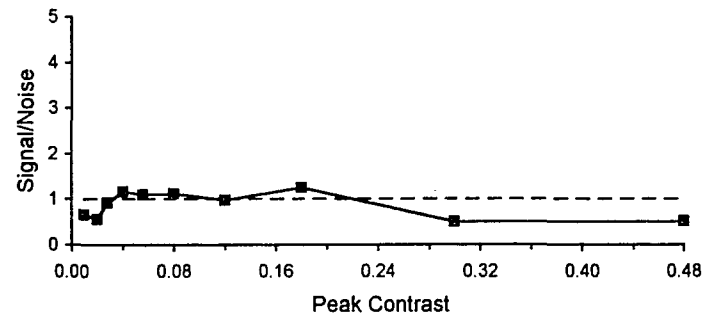
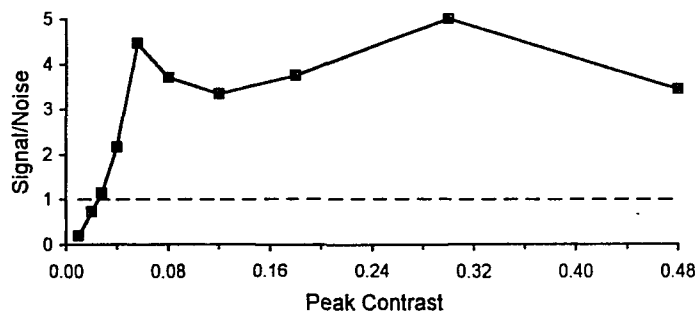
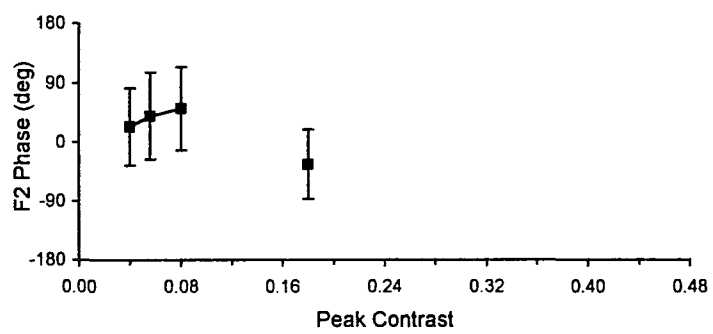
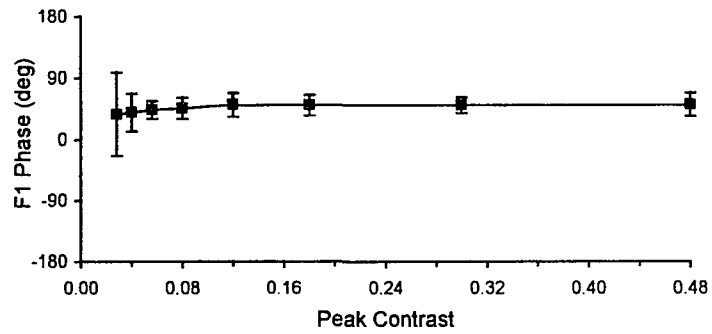
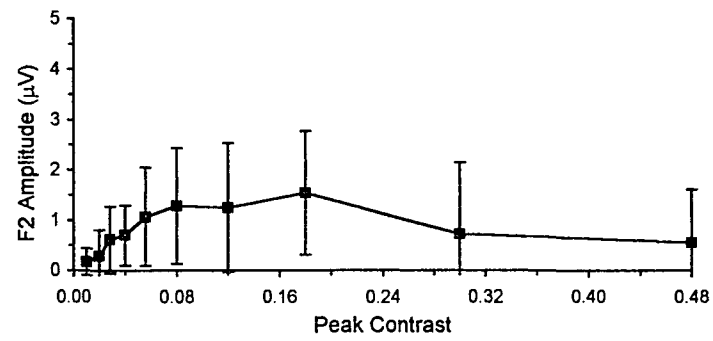
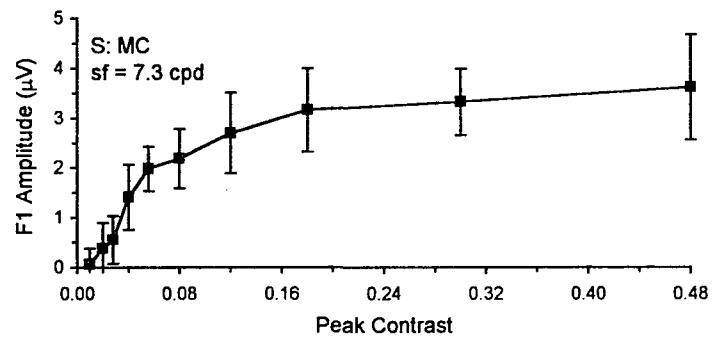


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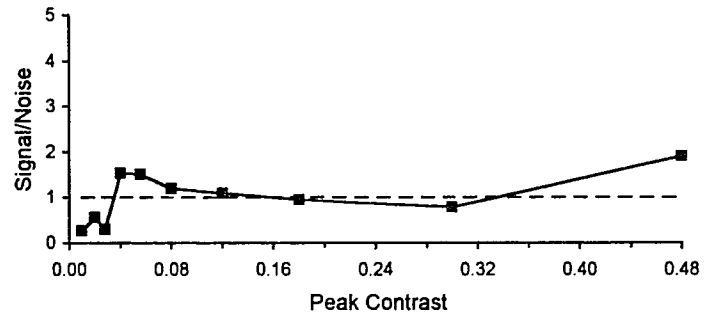
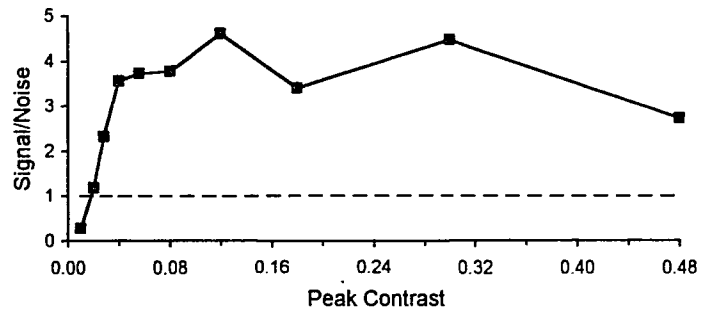
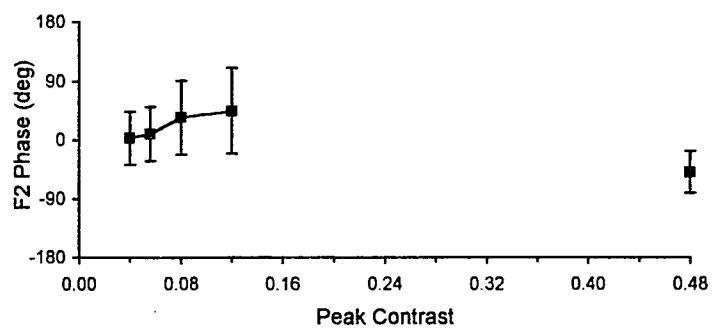
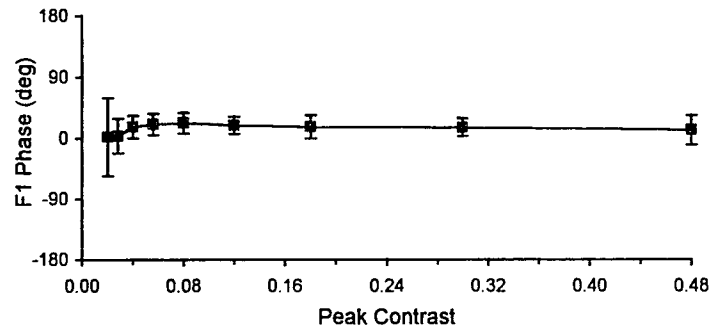
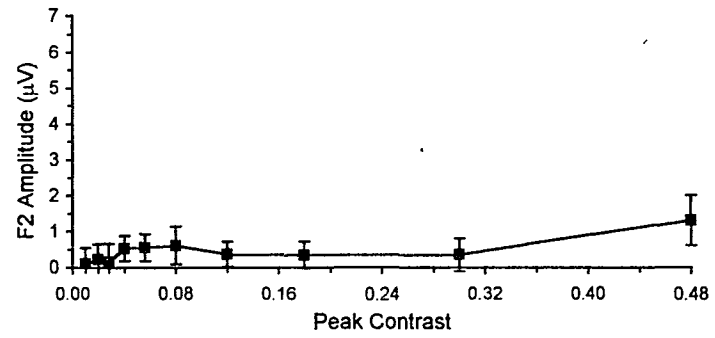
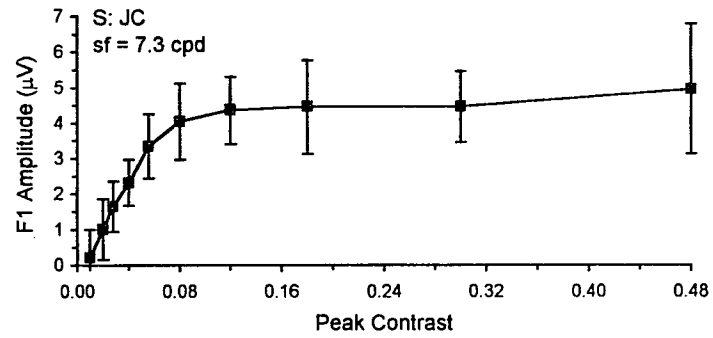


Figure 20b.

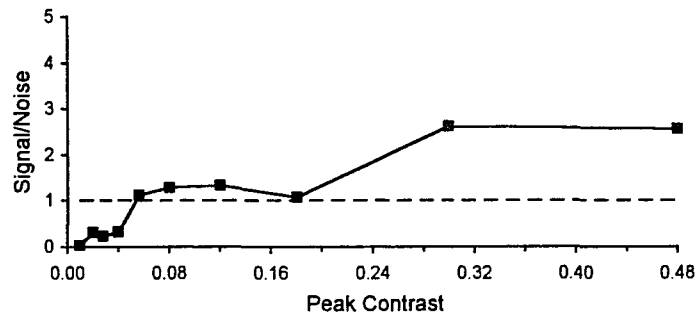
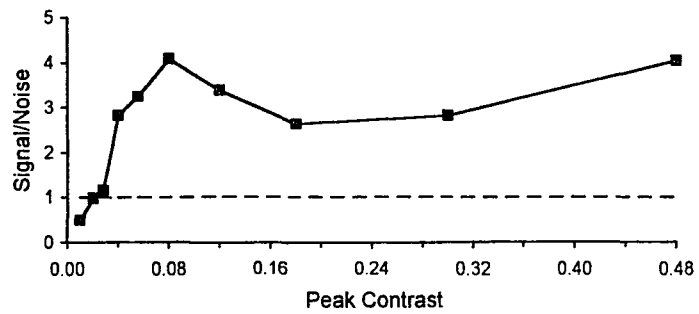
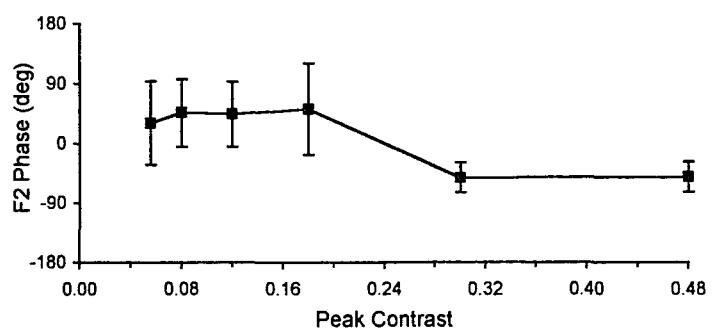
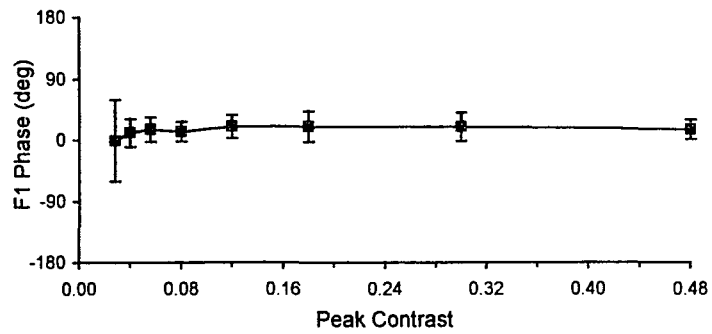
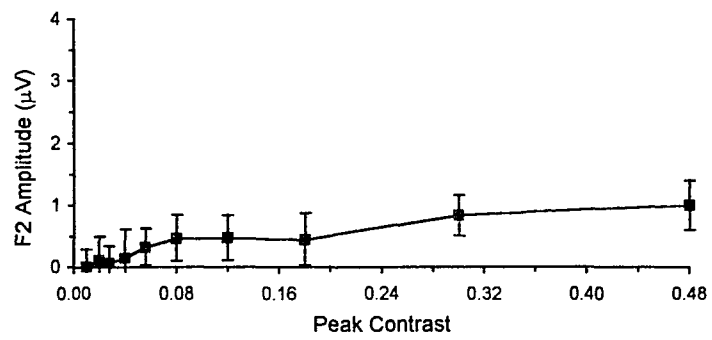
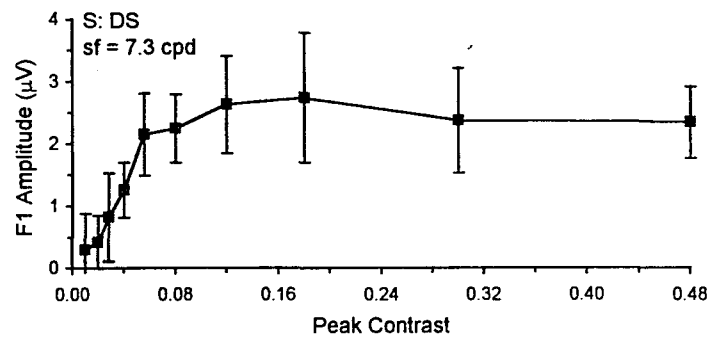


Figure 20c.

Figure 21.

The VEP contrast response function versus peak contrast (0.01 - 0.48).
Test distance: 114 cm. Temporal frequency = 6.27 Hz. Electrode placement: Oz-Cz.
Symbols and lines are used as in Figure 16. Subject: JC. 21a. 7.3 cpd, 21b. 10.0 cpd, 21c.
14.6 cpd.

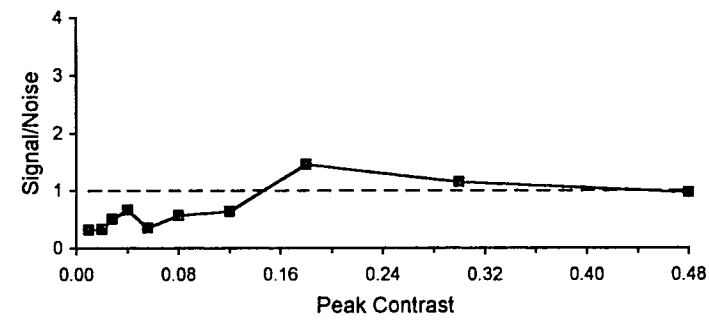
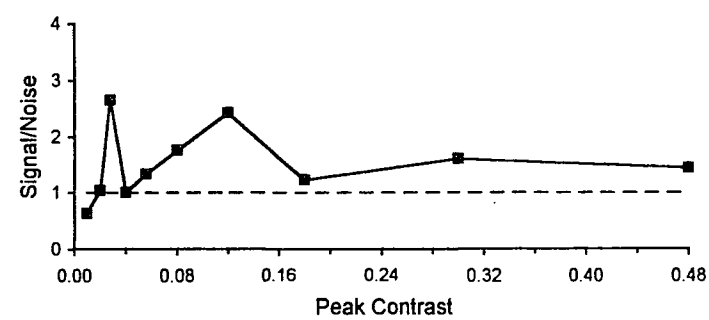
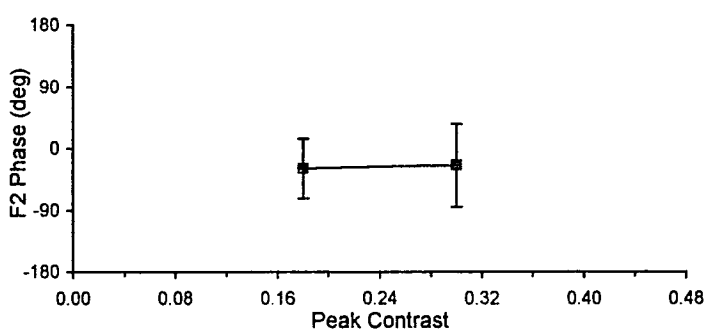
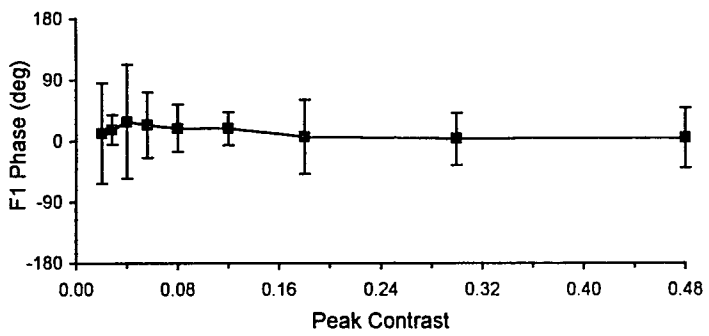
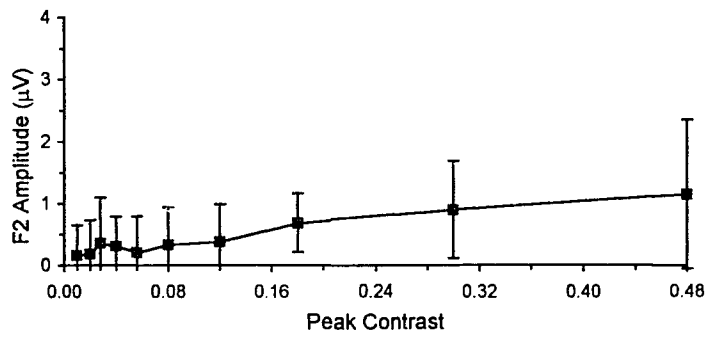
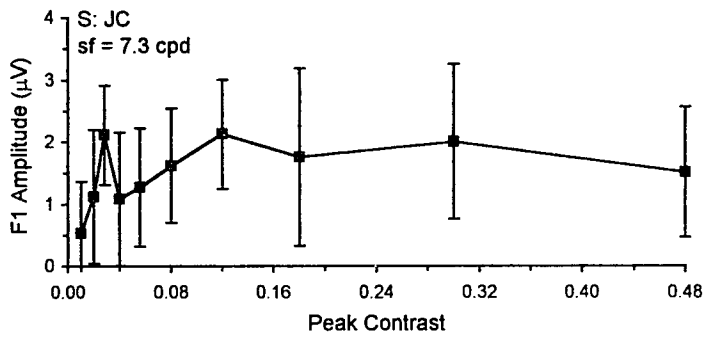


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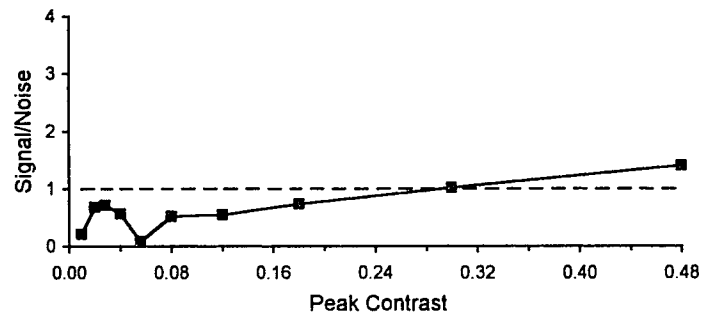
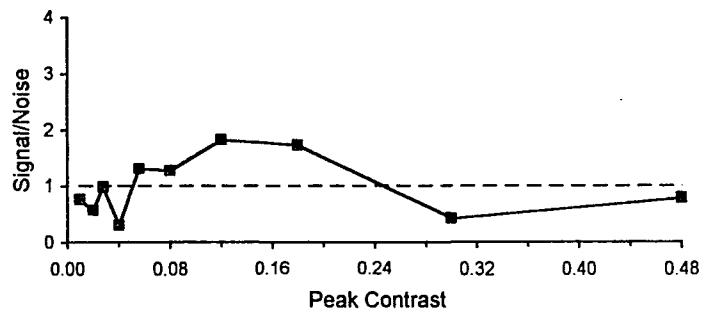
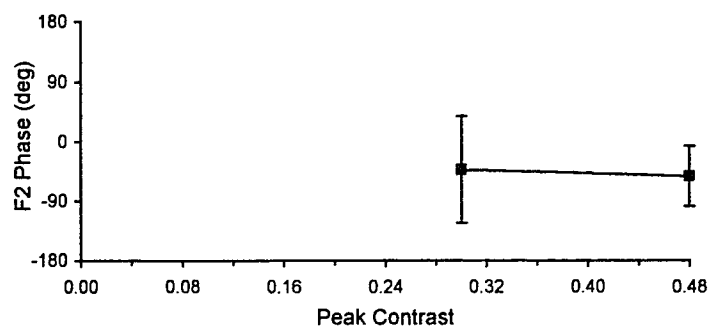
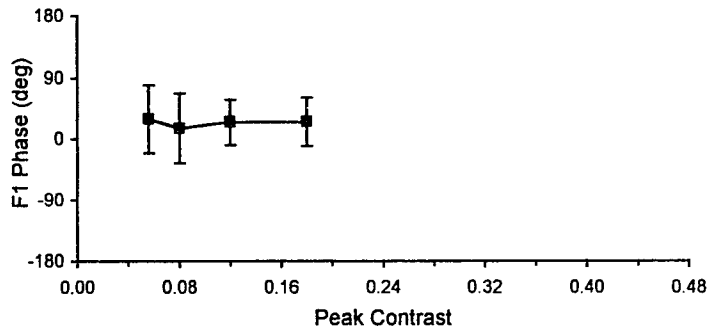
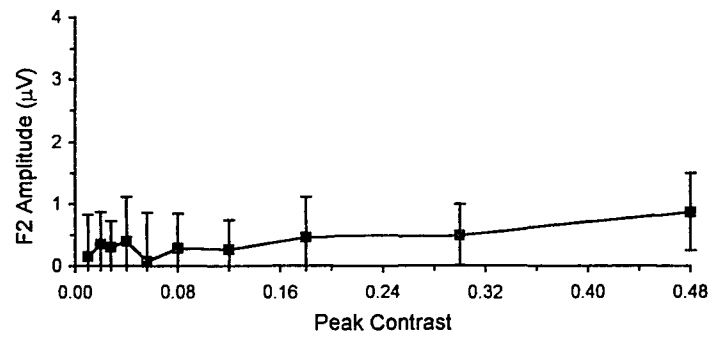
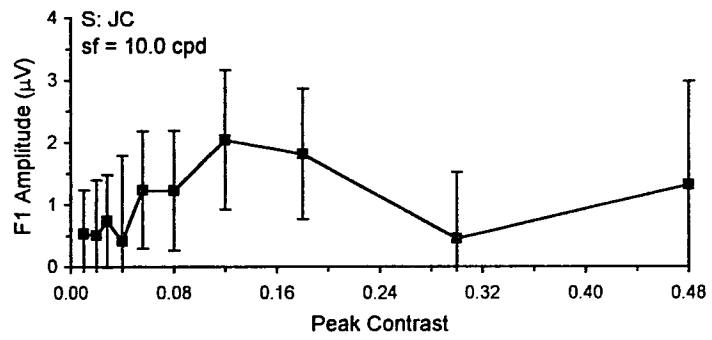


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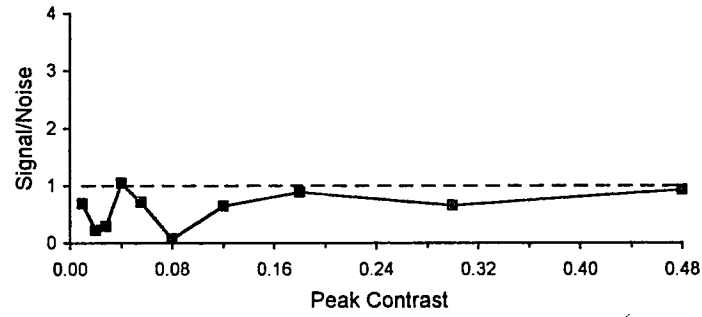
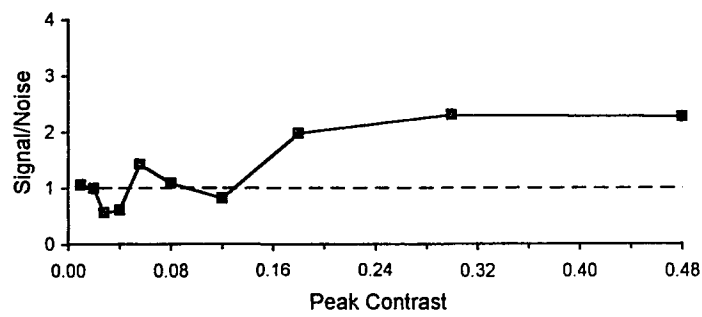
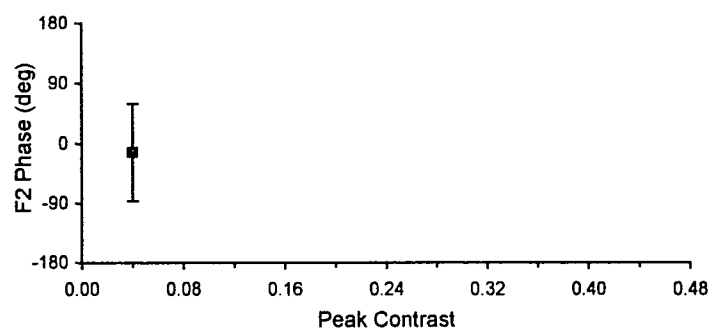
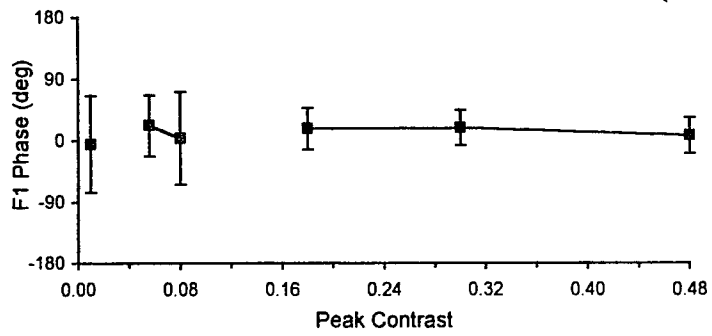
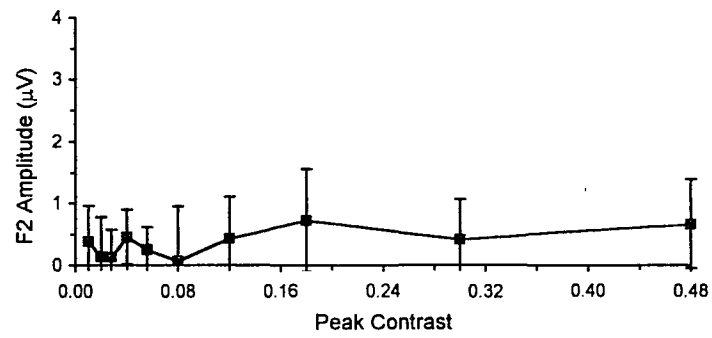
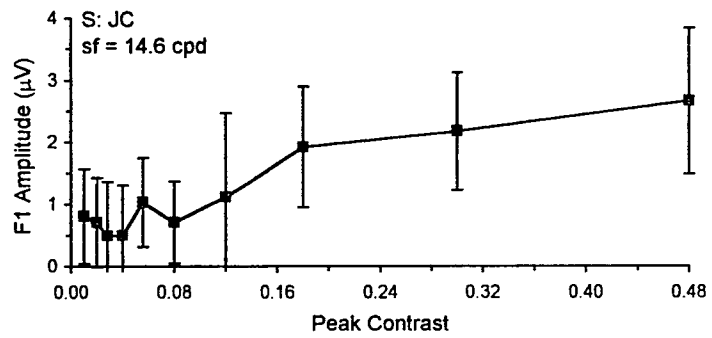
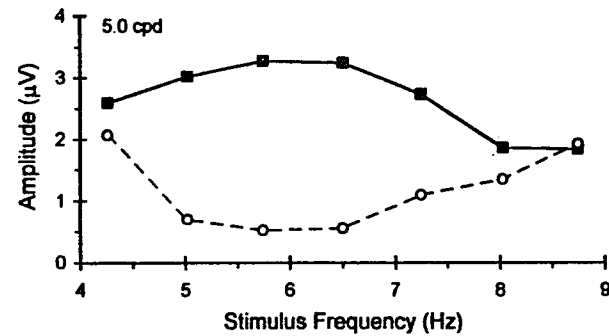
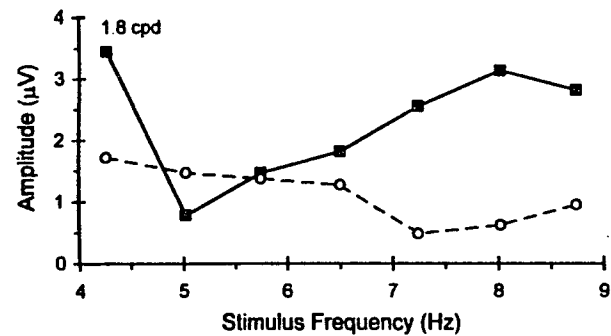
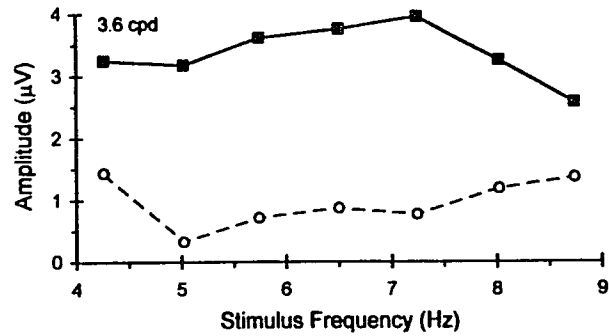
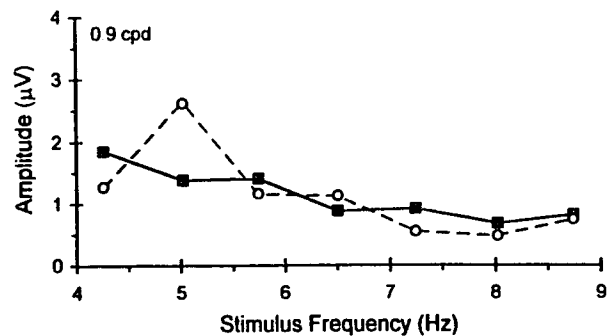


Figure 21c.

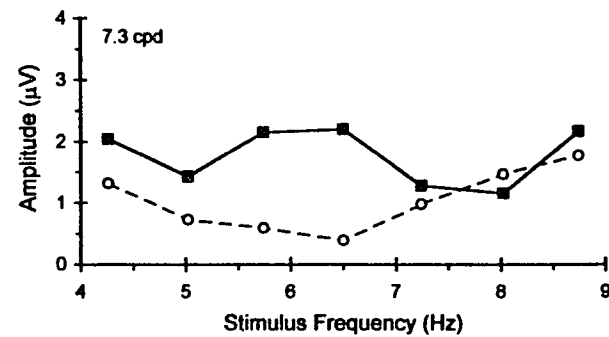
Figure 22.

VEP response amplitude as a function of stimulus frequency (4.26 - 8.74 Hz). Peak contrast = 0.15. Test distance: 57cm. Electrode placement: Oz-Cz. The fundamental (F1) component: filled symbols; second harmonic (F2): open symbols. Subject: JC.



S: JC
 —■— F1
 -○- F2
 peak contrast = 15%

Figure 22.



For observer JC (Figure 23b), the VEP-F1 function derived from MM gain was the closest match to the pattern detection function. This was based on good agreement between the functions for spatial frequencies 3.6 cpd and above. None of the VEP-F1 functions matched the band-pass or low-pass shapes of the psychophysical functions exactly. Unlike MC's data, both the VEP and psychophysical functions are broadly tuned. Like MC's data, the VEP-F1 $S/N = 2$ derivation produced the poorest fitting function to the psychophysical curves. Derivations from F1 phase, amplitude, and $S/N = 1$ did equally well in comparison to the pattern detection curves. For flicker detection, the $S/N = 1$ was the best VEP match to the psychophysics. Again, the VEP fails to describe the two lowest spatial frequencies (0.9 and 1.8 cpd). The discrepancy between the psychophysical and VEP data is now larger because of the increased psychophysical sensitivity to the lower spatial frequencies under the flicker detection condition. This mismatch is larger still when we look at the data from observer DS in Figure 23c. Although there are no derivations from the F1 component (except MM gain) for 0.9 cpd, the downward trend of the VEP functions at low spatial frequencies is clear. The pattern detection curve is not well matched by any of the VEP derivations except MM gain; and then only for 5.0 and 7.3 cpd. Flicker detection seemed to be matched best by the Rayleigh phase function but only for 3.6, 5.0, and 7.3 cpd. The F1 responses from DS were the smallest of all three subjects and this is evident from the missing data points; particularly for $S/N = 2$.

Derivations from the VEP-F2 component are compared with the psychophysical CSF in Figure 24. For MC, the F2 MM gain derivation matched behavioral sensitivities for 3.6, 5.0, and 7.3 cpd (Figure 24a). This was slightly better than the fit from $S/N = 1$ or any of the F1 comparisons. These VEP-F2 derived functions are not as narrowly tuned as the F1 functions, but still do not match the psychophysical curves. $S/N = 2$, once again, gave the poorest fit to the psychophysical CSF. The flicker detection function is matched by all five derivations for 5.0 and 7.3 cpd. But only the $S/N = 1$ curve follows

the downward trend in sensitivity for the three higher spatial frequencies: 3.6, 5.0, and 7.3 cpd. In Figure 24b we see the VEP-F2 derivations and pattern and flicker functions for observer JC. Here the VEP derivations fail to match the psychophysics at more than two consecutive data points with one exception. The $S/N = 2$ curve matches the shape, but not the absolute value, of the pattern detection CSF at 0.9, 1.8, and 3.6 cpd. A re-examination of the contrasts values that were obtained by meeting the $S/N = 2$ criterion showed that they were much greater than the contrasts derived from the other measures. In other words, the sensitivities derived from these higher contrast values were not threshold measurements at all, but from the suprathreshold range.

There was only one VEP versus psychophysical CSF comparison, for observer DS, which matched the entire spatial frequency range. Like the $S/N = 2$ match to pattern detection for observer JC described above, the contrast values (ranging from 0.11 to 0.27) that were obtained by meeting this criterion were above the threshold range. This is illustrated in Figures 24c. The VEP-F2 function derived from the $0.75 \mu\text{V}$ criterion matches the pattern detection curve in shape ($r^2 = 0.99$), but like JC's data, not the absolute value. A constant (1.25 log units) was added to each data point to translate the curve along the ordinate axis. If the psychophysical sensitivities measured represented absolute threshold, then an increase of one log unit in VEP derived sensitivity would require 100 times the amount of data currently collected. This would be equal to 300 minutes of data collection at each of 10 contrast levels or fifty hours per experimental session! Close inspection of the curves shows that the MM gain function would also have matched the pattern detection curve. There was no consistent match to the flicker detection curve except by the MM gain or .75 Amp functions at 5.0 and 7.3 cpd.

The best-fitting VEP derived measures to the psychophysical CSFs for each observer are shown in the final figures. In Figure 25, the pattern detection functions are fit by the F2 - MM gain for MC, the F1 - MM gain for JC, and the F2 - $.75 \mu\text{V}$ criterion amplitude for DS. It is clear that only at higher spatial frequencies do the functions

match for all three observers. The good agreement between the psychophysical CSF and VEP curves from observer JC at 10.0 and 14.6 cpd suggests strongly that extending the spatial frequency range for MC and DS would have produced similar results. In Figure 26, the flicker detection functions are fit by the F2 - $S/N = 1$ for observer MC, F1 - $S/N = 1.0$ for JC, and F1 - Rayleigh phase for DS. Again, it is clear that at only the highest spatial frequencies is there a relationship between the VEP and psychophysical CSF. From Figures 25 and 26, we see that the best-fitting VEP functions included three from the F1 component: one from MM gain, one from the $S/N = 1$ ratio, and one from Rayleigh phase; and three from the F2 component: MM gain, $S/N = 1$, and .75 Amp. But there is no correspondence between F1 derived functions and the pattern detection curves or the F2 and flicker detection curves. For MC, both psychophysical functions are best-fit by F2 derived thresholds. The opposite is true for JC; both functions are best-fit by F1 derivations. For DS, there is an almost perfect correlation between the pattern CSF and the F2-.75 Amp derivation. The best-fit (albeit a poor one) to the flicker detection CSF for this observer was the F1-Rayl phase.

Figure 23.

Comparisons between the F1 response component and pattern (left) and flicker (right) detection contrast sensitivity functions. Psychophysical sensitivities (filled symbols) are plotted as functions of log spatial frequency. The five VEP derivations (open symbols) include: 0.75 μV criterion response (.75 Amp), Rayleigh phase coefficient (Rayl), Signal-to-Noise ratios of 1 and 2 ($S/N = 1$ and $S/N = 2$), and contrast gain derived from the Michaelis-Menten function (MMgain). 23a. MC, 23b. JC, 23c. DS.

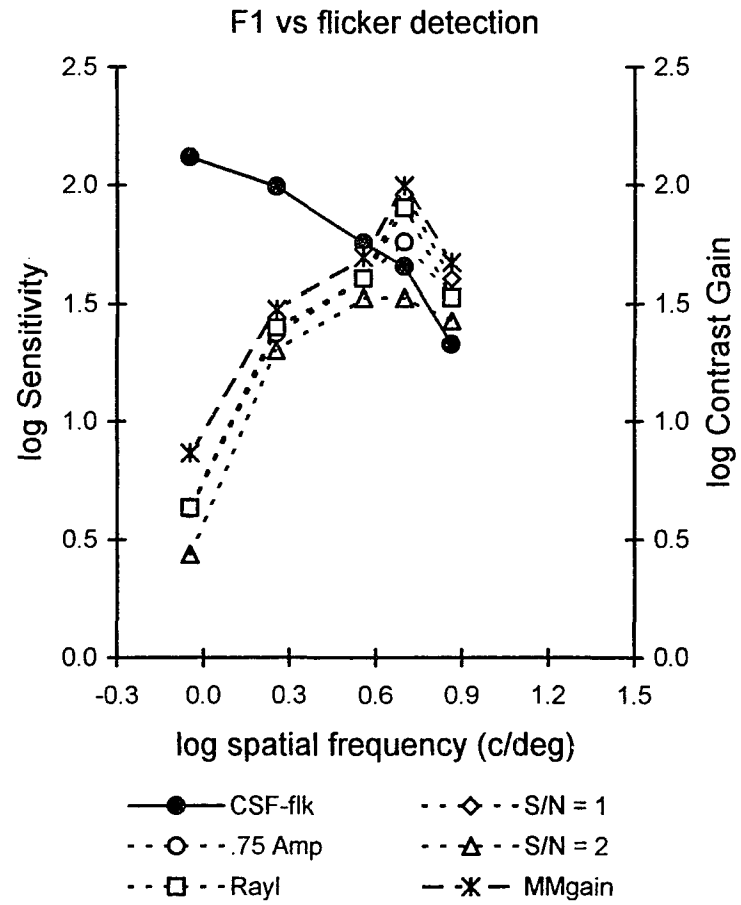
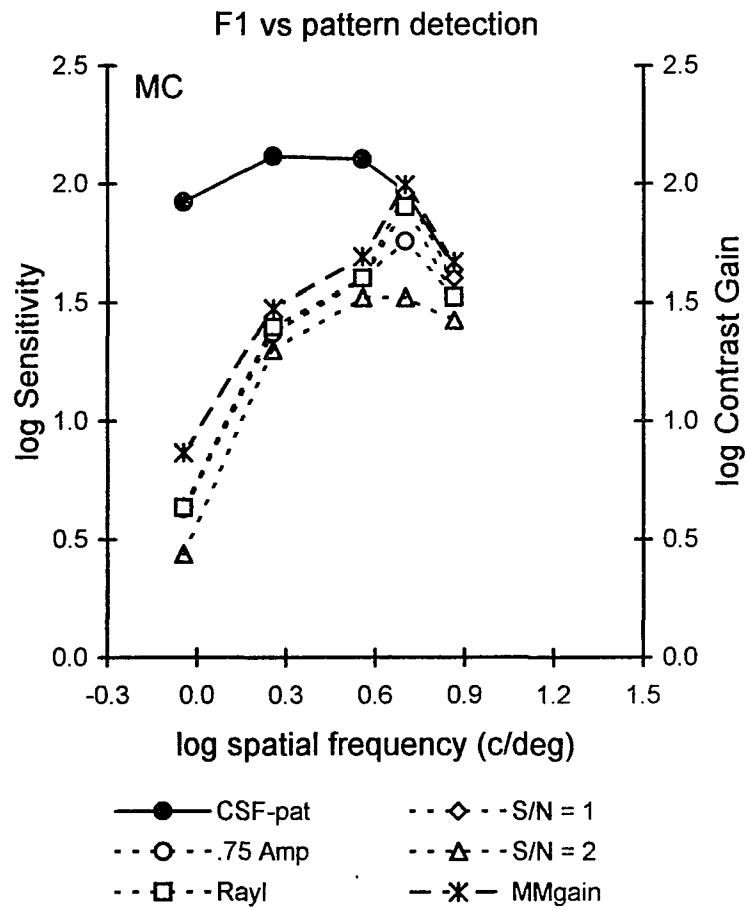


Figure 23a.

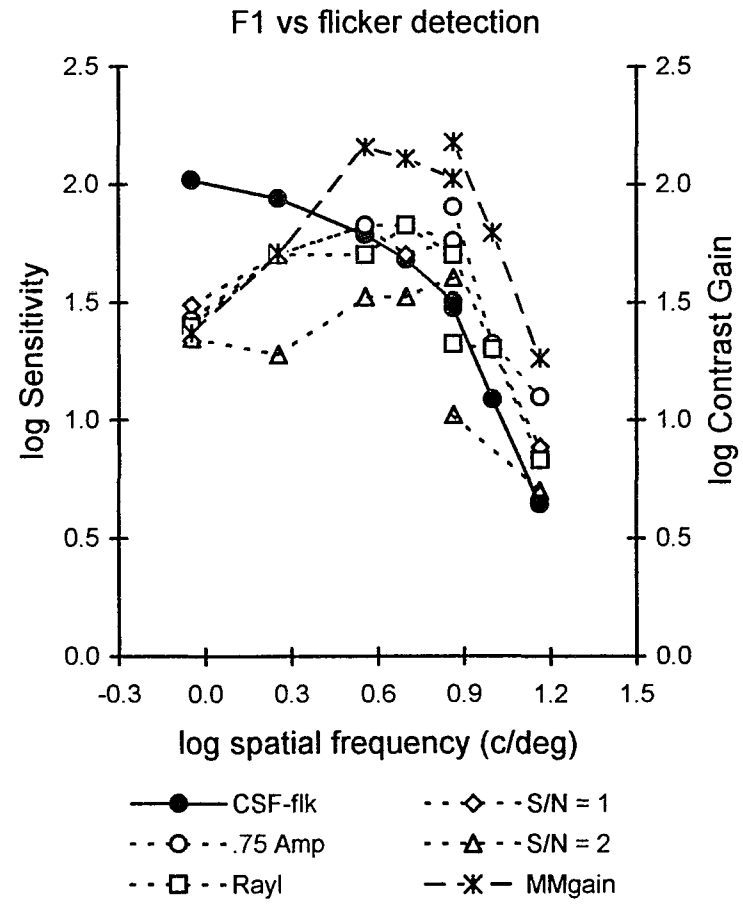
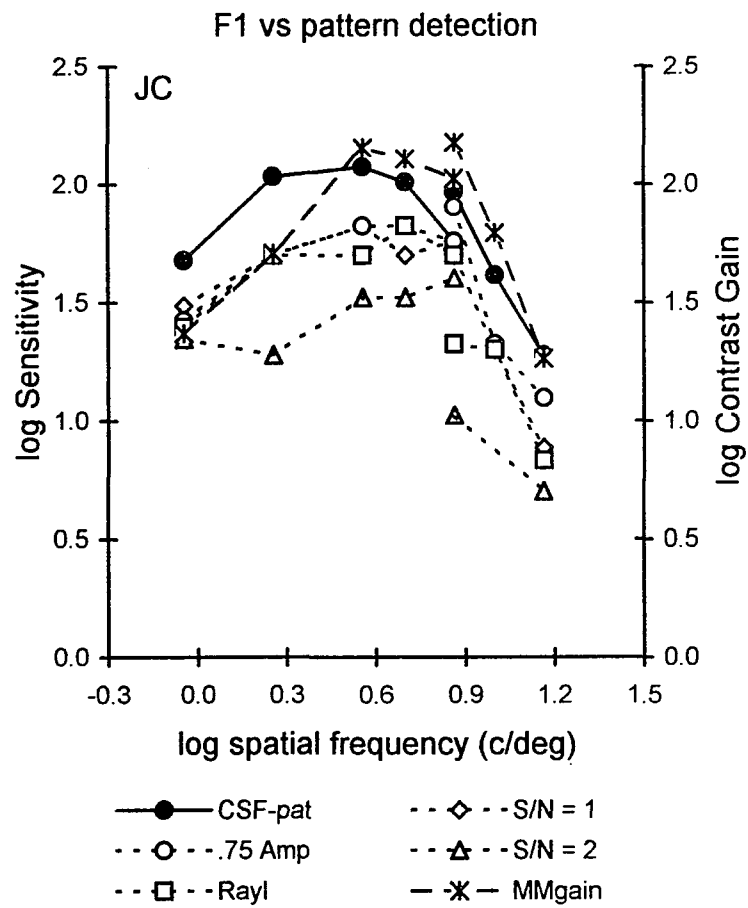


Figure 23b.

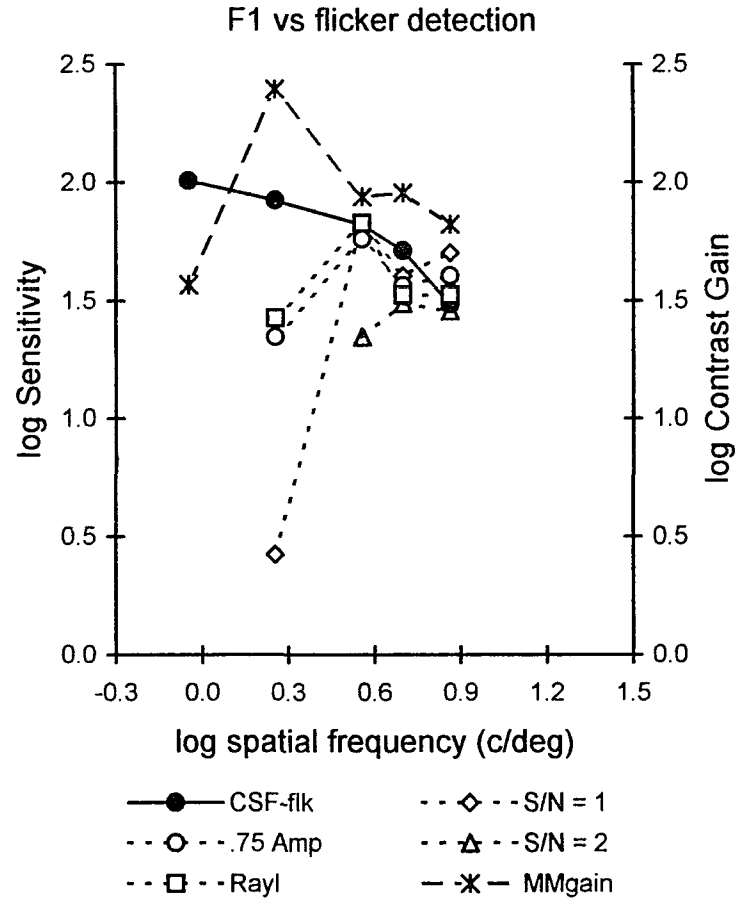
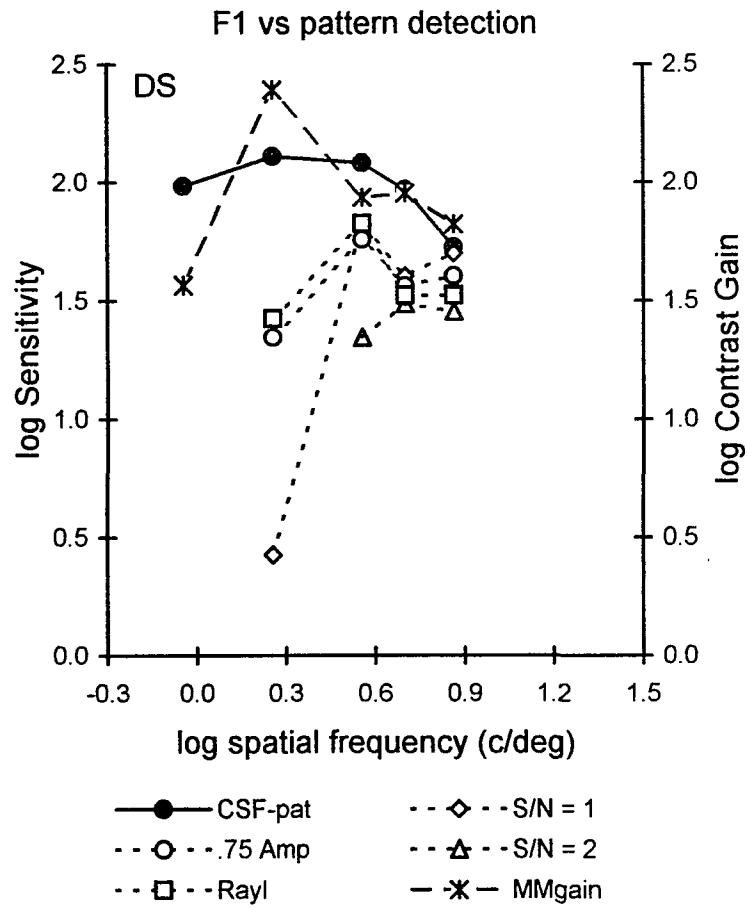


Figure 23c.

Figure 24.

Comparisons between the F2 response component and pattern (left) and flicker (right) detection contrast sensitivity functions. Psychophysical sensitivities (filled symbols) are plotted as functions of log spatial frequency. The five VEP derivations (open symbols) are as described in Figure 23. 24a. MC, 24b. JC, 24c. DS.

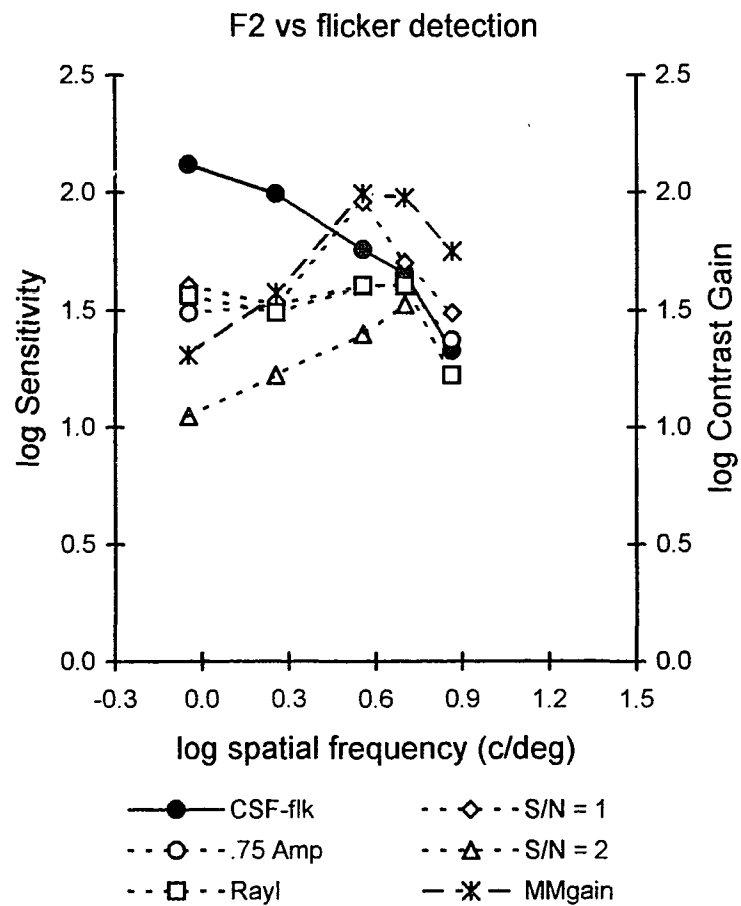
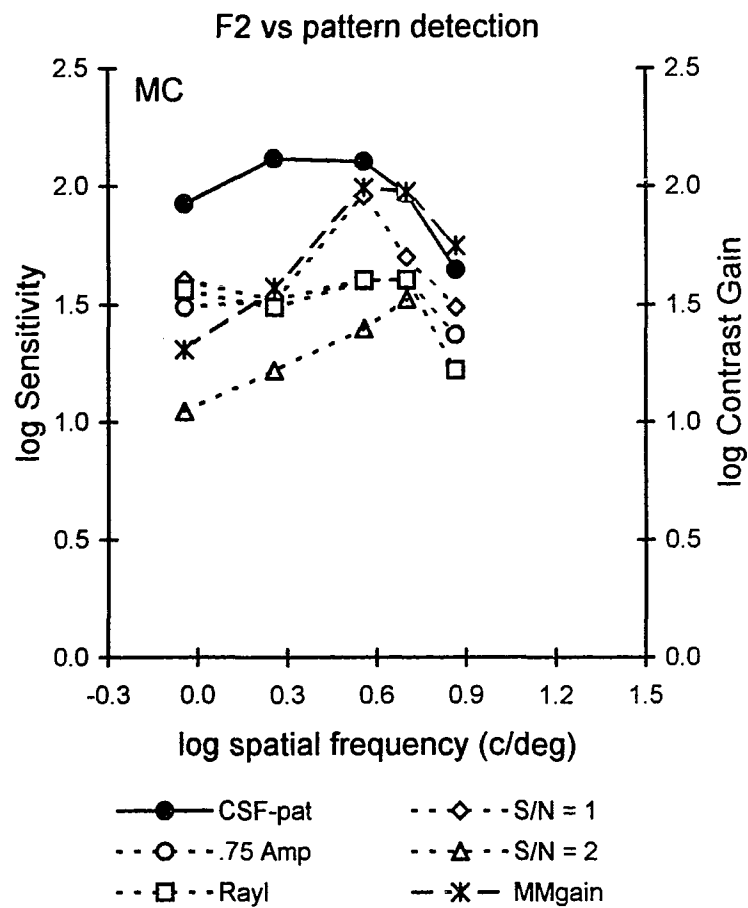


Figure 24a.

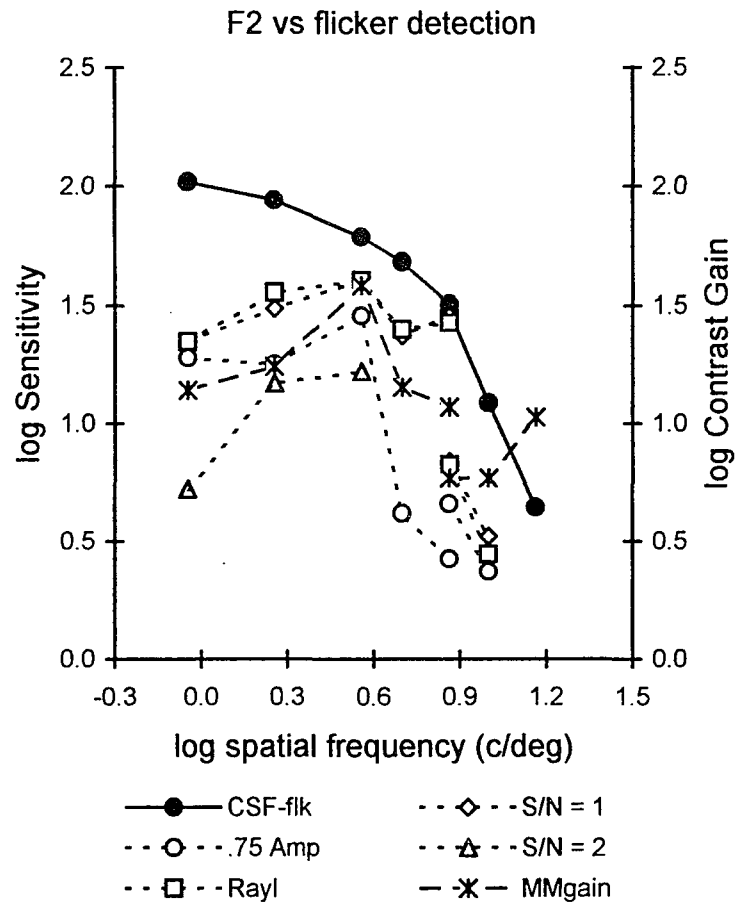
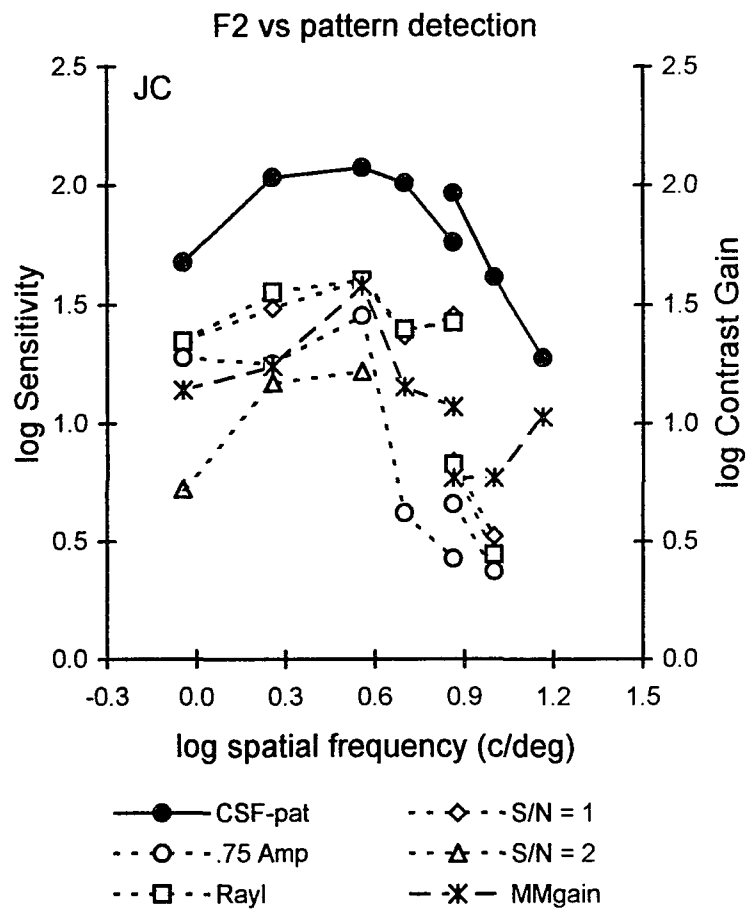


Figure 24b.

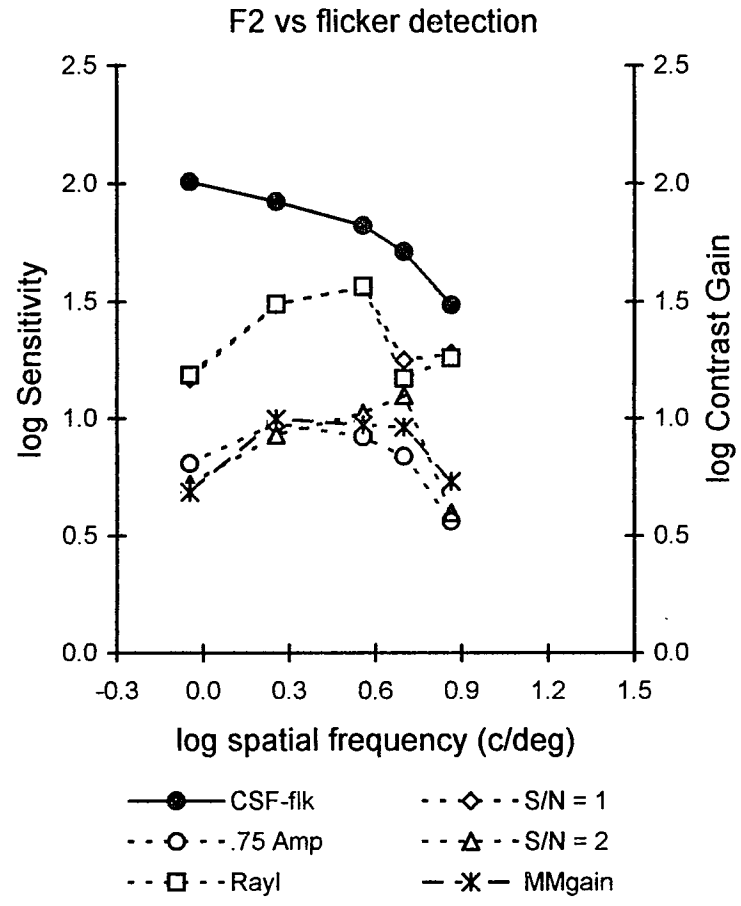
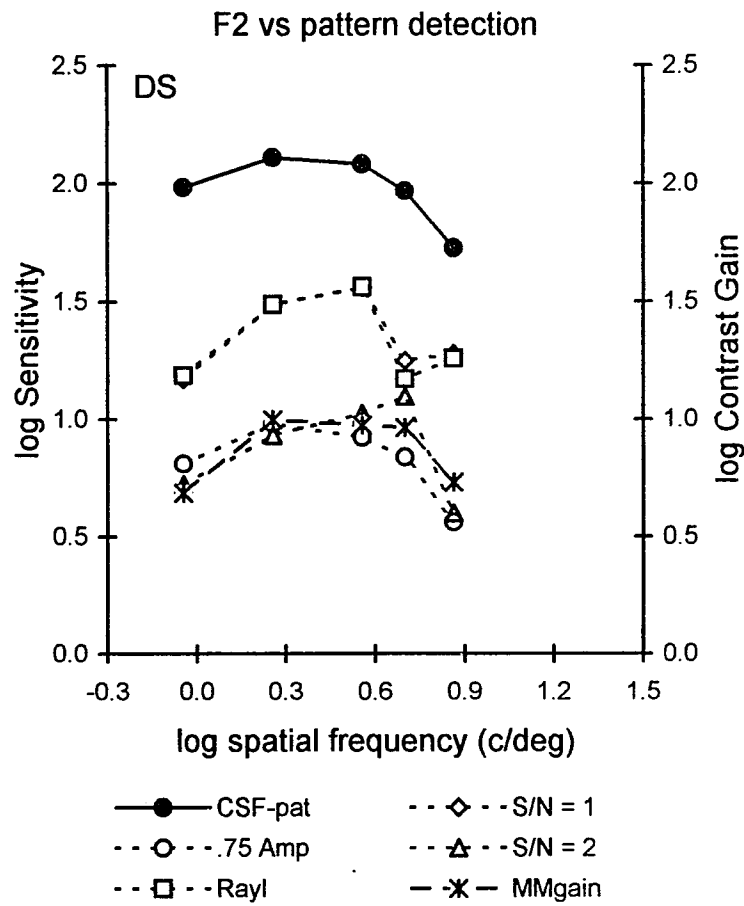


Figure 24c.

Figure 25.

Best-fitting VEP derived sensitivity function compared with the psychophysical CSF to pattern detection criteria. Filled symbols: psychophysics. Subjects: MC, JC, DS.

Psychophysical contrast sensitivity by pattern criteria vs best-fitting VEP derived measure

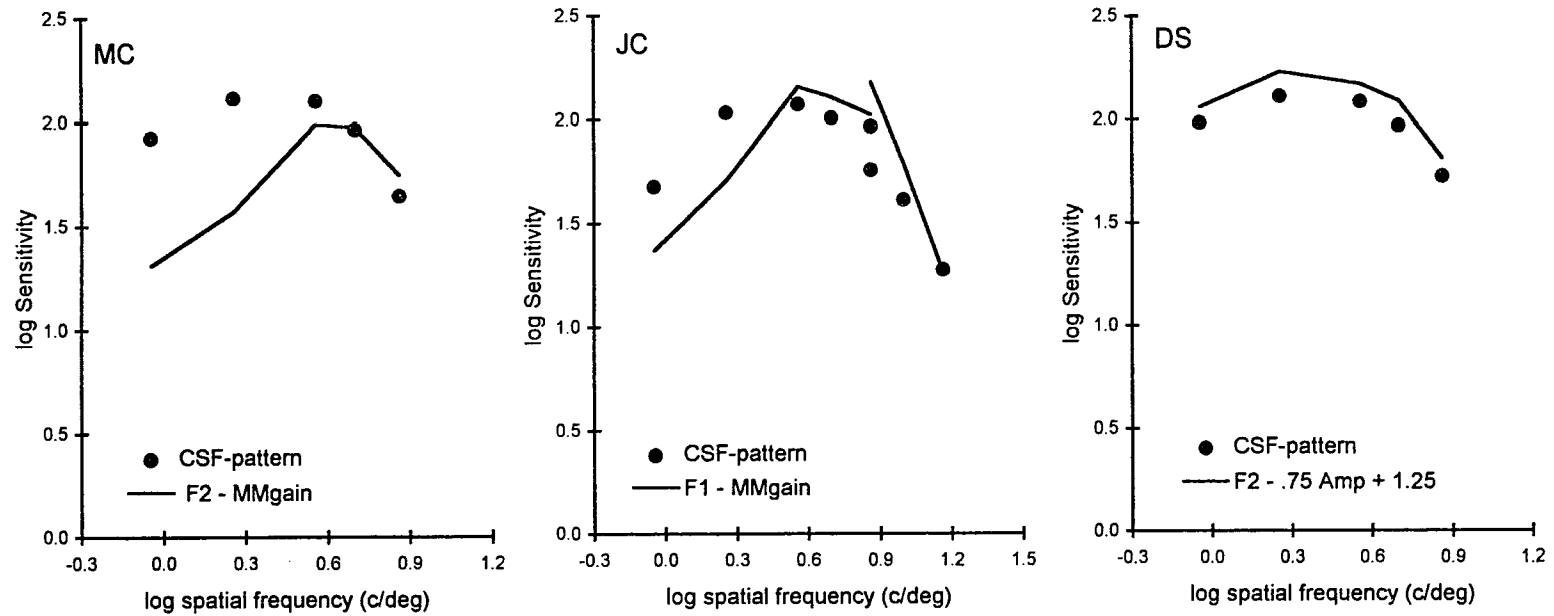


Figure 25.

Figure 26.

Best-fitting VEP derived sensitivity function compared with the psychophysical CSF to flicker detection criteria. Filled symbols: psychophysics. Subjects: MC, JC, DS.

Psychophysical contrast sensitivity by flicker criteria vs best-fitting VEP derived measure

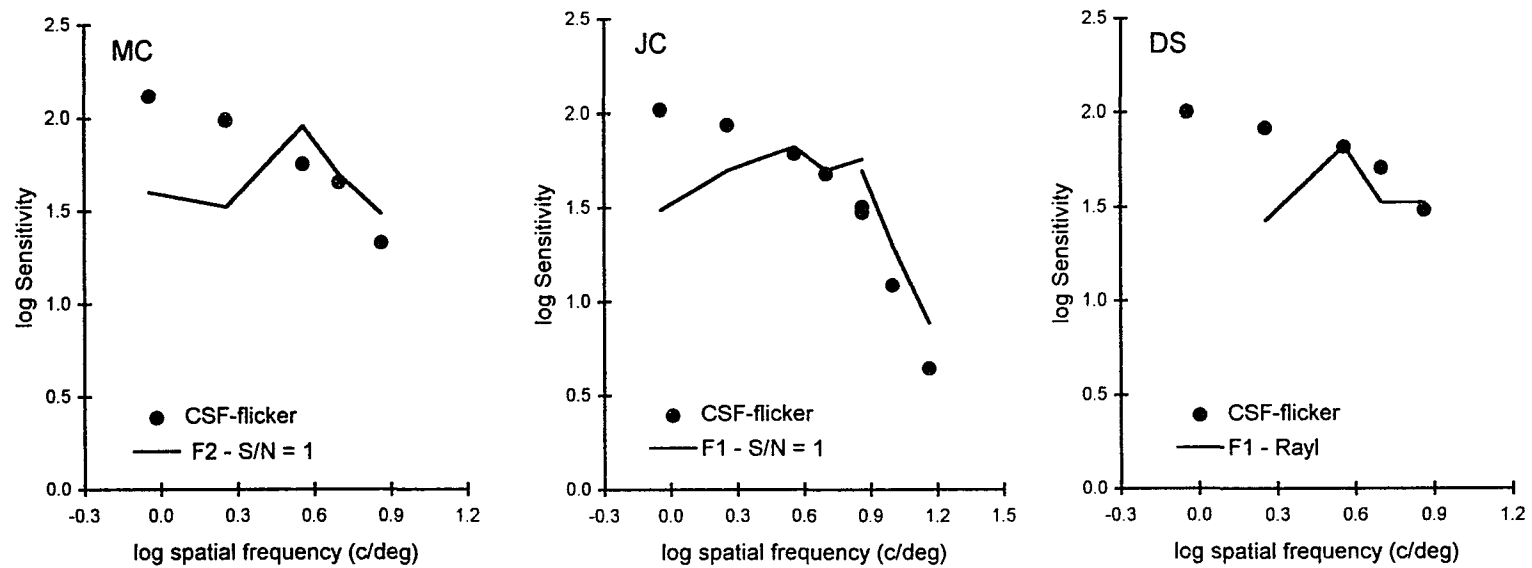


Figure 26.

DISCUSSION

This thesis has attempted to describe the relationship between the human contrast sensitivity function and the visual evoked potential. This section will summarize these results and then relate them to previous experimental work. It will also discuss the possible implications of these findings in terms of underlying functional and structural mechanisms.

Summary and Comparison with Previous Findings

In various experimental paradigms, VEPs and psychophysics have provided similar and dissimilar information about luminance contrast sensitivity. Contradictory findings in the literature suggested that methodological differences were involved and prompted an exploration in this area. Generally, our results indicate that there is not a simple relationship between psychophysical and electrophysiological threshold measures. We did not find a consistent correlation between these measures for all observers. It is unlikely that unreliability of our VEP data can account for these discrepancies. Rather, we suggest that psychophysical/VEP mismatches are due to subject individual differences. There was no consistent correlation between the fundamental (F1) component and pattern detection, or the second harmonic and flicker detection across the entire spatial frequency range. Derivations from both the fundamental and the second harmonic matched the psychophysical sensitivities for the higher spatial frequencies (above 3.6 cpd) for all observers. Our results agree with all previous studies which used single spatial frequencies (6, 10, 12, or 14 cpd) and reported good-to-excellent agreement with psychophysical pattern detection (Campbell and Maffei, 1970; Bodis-Wollner and Hendley, 1979; Bobak et al., 1984; Allen et al., 1986; Chen et al., 1990) regardless of threshold derivation method, type of stimulus modulation, or Fourier component examined. Results demonstrate both broad (JC and DS) and narrow (MC) spatial

frequency tuning of the VEP. The narrow tuning of the VEP-F1 responses for observer MC concurs with VEP data presented by Tyler and Apkarian (1985), and resembles the tuning functions of cortical cells from the cat and monkey (De Valois, De Valois, and Yund, 1979; Nakayama and Mackeben, 1982). The broad VEP spatial frequency tuning observed for observers JC and DS agrees with everyone else. For DS, the VEP-F2 function derived from the 0.75 amplitude criterion correlated almost perfectly with pattern detection ($r^2 = 0.99, p < 0.05$). There was also a suggestion of this F2/pattern detection agreement for the three lowest spatial frequencies for observer JC. However, both of these matches to psychophysics come from VEP criteria responses derived from the suprathreshold contrast range. With these exceptions, all other comparisons failed to agree at low spatial frequencies. We found no clear difference in predictability strength for four of the five derivation methods used. At first, it was surprising to find that the most arbitrary (0.75 Amp) derivation method did as well as a "statistically rigorous" (S/N = 1) method. In hindsight, it should not be so surprising given the amount of VEP data collected and that trained observers were used. A truer test of the statistical strength of a derivation method occurs when data are noisy, or incomplete. This was certainly not the case in the present study. In general, four of the five derivation methods produced sensitivity functions which were similar to the psychophysical sensitivity functions. When the individual VEP response components were too small to meet a given criterion, it was not possible to derive a contrast sensitivity measure. The S/N = 2, for example, proved too high a criterion given the overall size of the VEP responses. In fact, most of the sensitivities derived using this criterion were outside of the near-threshold range.

Contrast Sensitivity and Excitation/Inhibition

The results summarized above agree with the notion that channels processing low spatial frequency information (less than 4.0 cpd) must have different temporal characteristics from those processing high spatial frequency information. A

parsimonious explanation, given all of the data, is that a single mechanism which is temporally insensitive at higher spatial frequencies generates both the F1 and F2 VEP components. Either Fourier component can account for pattern and/or flicker sensitivities for spatial frequencies above 3.6 cpd. Stimulus conditions will optimize the strength of either the F1 or F2 component for a given observer. For observer MC, VEP derivations from the F2 component made for better comparisons with psychophysics, regardless of pattern or flicker criteria. On the other hand, for JC, the F1 component derivations fit the psychophysical data better. Observer DS provided the only (near) perfect correlation between psychophysics and VEPs; but for pattern detection only and not from a near-threshold contrast range. Obtaining this correlation may explain much of the previous work which claimed the one-to-one correspondence between these two measures. At low spatial frequencies, temporal sensitivity is more specific or narrowly tuned and VEP responses at 6.27 (F1) and 12.54 Hz (F2) may fall outside this temporal tuning band. The type of stimulus modulation, appearance-disappearance, and the temporal frequency used, both favored a stronger F1 response component over the F2 response (see Figure 22) for observer JC. Given his responses to a contrast of 0.15, a modulation frequency of 4 Hz, for instance, may have produced larger F2 responses over the entire contrast range (0.01 - 0.48). With a more optimal temporal frequency for the F2 response, sensitivities derived using this component may have come closer to matching the pattern detection functions for all three observers; not just DS. Previous investigators reported excellent correlations between psychophysics and VEPs for pattern detection at higher spatial frequencies and with 6 to 8 Hz contrast-reversal modulation. As mentioned earlier, this type of stimulus modulation elicits only even (F2, F4, etc.) harmonic responses in the VEP. It is possible that modulation at lower temporal frequencies would have produced psychophysical and VEP functions which matched at lower spatial frequencies as well.

Another possibility is that the psychophysical sensitivities to low spatial frequencies cannot be accounted for by a corresponding VEP derived measure. Burbeck and Kelly (1980) modeled the spatiotemporal threshold surface as the linear difference between two separable mechanisms - one excitatory and the other inhibitory. One mechanism accounts for the peak of the sensitivity curve and the high spatial frequency falloff; while the second mechanism inhibits the first in the low frequency region. Following their reasoning, the VEP may be influenced predominantly by inhibitory cortical interactions at low spatial frequencies, and no single Fourier component may adequately reflect the excitatory signal that determines psychophysical performance. This seems to be plausible given the mismatch at low spatial frequencies for JC and for MC's VEP functions which demonstrate a sharp spatial tuning. The lower contrast sensitivity (higher contrast thresholds) implies that although the low spatial frequencies are visible, they elicit little response from the cortex at the electrode site. Observer DS may have a different temporal tuning than MC or JC in the low spatial frequency region. If this is the case, then his VEPs at this temporal frequency (6.27 Hz) may be less influenced by inhibitory intracortical interactions.

Psychophysics, by definition indicates the overall performance of the neural system. The relationship of the VEP to psychophysics is a measure of the neural mechanisms relevant to spatial vision. The VEP measures population-averaged signals at the occipital pole. Dipole modeling of the source of the appearance-disappearance VEP suggests that it originates in primary visual cortex (Maier, Dagnelie, Spekreijse, and Van Dijk, 1987). A possible explanation for psychophysical and VEP discrepancies lies in the underlying anatomical structure of the visual cortex. Cortical visual neurons receive a wide variety of inputs including intracortical, transcallosal and thalamic, in addition to specific afferent influences from the LGN. In 1991, Felleman and Van Essen described 25 cortical areas in the macaque which are predominantly or exclusively visual in function. These areas plus seven other associated regions share a 40% connectivity

between them. Even though the VEP is primarily foveal and, therefore of V1/V2 origin, surface recordings at the occiput likely include the summed input from associated visual areas as well. Areas such as V3, V4, and MT, for example, may contribute to the behavioral measure of contrast sensitivity, but their relative contributions to the VEP are not known. Local inhibitory interactions within V1 alone may account for the narrow VEP spatial frequency tuning of the F1 component we see in observer MC.

Contrast Sensitivity and M/P cell Similarities

It is tempting to propose that the magnocellular pathway makes the dominant contribution to the visual evoked potential at near-threshold contrasts. Similarities between VEP and M/P cell data, presented here and elsewhere, cause us to consider this relationship very carefully. The majority of the VEP sensitivities derived here were from the 0.02 to 0.08 contrast range. Tootell, Hamilton, and Switkes (1988) determined that the use of low contrast stimuli (less than 0.10) strongly biases cortical input in favor of the magnocellular pathway, and minimizes input from the parvocellular pathway. Additional evidence comes from examination of the spatial contrast sensitivity function for monkey M and P cells. Both are band-pass in shape but the sensitivity of M cells matches behavioral threshold more closely. The sensitivity of P cells is substantially lower than psychophysically determined sensitivities (Kaplan, Shapley and Purpura, 1989). The VEP-F1 and -F2 contrast response functions resemble the functions obtained from macaque magnocellular and parvocellular layers, respectively. This is particularly true for the higher spatial frequencies (i.e., 5.0 and 7.3 cpd). The slope of the contrast response function is steeper (like the VEP-F1) for LGN magnocellular layers than for parvocellular layers (like the VEP-F2). The high sensitivity of the VEP-F1 response and low contrasts at which this response saturates (approximately 0.08 - 0.10) mimics the functions obtained from magnocellular neurons in the monkey. Responses obtained from parvocellular neurons are relatively insensitive to contrast and exhibit nonsaturating

functions (Kaplan and Shapley, 1986). This is similar to how we would describe the VEP-F2 contrast response functions. Finally, the difference in contrast gains reported by Kaplan and Shapley (1986) for magnocellular versus parvocellular cells (8 -10:1) are almost identical to the F1/F2 contrast gain ratios (10 - 12:1) observed here. The parallels noted above, make for a compelling hypothesis. However, the parsimonious explanation is that the individual VEP response components are not generated by different parallel pathways, but that a single mechanism can produce both responses. The F1 and F2 responses cannot be singled out as characteristic of a particular neural pathway or group. The slight phase advance with increases in contrast in the threshold range was evident in both the F1 and F2 response functions. This behavior at low contrasts along with the steeply rising amplitudes are believed to be the signature of contrast gain control for the magnocellular pathway. The phase lag at higher contrasts (0.30 - 0.48) at the highest spatial frequencies may be indicative of parvocellular inputs in the cortex (Zemon, personal communication). Again, it seems clear that both the F1 and F2 contrast response functions reflect magnocellular and parvocellular contributions depending on the spatial frequency and contrast range.

Summary and Future Considerations

The current study attempted to determine what relationship individual VEP response components have to psychophysical contrast sensitivity functions. We determined that the sensitivities derived from both F1 and F2 components agreed well with psychophysical sensitivities for spatial frequencies above 3.6 cpd. The good agreement between these two measures of contrast sensitivity at higher spatial frequencies demonstrates that the VEP can be used to investigate fine spatial pattern processing. A consistent psychophysical/VEP correspondence at low spatial frequencies, however, was not observed. VEP contrast sensitivities were derived in several ways by meeting specific criteria. The derivation methods produced functions which were, in

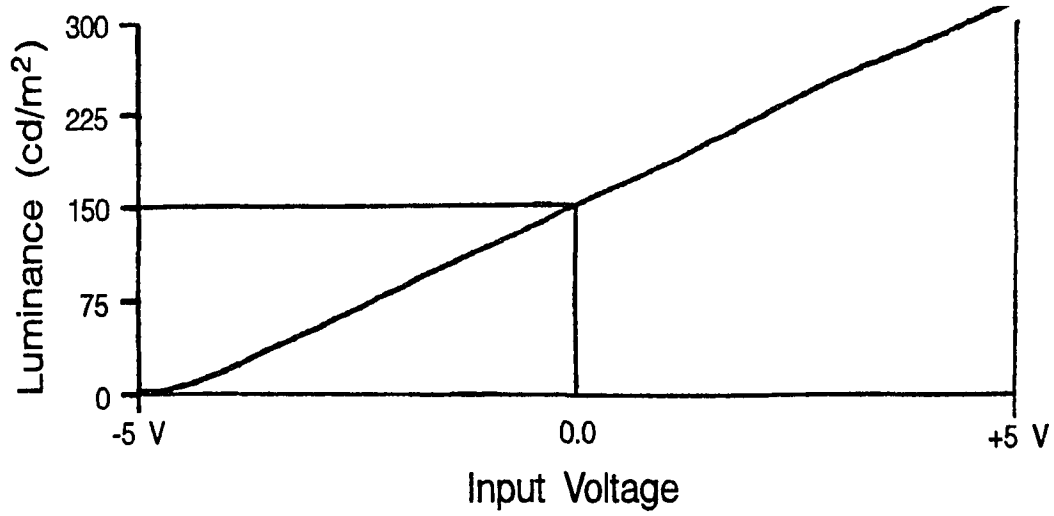
most cases, similar to each other but not necessarily similar to the psychophysical functions over the entire spatial frequency range. Results of the VEP temporal tuning experiment indicated that our choice of modulation frequency favored one VEP response component (F1) over the other (F2). We propose that future studies determine each individual's VEP temporal tuning function prior to obtaining a contrast response function. In this way, a modulation frequency can be chosen which will optimize the VEP response components of interest. Given that either harmonic component agrees well with the psychophysical CSF at higher spatial frequencies, one could focus on a single VEP response component. To examine the temporal tuning mechanism present at low spatial frequencies, one could use an adaptation paradigm in which frequencies close to the stimulus frequency act to silence or "adapt out" the temporal contribution to the VEP. Another approach is suggested by the work of Zemon, Conte, Jindra, and Camisa (1985) on "local excitatory" and "lateral inhibitory" cortical processing. Using a radial spatial pattern and pairs of modulation frequencies, they reported that the VEP temporal tuning function of the "inhibitory" mechanism is low-pass in shape, peaks at 10 Hz, and falls off above this frequency. In this case, modulation frequencies above 10 Hz perhaps can suppress the inhibitory contributions to the VEP at low spatial frequencies.

Finally, we have demonstrated that the T_{circ}^2 statistic is useful in determining the presence of a reliable VEP response at near threshold contrasts. It can be used to derive a criterion VEP response measure of contrast sensitivity which approximates the psychophysical thresholds under specific spatial conditions. This can be an important statistical tool in the clinical setting where EEG recordings can be noisy or when only a small amount of data can be obtained from a patient. The VEP has been used clinically as an objective means of detecting visual abnormalities, either when sensory symptoms are equivocal, or with uncooperative patients. Studies of early visual development in infants posed an experimental challenge to VEP investigators. This led to the development of the swept-parameter VEP technique. This technique was developed

primarily for speed since the attention span of an infant is short; any reliable VEP recordings must be obtained quickly. Swept-stimulus parameters can be contrast, spatial frequency or orientation, for example. Within a single 10-sec sweep, an entire contrast response function may be obtained (Regan, 1989). The addition of the T_{circ}^2 as a measure of signal integrity would strengthen the conclusions drawn from VEP data collected in this manner. Contrast gain may be determined concurrently from a contrast response function obtained using the rapid sweep-VEP technique.

Appendix A

Luminance calibration of Tektronix 608 oscilloscope



Appendix B

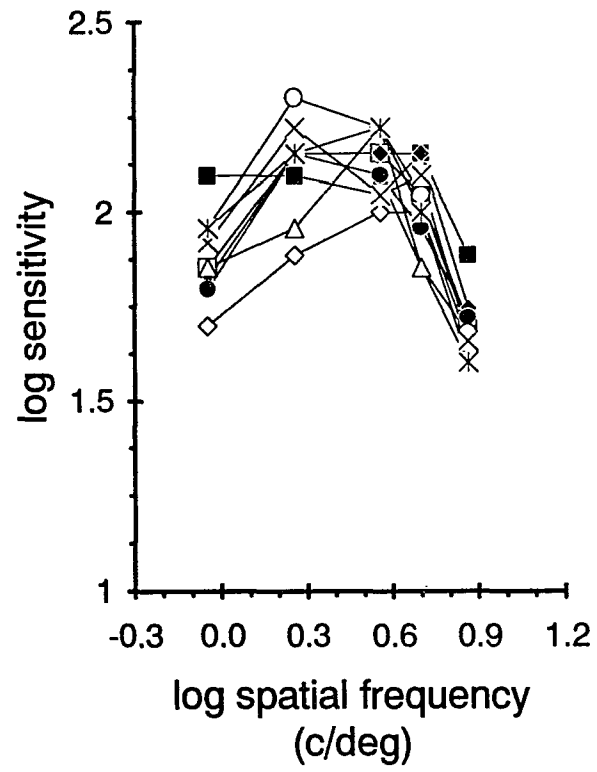
S: MC Psychophysical judgements (n = 10 trials)				
temp. frequency = 2.08 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.892	0.035	1.992	0.023
1.8	2.124	0.038	1.969	0.039
3.6	2.126	0.026	1.802	0.039
5.0	2.017	0.034	1.607	0.035
7.3	1.693	0.026	1.325	0.051
temp. frequency = 4.19 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.899	0.024	2.086	0.023
1.8	2.132	0.027	1.975	0.029
3.6	2.166	0.022	1.748	0.030
5.0	2.000	0.020	1.605	0.036
7.3	1.682	0.020	1.356	0.039
temp. frequency = 6.27 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.923	0.024	2.117	0.017
1.8	2.117	0.017	1.991	0.018
3.6	2.104	0.027	1.755	0.039
5.0	1.967	0.021	1.654	0.030
7.3	1.645	0.032	1.327	0.034
temp. frequency = 8.42 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.831	0.026	2.084	0.017
1.8	2.108	0.024	2.011	0.052
3.6	2.096	0.021	1.722	0.022
5.0	1.948	0.032	1.603	0.039
7.3	1.653	0.022	1.349	0.054
temp. frequency = 12.44 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.781	0.023	1.939	0.026
1.8	2.110	0.044	1.764	0.020
3.6	2.109	0.034	1.569	0.029
5.0	1.949	0.031	1.474	0.019
7.3	1.613	0.026	1.212	0.050

S: JC Psychophysical judgements (n = 10 trials)				
temp. frequency = 2.08 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.728	0.029	1.916	0.015
1.8	2.105	0.017	1.930	0.023
3.6	2.160	0.022	1.900	0.026
5.0	2.083	0.034	1.839	0.029
7.3	1.822	0.034	1.610	0.021
temp. frequency = 4.19 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.728	0.033	1.948	0.022
1.8	2.130	0.022	1.929	0.011
3.6	2.073	0.027	1.804	0.016
5.0	2.022	0.021	1.721	0.035
7.3	1.784	0.018	1.452	0.024
temp. frequency = 6.27 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.677	0.036	2.017	0.019
1.8	2.032	0.031	1.938	0.016
3.6	2.074	0.037	1.785	0.027
5.0	2.008	0.035	1.679	0.023
7.3	1.758	0.039	1.504	0.045
7.3*	1.965	0.058	1.473	0.036
10.0*	1.615	0.013	1.087	0.020
14.6*	1.276	0.057	0.643	0.017
temp. frequency = 8.42 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.698	0.029	2.002	0.024
1.8	2.081	0.021	1.924	0.017
3.6	2.127	0.027	1.780	0.018
5.0	1.952	0.028	1.672	0.029
7.3	1.717	0.031	1.472	0.026
temp. frequency = 12.44 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.620	0.028	1.909	0.030
1.8	2.001	0.037	1.825	0.020
3.6	2.112	0.030	1.679	0.022
5.0	1.962	0.030	1.557	0.019
7.3	1.754	0.044	1.340	0.021
* at 114 cm. test distance				

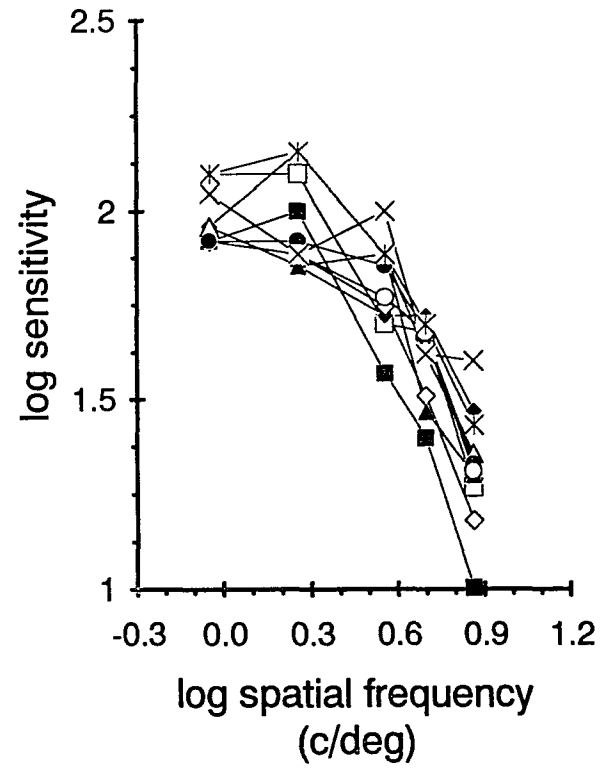
S: DS Psychophysical judgements (n = 10 trials)				
temp. frequency = 2.08 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.999	0.040	1.982	0.035
1.8	2.135	0.068	1.972	0.042
3.6	2.134	0.054	2.019	0.025
5.0	2.030	0.063	1.870	0.031
7.3	1.805	0.045	1.705	0.031
temp. frequency = 4.19 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	2.003	0.026	1.943	0.041
1.8	2.073	0.026	1.948	0.036
3.6	2.115	0.044	1.855	0.042
5.0	1.973	0.034	1.801	0.028
7.3	1.783	0.049	1.543	0.035
temp. frequency = 6.27 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.983	0.019	2.005	0.039
1.8	2.110	0.043	1.921	0.019
3.6	2.083	0.035	1.819	0.024
5.0	1.969	0.025	1.709	0.034
7.3	1.725	0.074	1.484	0.031
temp. frequency = 8.42 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	2.005	0.022	1.973	0.030
1.8	2.043	0.041	1.941	0.022
3.6	2.076	0.059	1.827	0.030
5.0	1.976	0.044	1.730	0.033
7.3	1.759	0.047	1.516	0.036
temp. frequency = 12.44 Hz				
	Pattern Detection		Flicker Detection	
SF(cpd)	MEAN	SEM	MEAN	SEM
0.9	1.874	0.032	1.883	0.052
1.8	2.064	0.052	1.771	0.029
3.6	2.112	0.062	1.756	0.048
5.0	1.975	0.035	1.588	0.034
7.3	1.653	0.059	1.410	0.044

S: MC
2.08 Hz

pattern detection



flicker detection

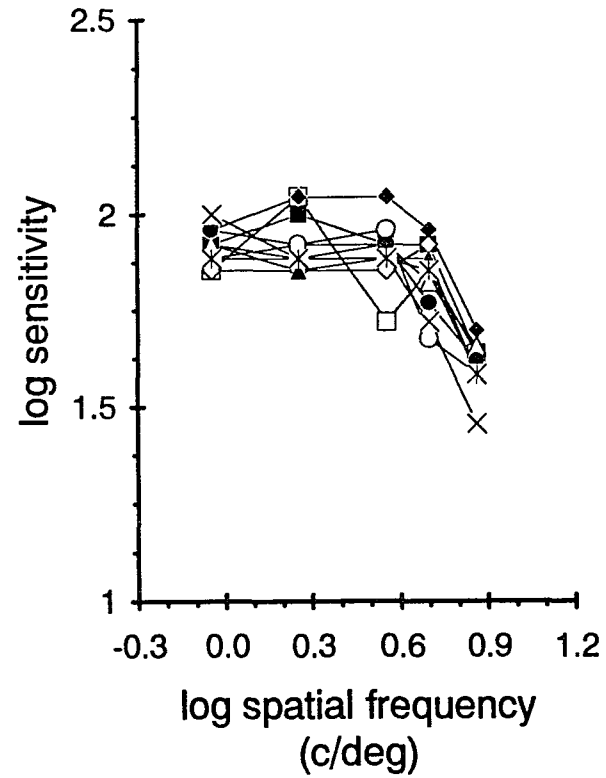
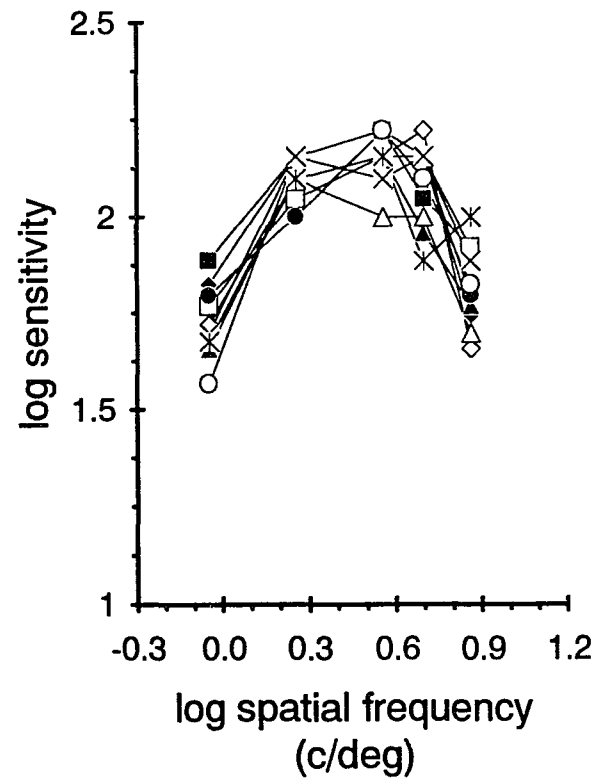


S: JC

2.08 Hz

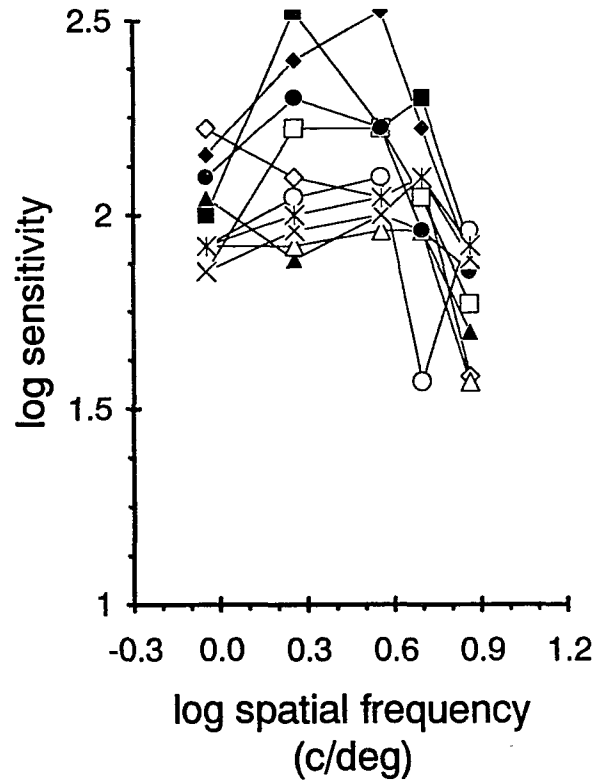
pattern detection

flicker detection

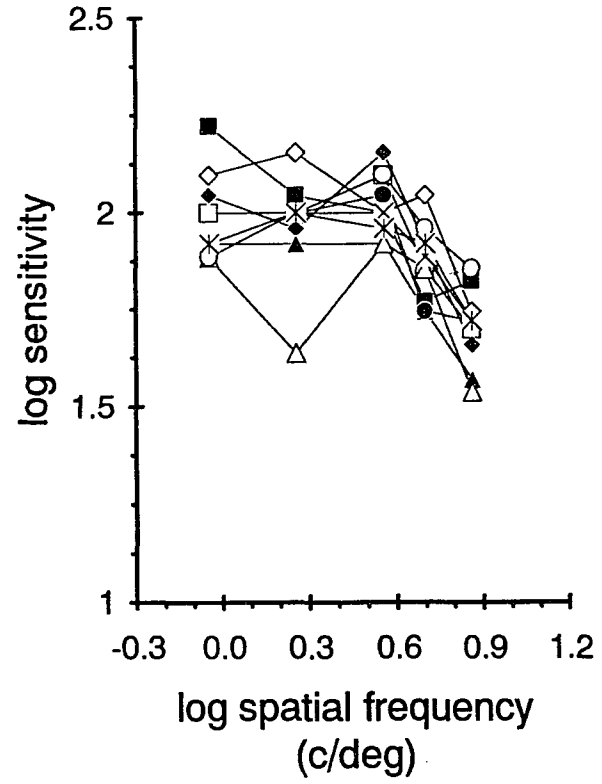


S: DS
2.08 Hz

pattern detection

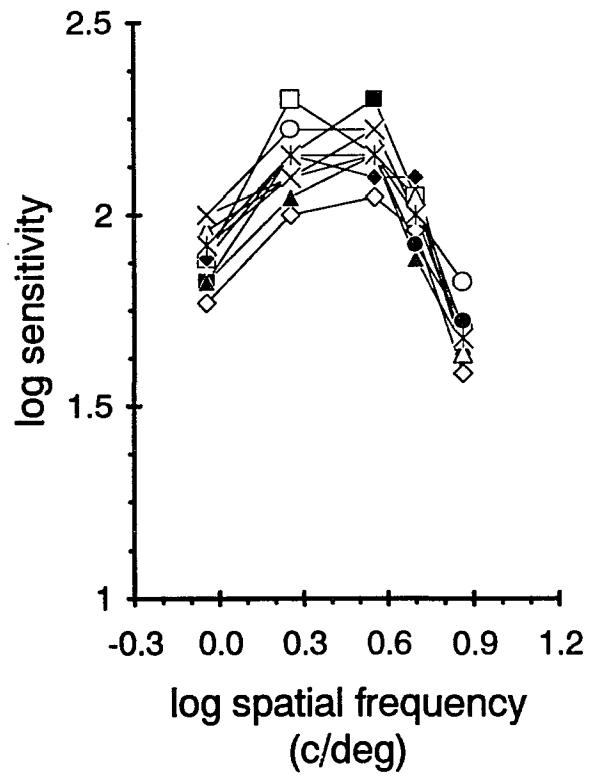


flicker detection

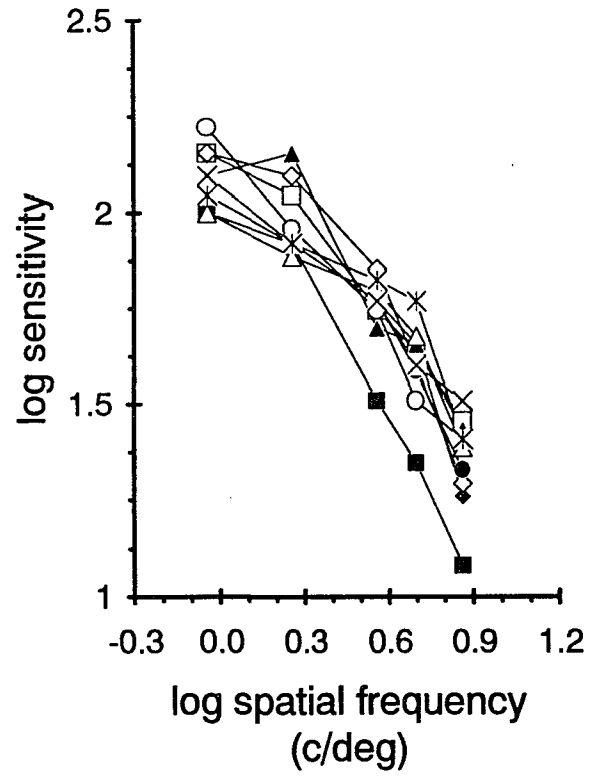


S: MC
4.19 Hz

pattern detection

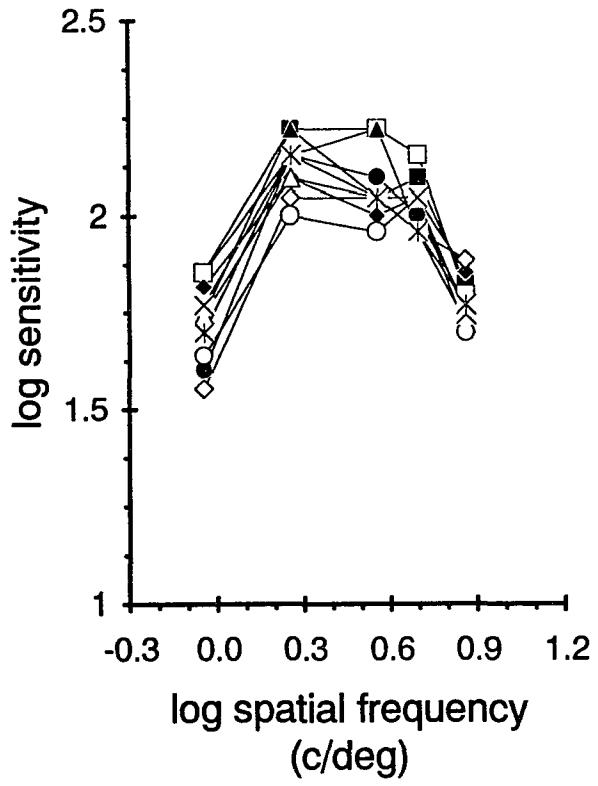


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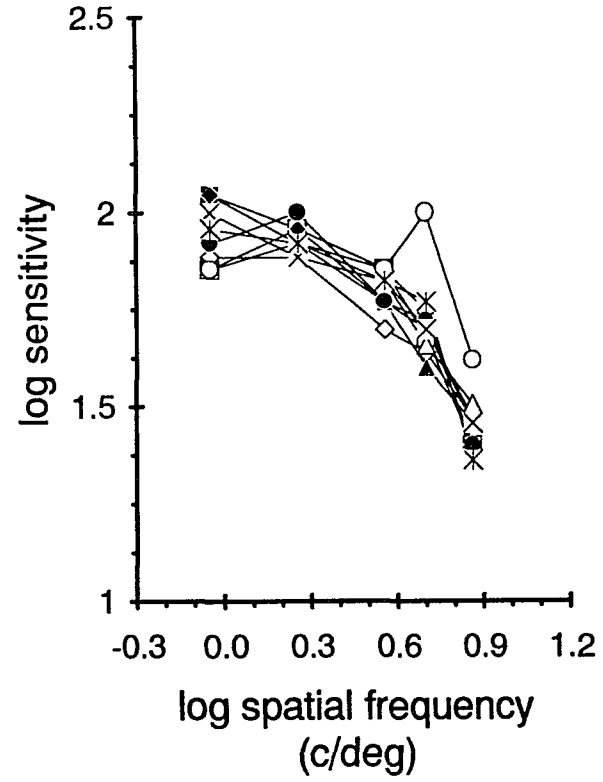


S: JC
4.19 Hz

pattern detection

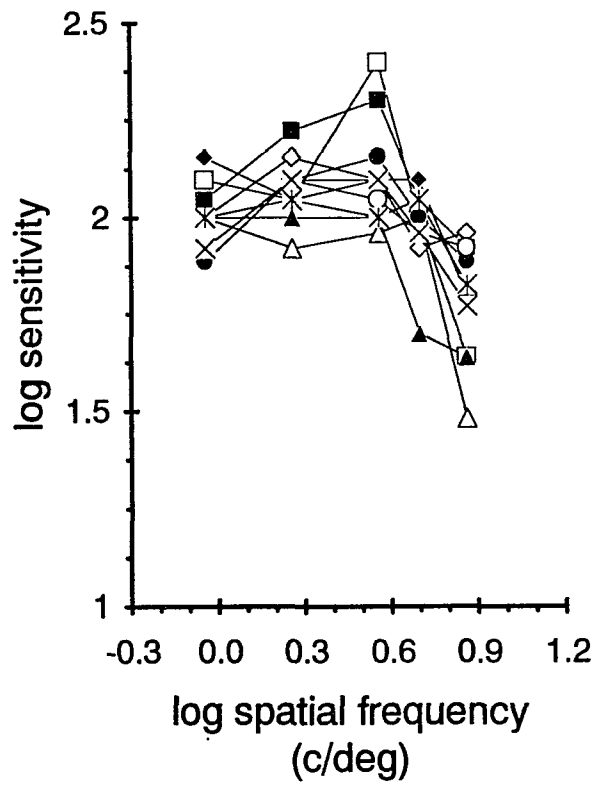


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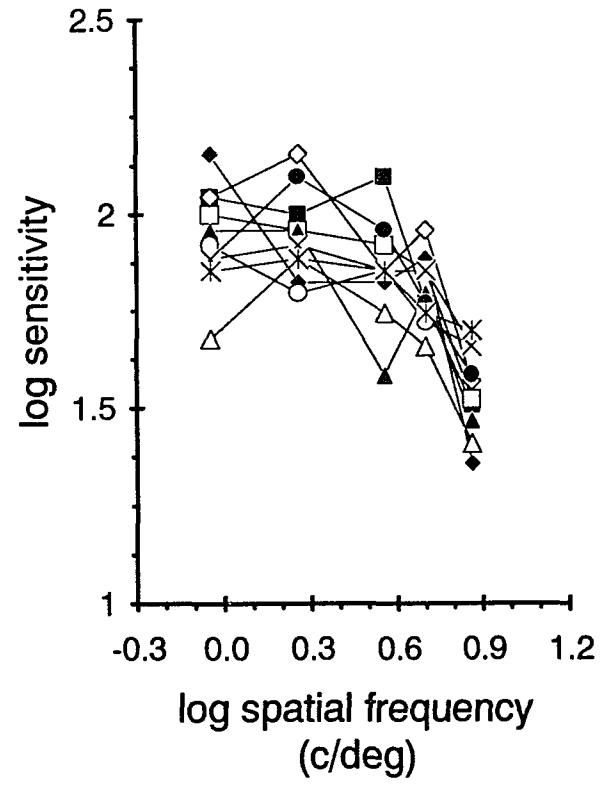


S: DS
4.19 Hz

pattern detection

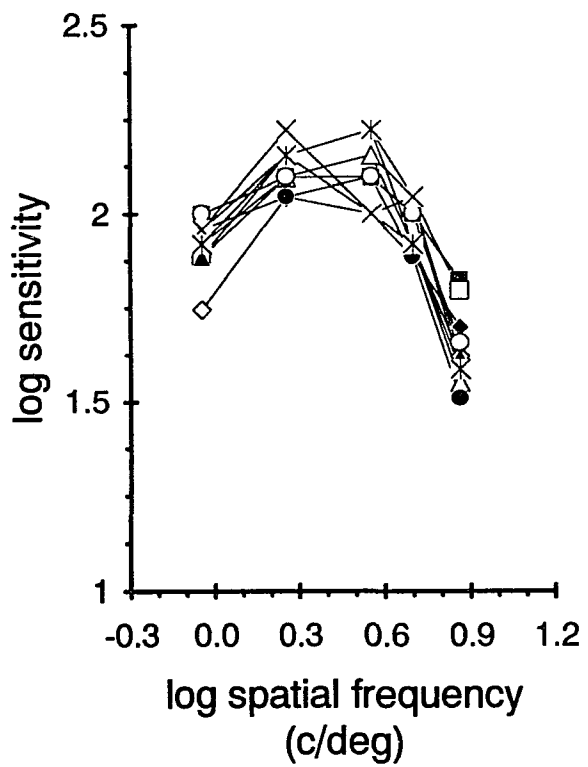


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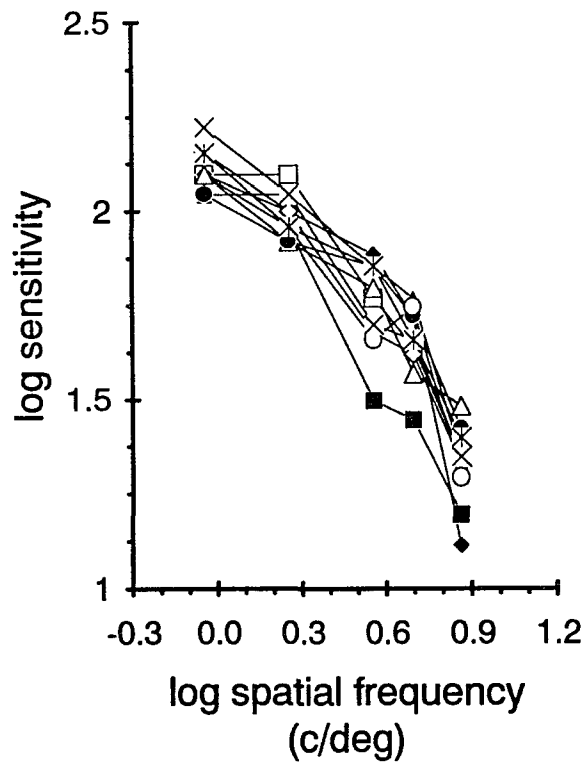


S: MC
6.27 Hz

pattern detection

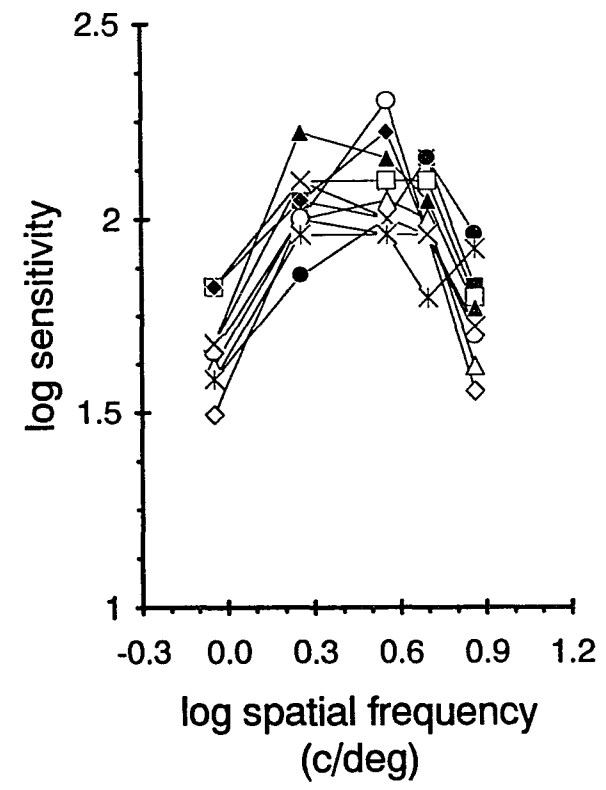


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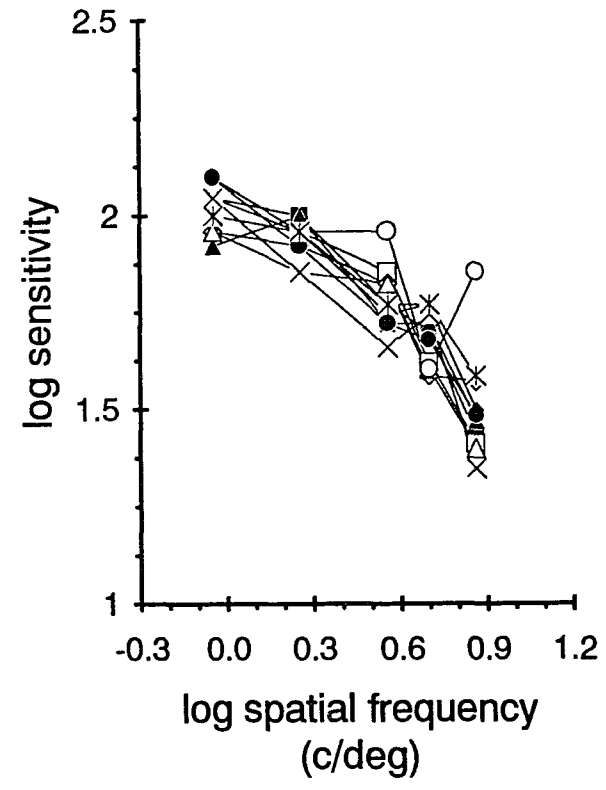


S: JC
6.27 Hz

pattern detection

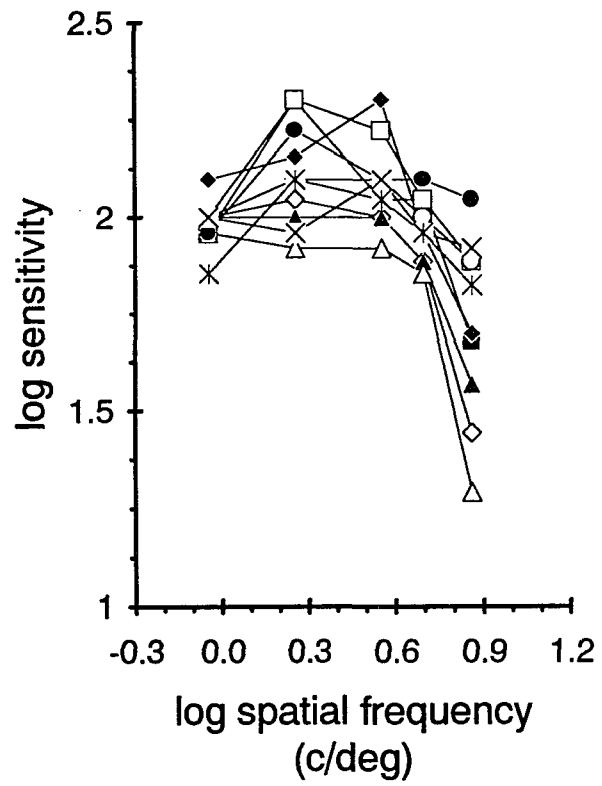


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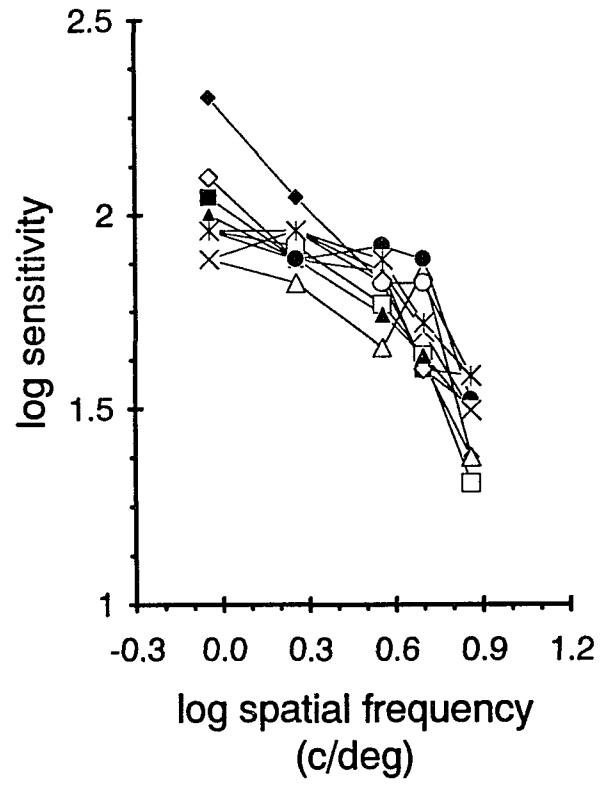


S: DS
6.27 Hz

pattern detection

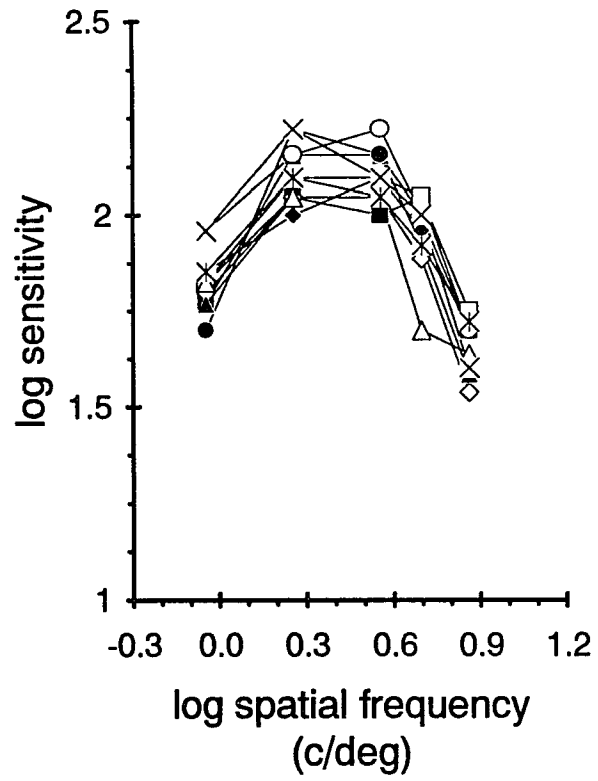


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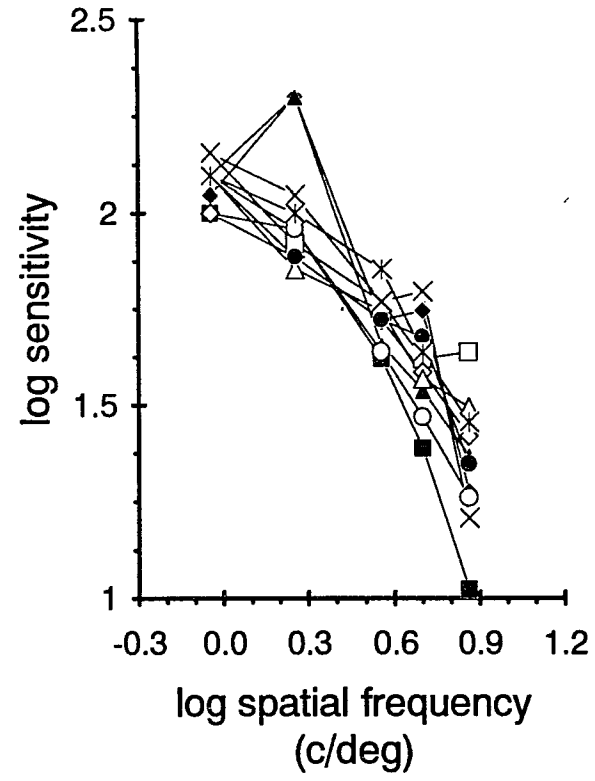


S: MC
8.42 Hz

pattern detection



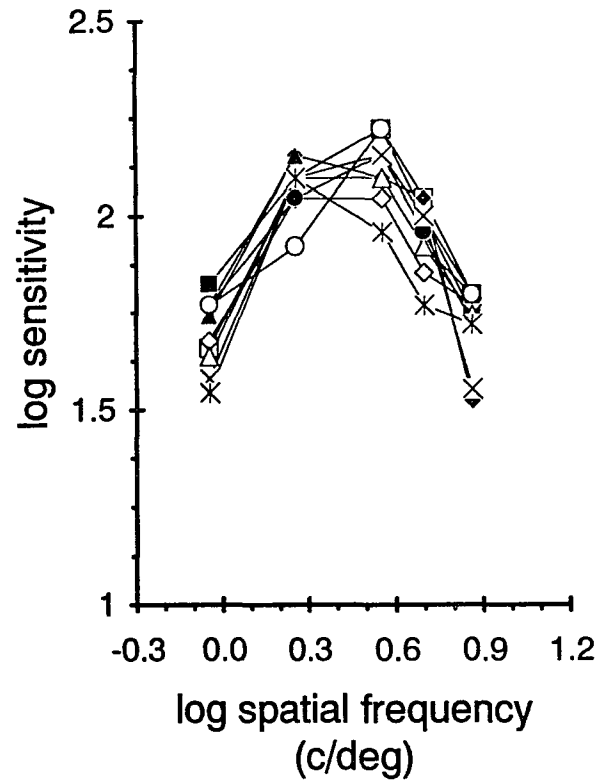
flicker detection



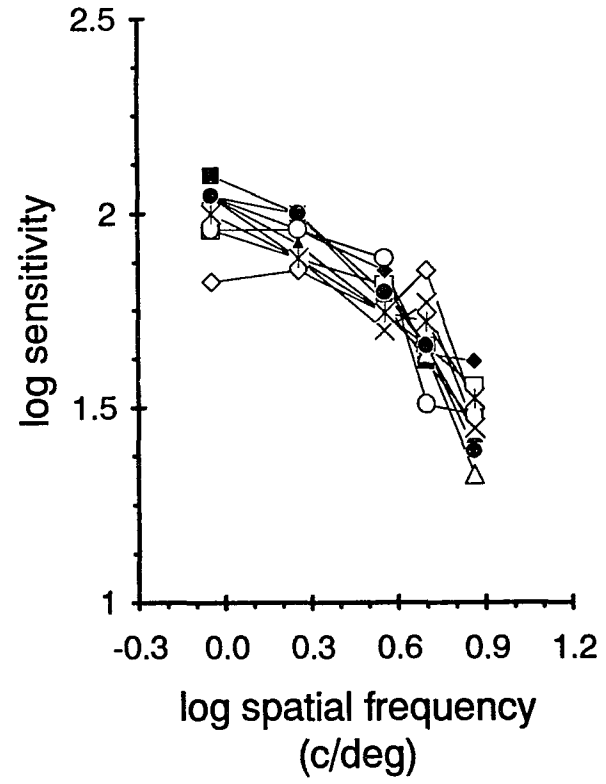
S: JC

8.42 Hz

pattern detection

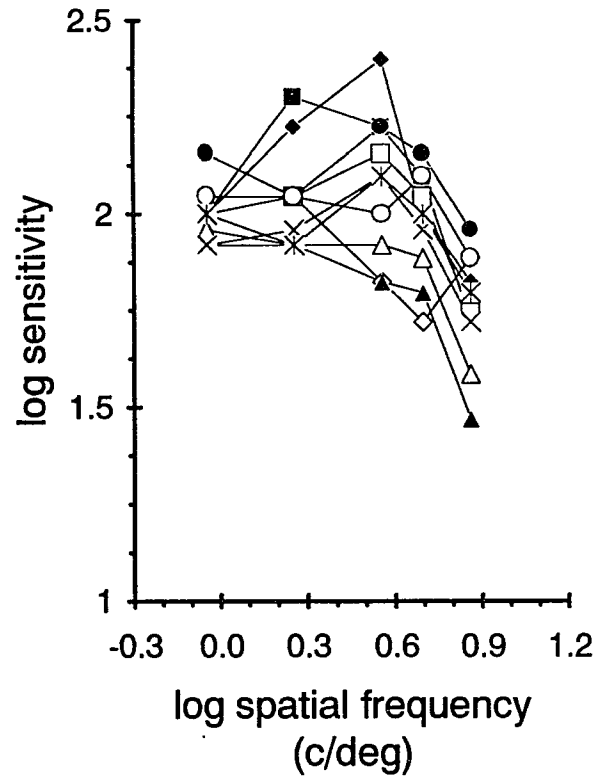


flicker detection

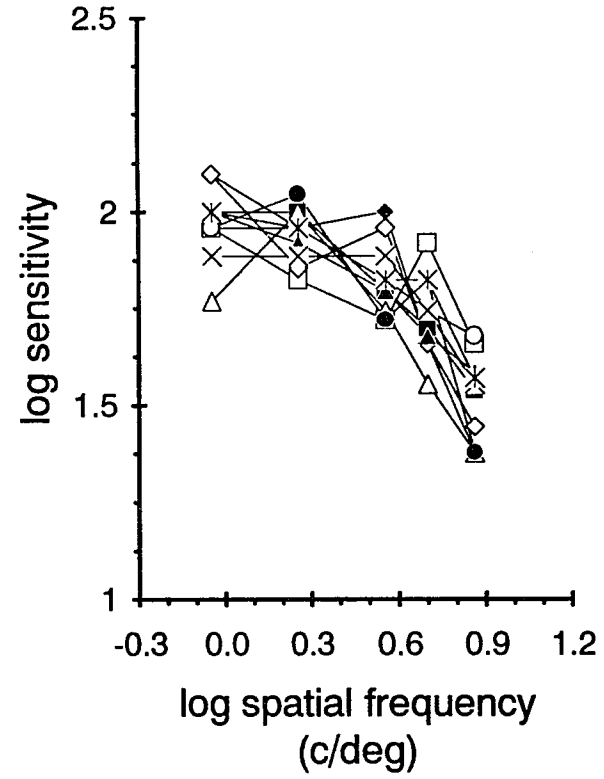


S: DS
8.42 Hz

pattern detection



flicker detection

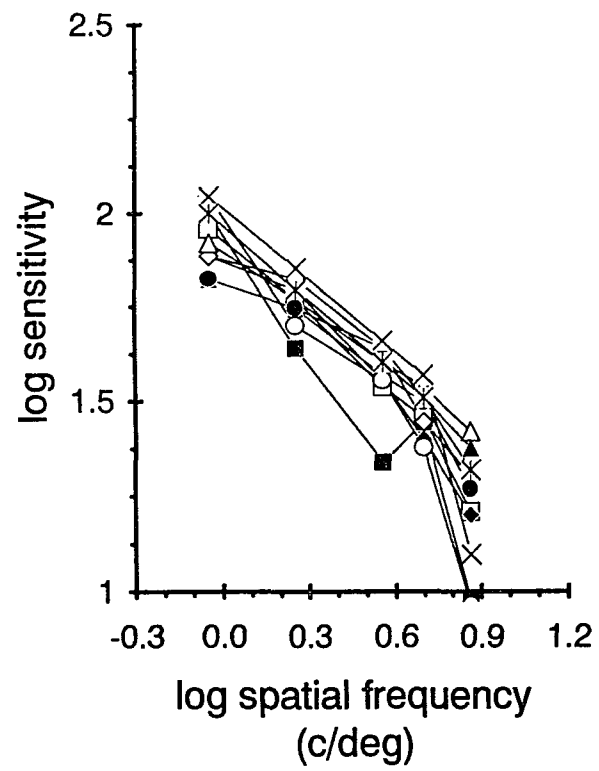
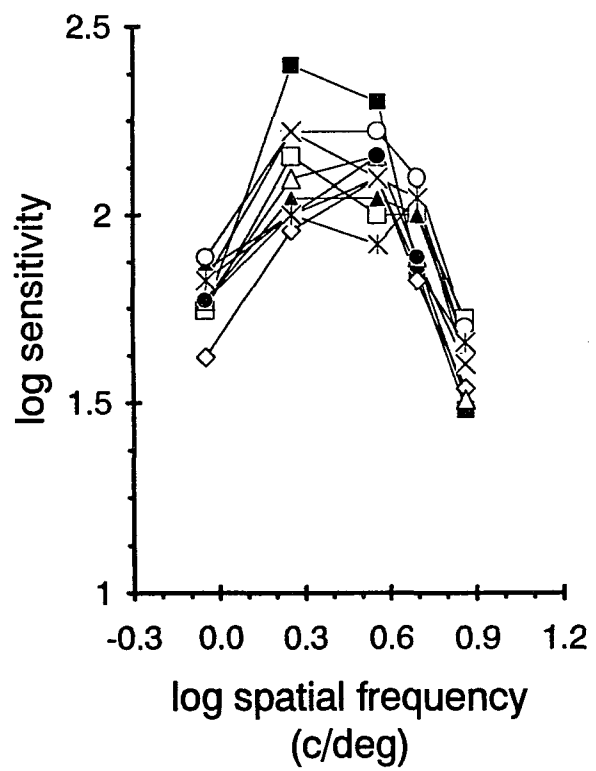


S: MC

12.44 Hz

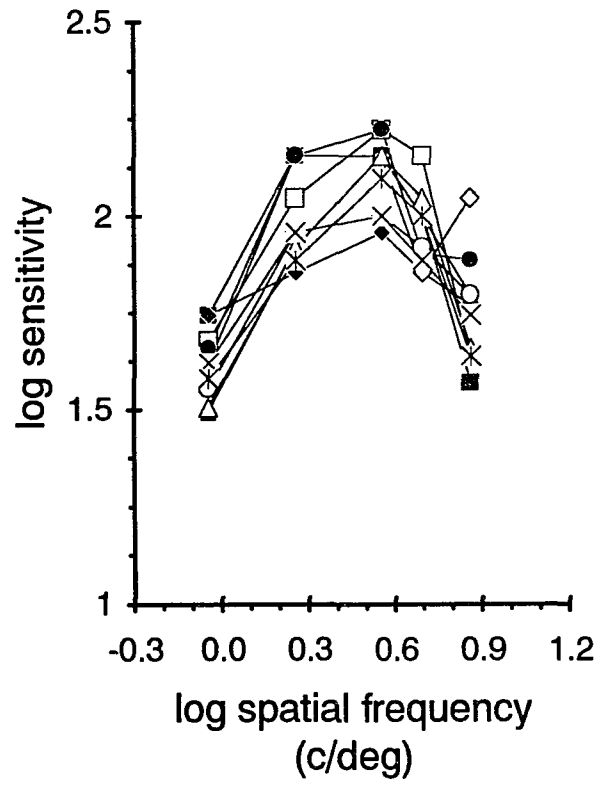
pattern detection

flicker detection

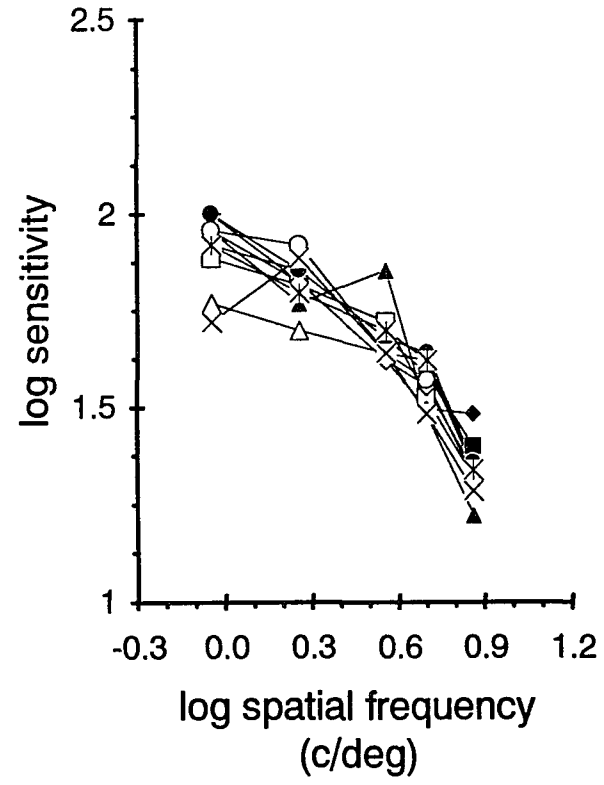


S: JC
12.44 Hz

pattern detection

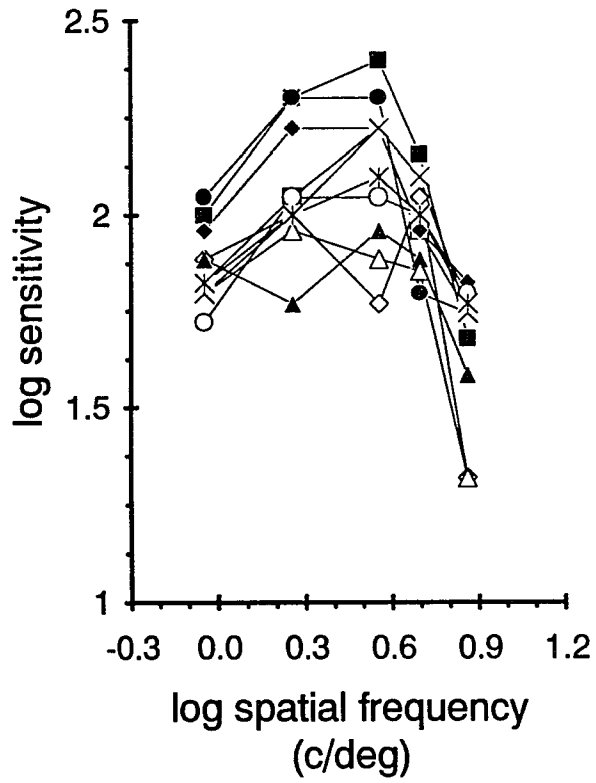


flicker detection

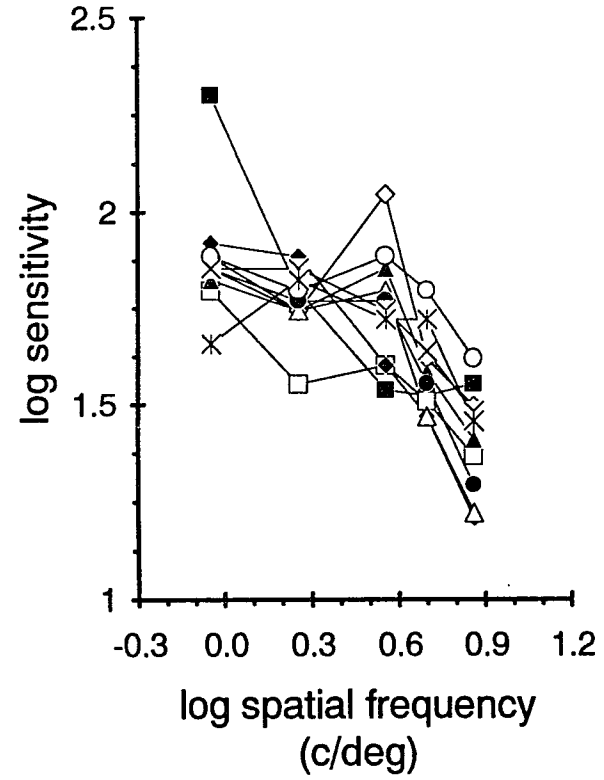


S:DS
12.44 Hz

pattern detection

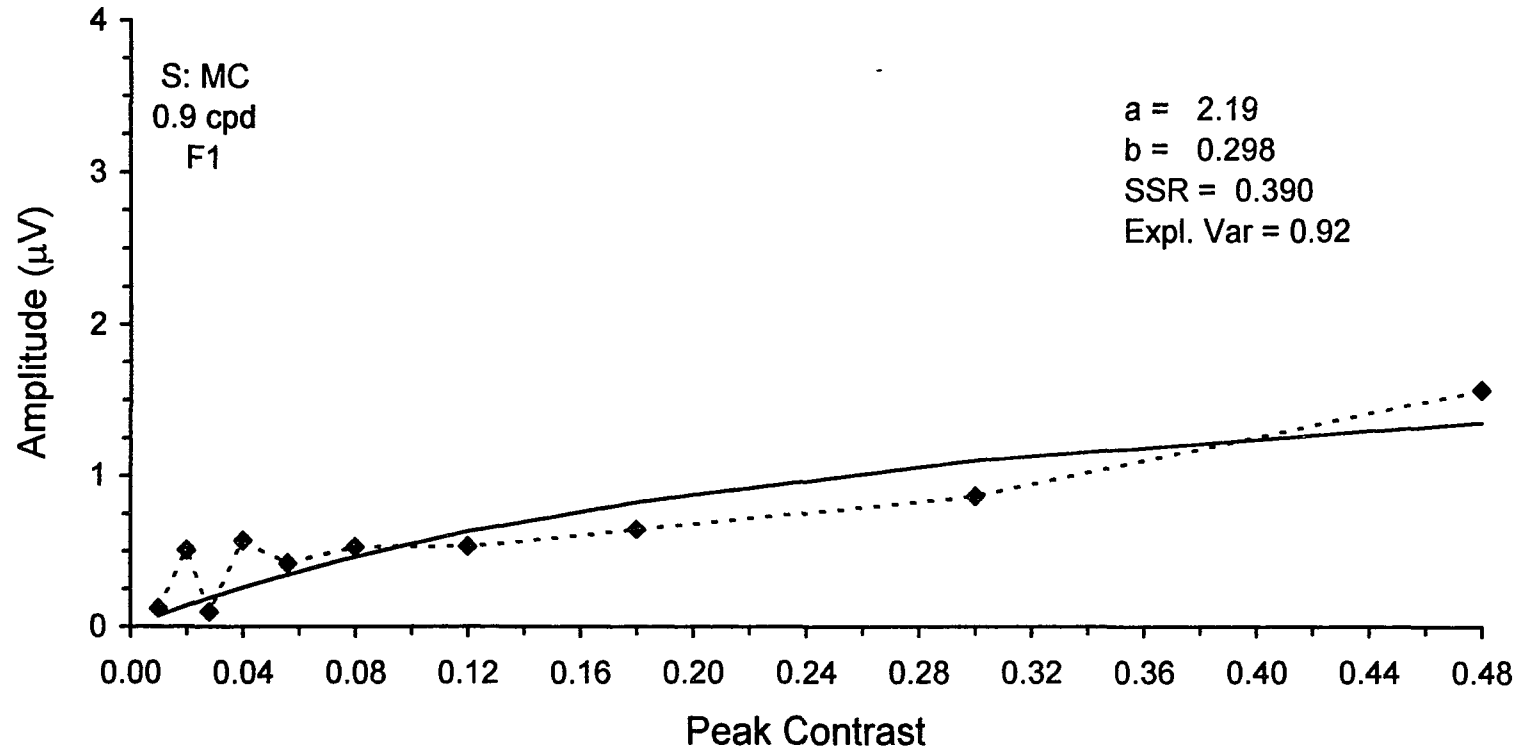


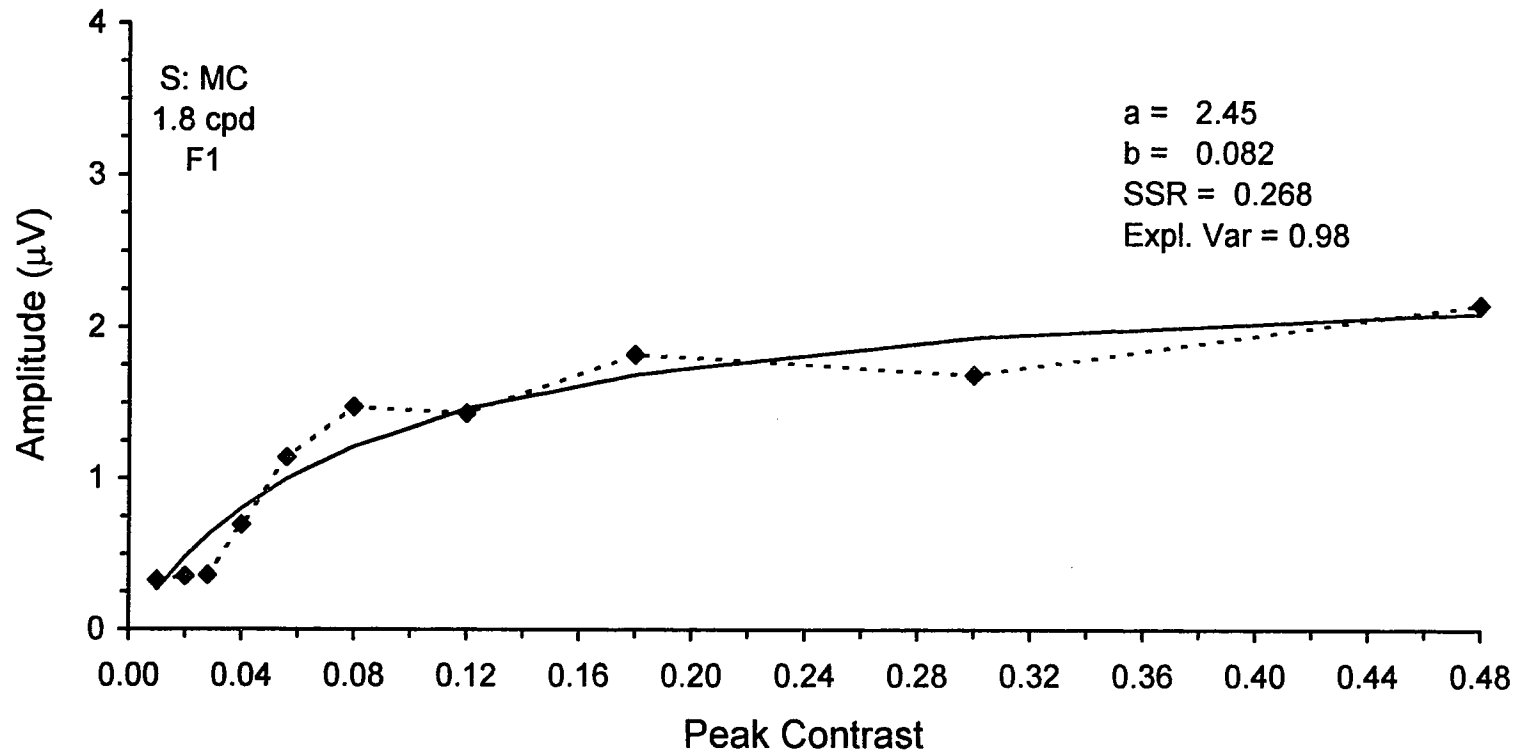
flicker detection

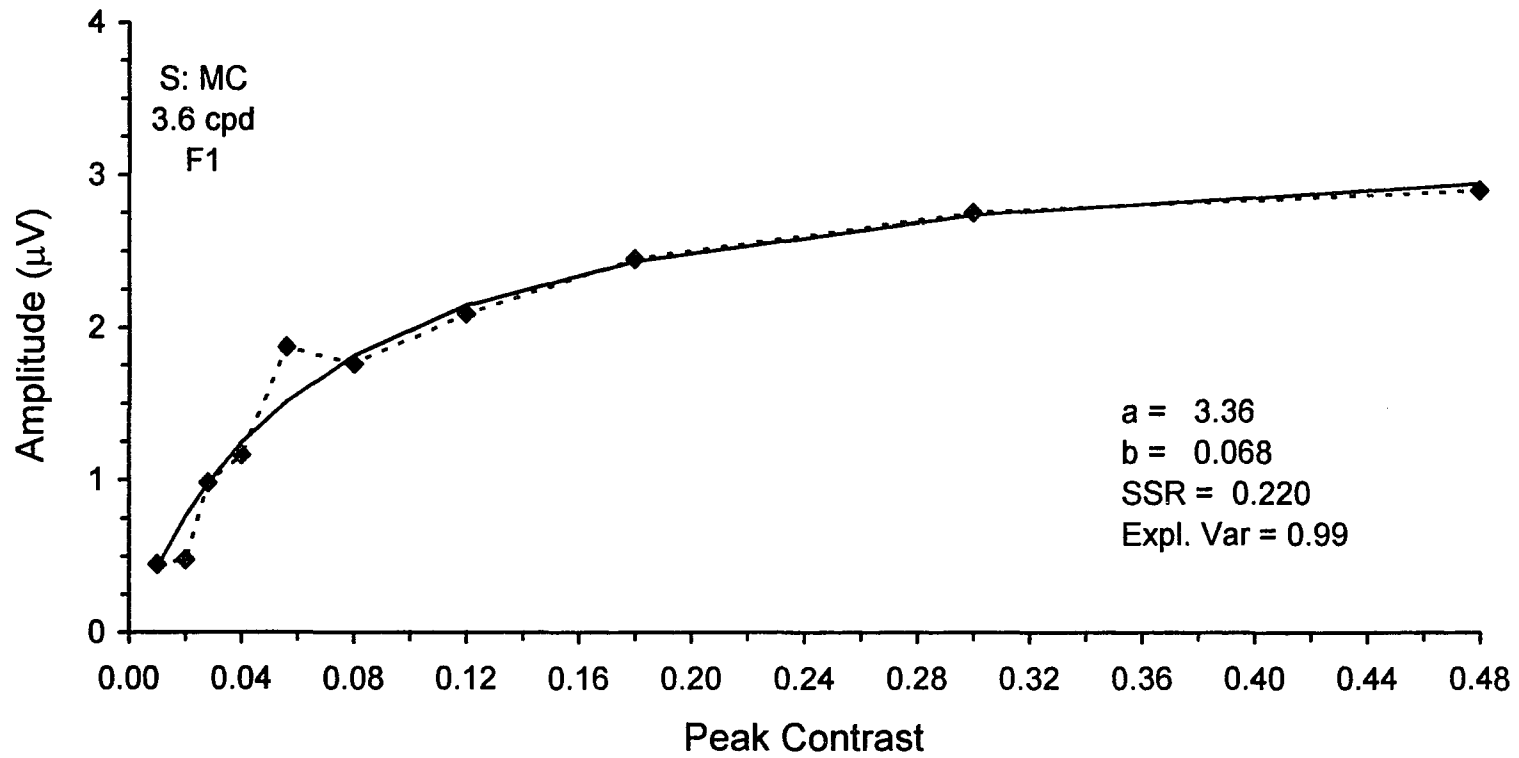


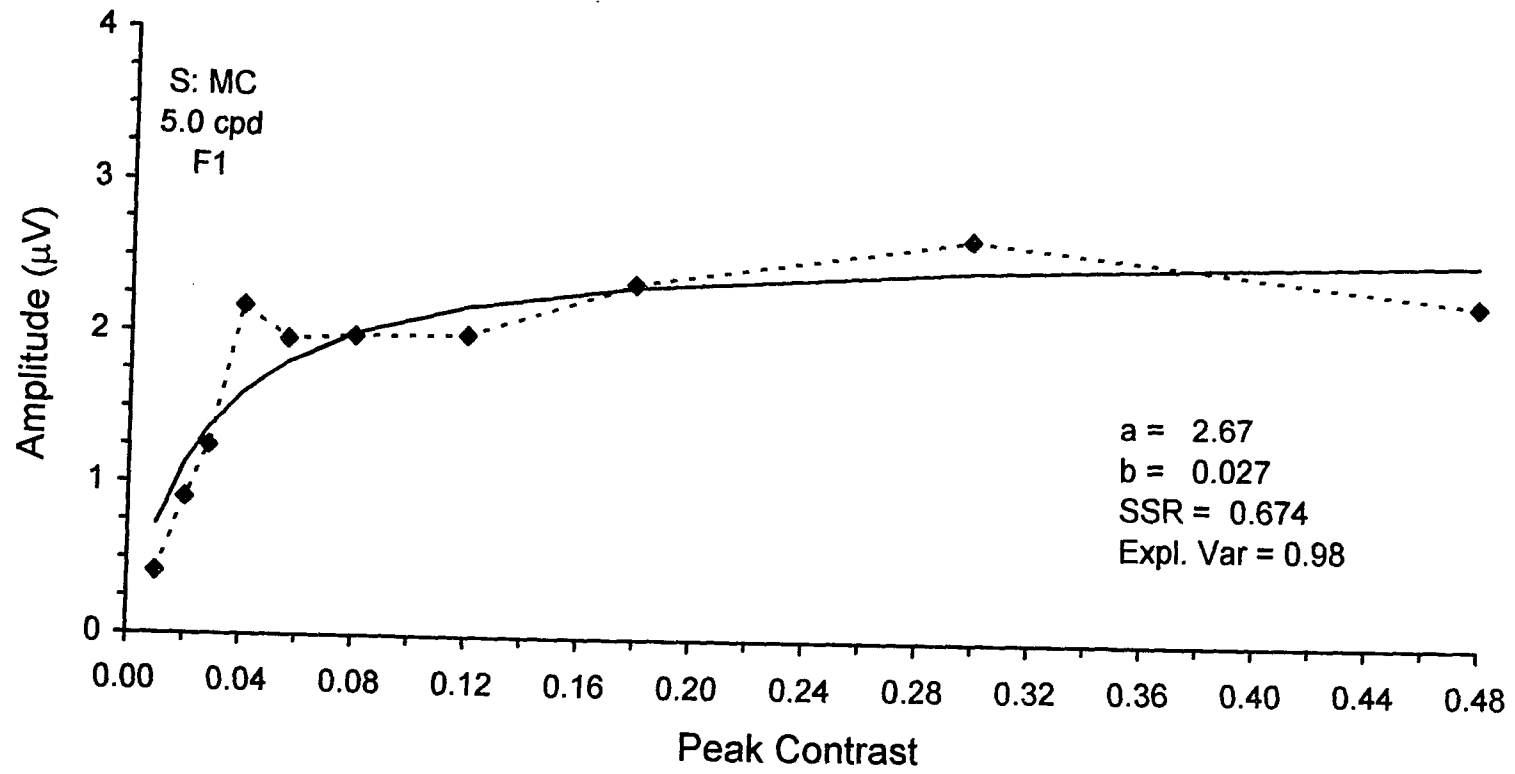
Appendix C

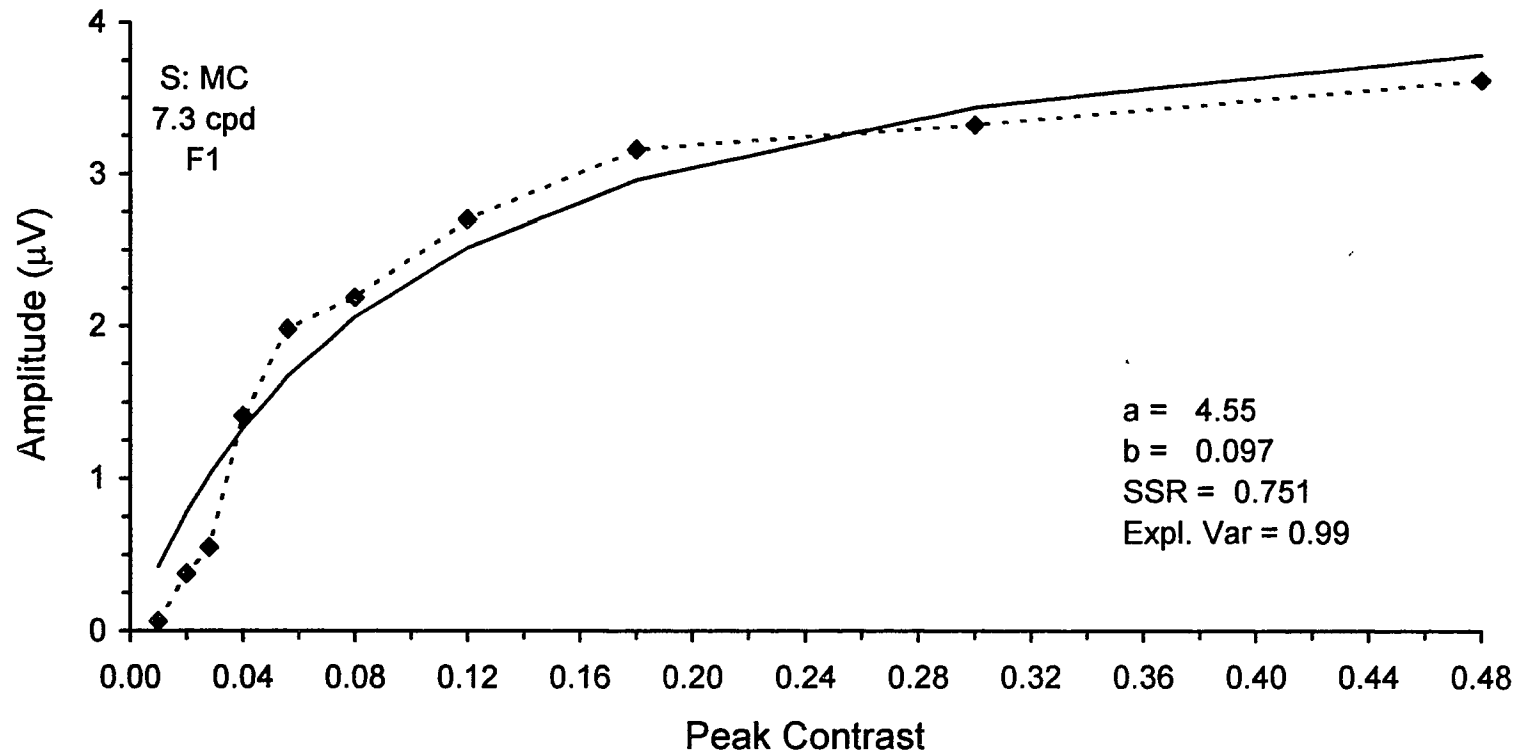
Michaelis-Menten Equation		$Y = aX / (b + X)$							
S: MC									
Fundamental (F1)					Second Harmonic (F2)				
SF (cpd)	a	b	SSR	Var(expl)	a	b	SSR	Var(expl)	
0.9	2.19	0.298	0.390	0.92	5.40	0.265	0.236	0.99	
1.8	2.45	0.082	0.268	0.98	4.37	0.117	1.051	0.98	
3.6	3.36	0.068	0.220	0.99	1.31	0.013	0.822	0.93	
5.0	2.67	0.027	0.674	0.98	1.53	0.016	2.086	0.87	
7.3	4.55	0.097	0.751	0.99	1.15	0.021	1.081	0.87	
S: JC									
Fundamental (F1)					Second Harmonic (F2)				
SF (cpd)	a	b	SSR	Var(expl)	a	b	SSR	Var(expl)	
0.9	3.15	0.135	0.670	0.97	4.79	0.346	0.138	0.99	
1.8	4.54	0.089	1.076	0.98	3.48	0.199	0.209	0.99	
3.6	4.67	0.033	3.415	0.97	1.21	0.032	0.458	0.94	
5.0	4.86	0.038	1.874	0.98	1.38	0.097	0.423	0.92	
7.3	5.74	0.054	1.801	0.98	0.94	0.080	0.646	0.80	
7.3*	1.91	0.013	1.266	0.95	1.86	0.317	0.097	0.97	
10.0*	1.47	0.024	2.107	0.85	0.96	0.163	0.233	0.87	
14.6*	3.70	0.202	0.833	0.96	0.67	0.063	0.307	0.83	
S: DS									
Fundamental (F1)					Second Harmonic (F2)				
SF (cpd)	a	b	SSR	Var(expl)	a	b	SSR	Var(expl)	
0.9	0.30	0.008	0.123	0.84	8.05	1.663	0.083	0.99	
1.8	0.64	0.003	0.498	0.88	3.47	0.349	0.068	0.99	
3.6	1.78	0.021	1.251	0.93	3.41	0.363	0.105	0.99	
5.0	2.16	0.024	1.340	0.95	1.89	0.206	0.093	0.98	
7.3	3.03	0.046	1.329	0.96	1.59	0.296	0.057	0.98	
* at 114cm. test distance									

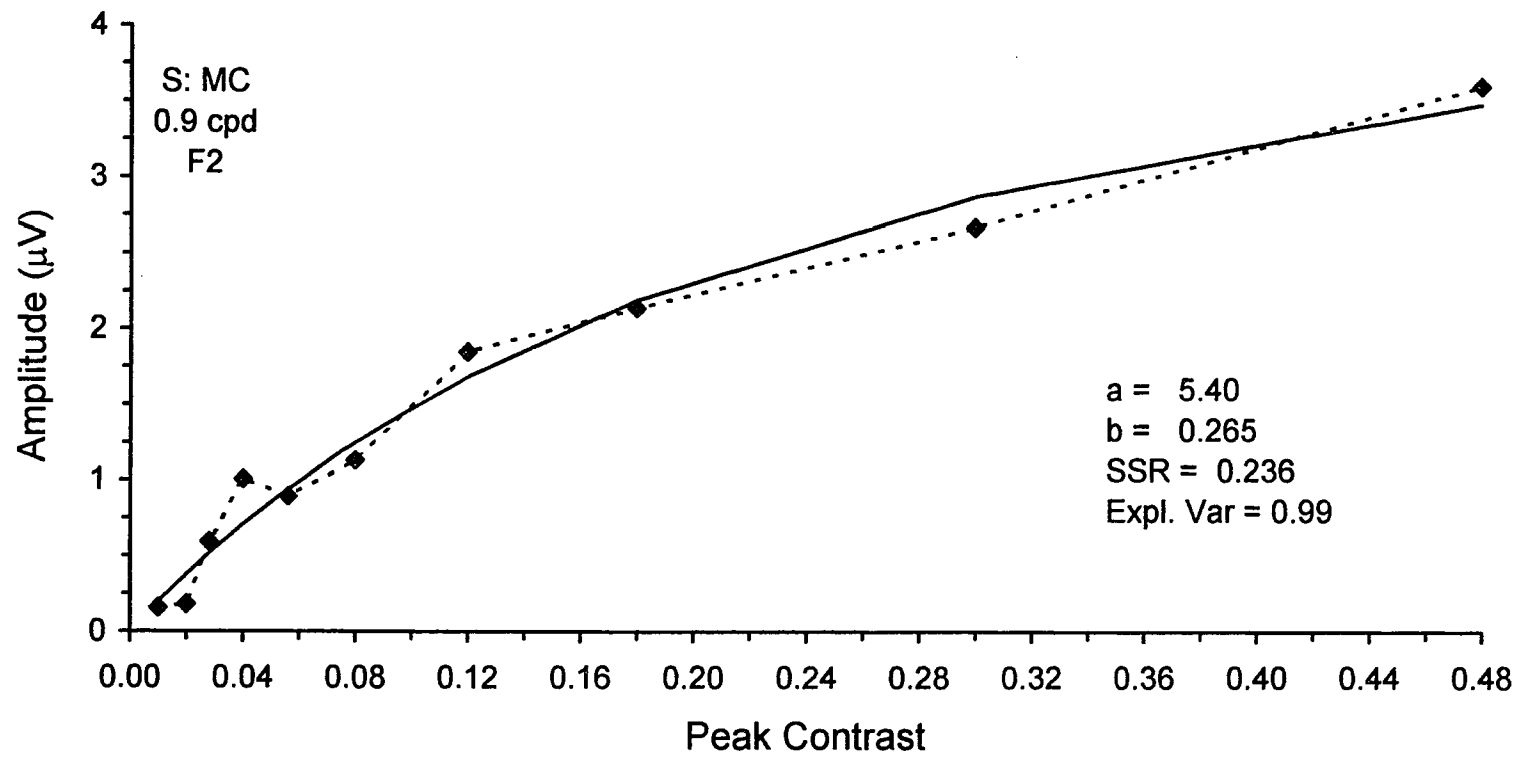


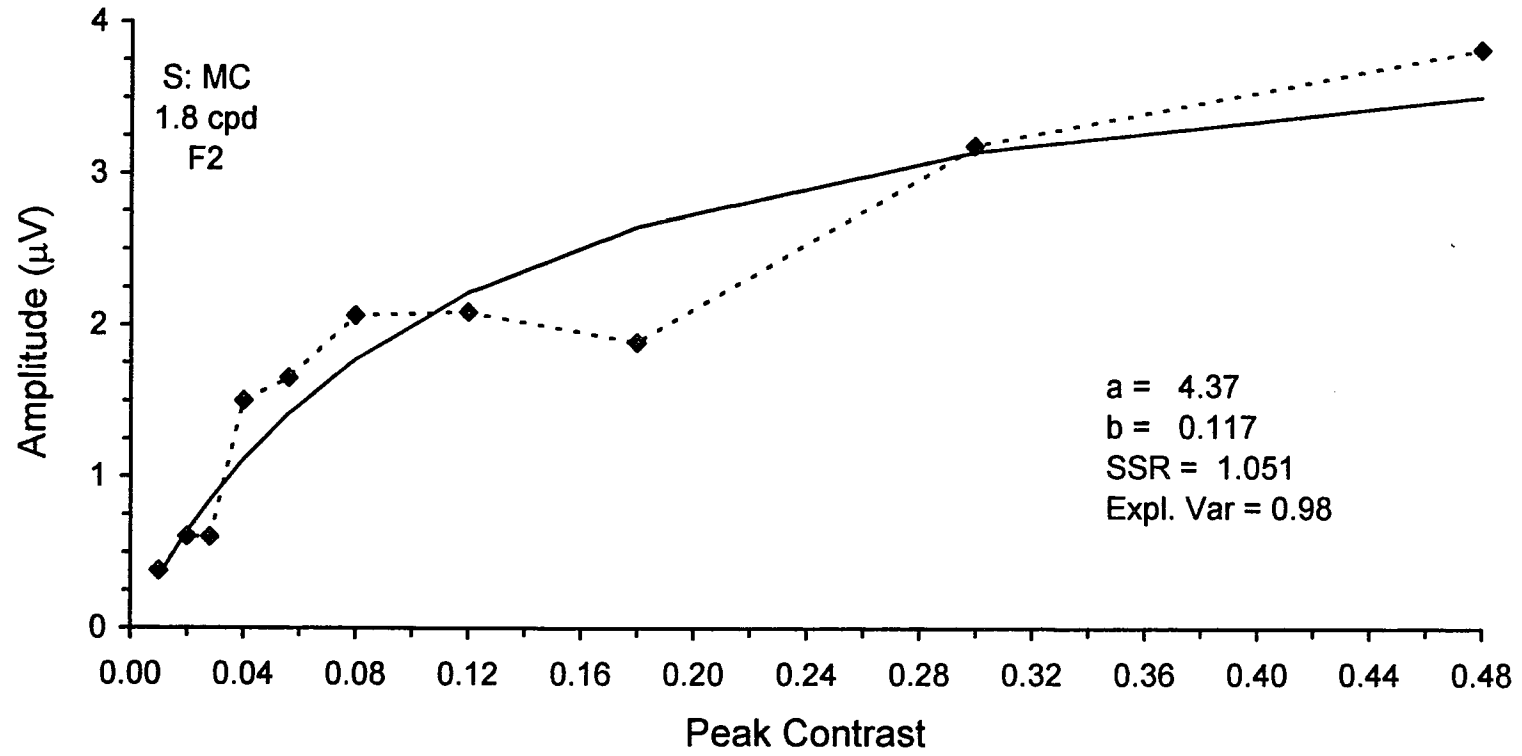


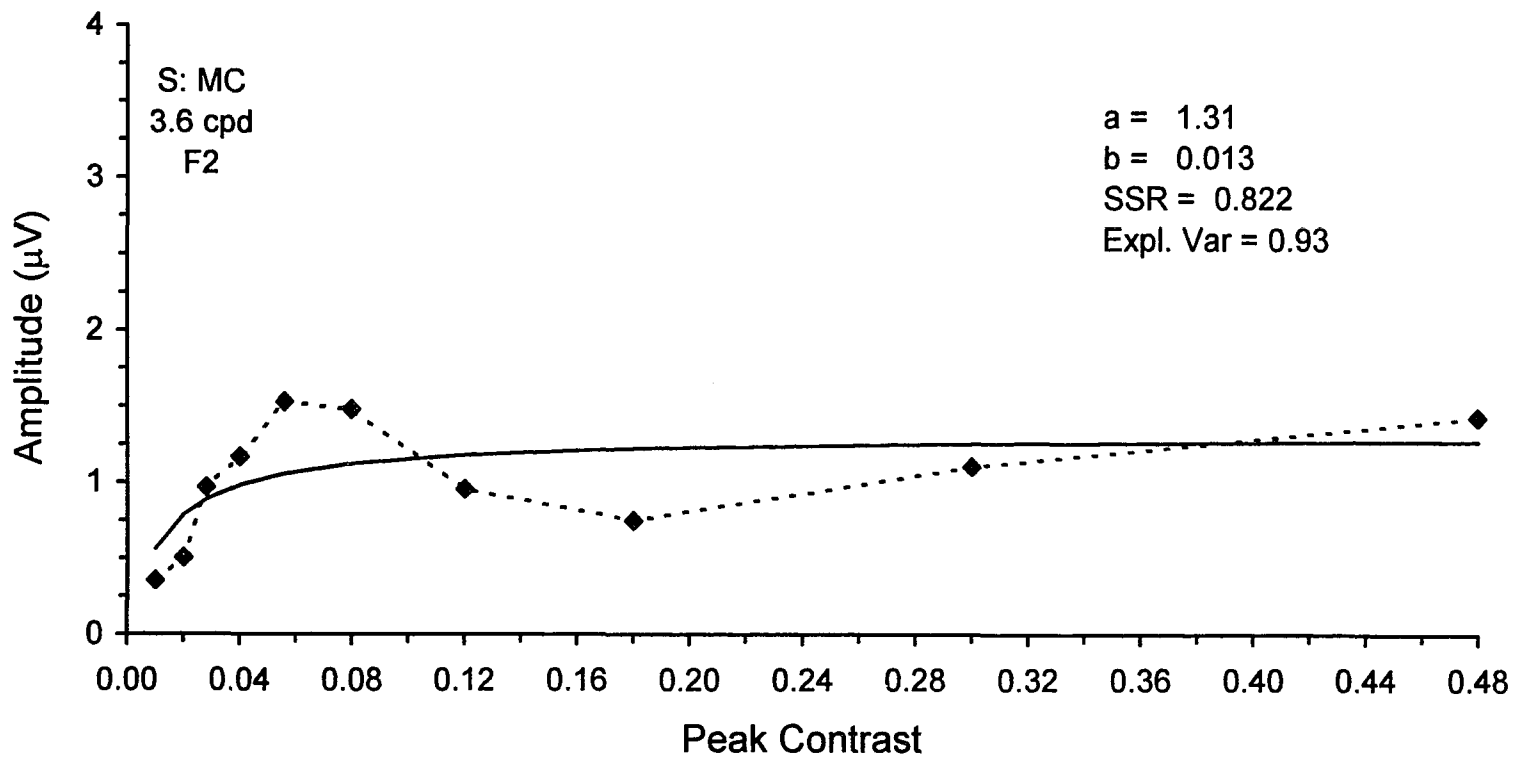


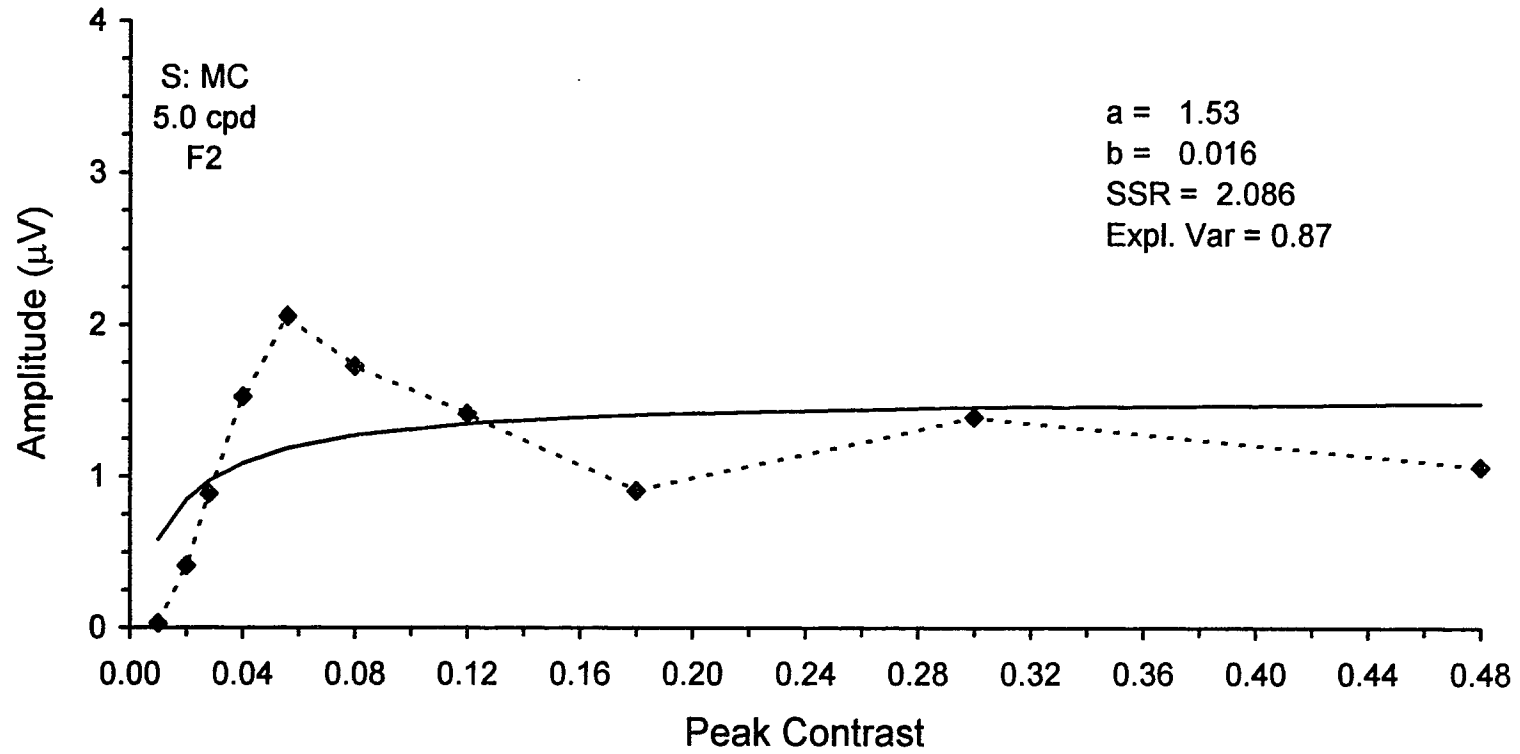


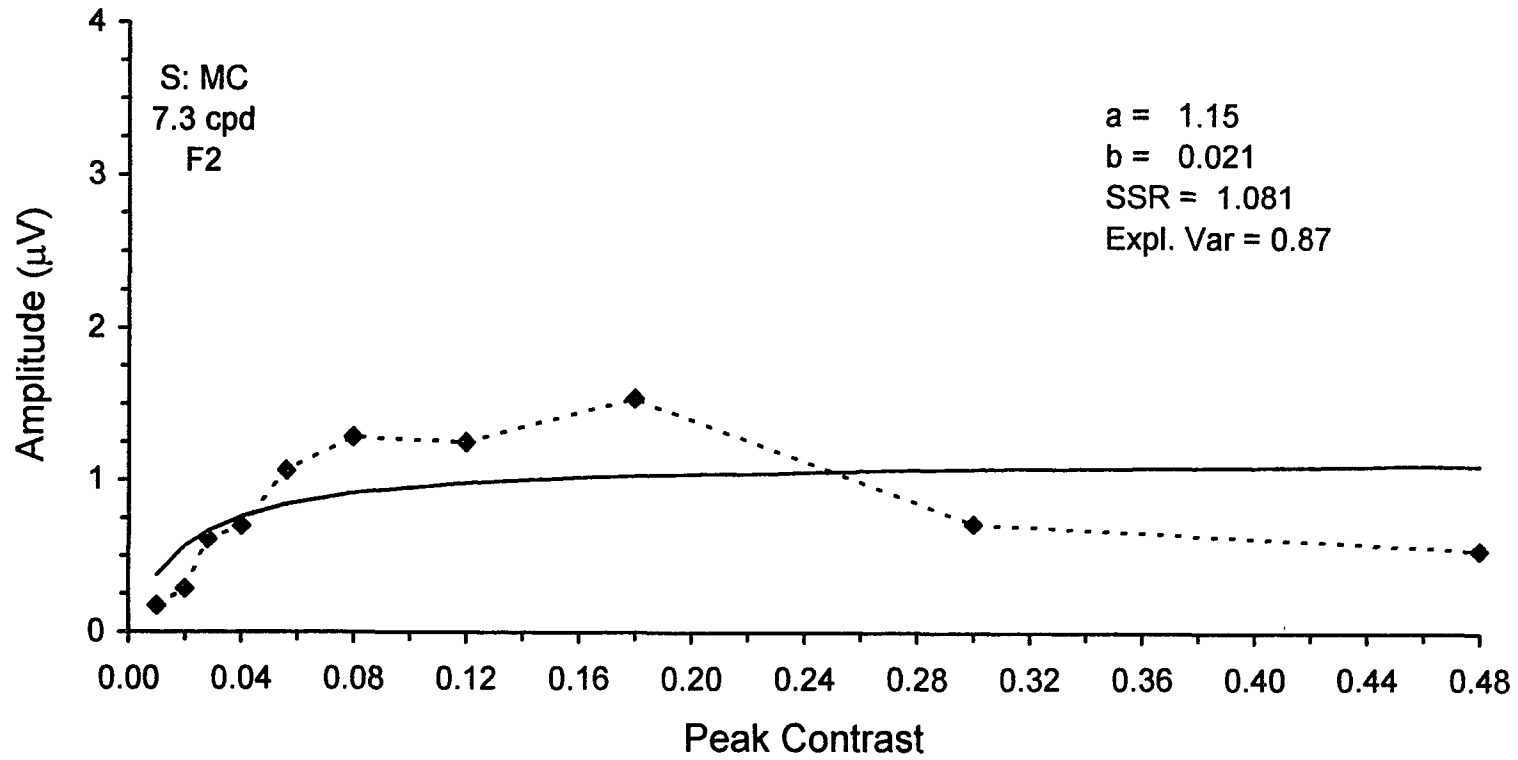


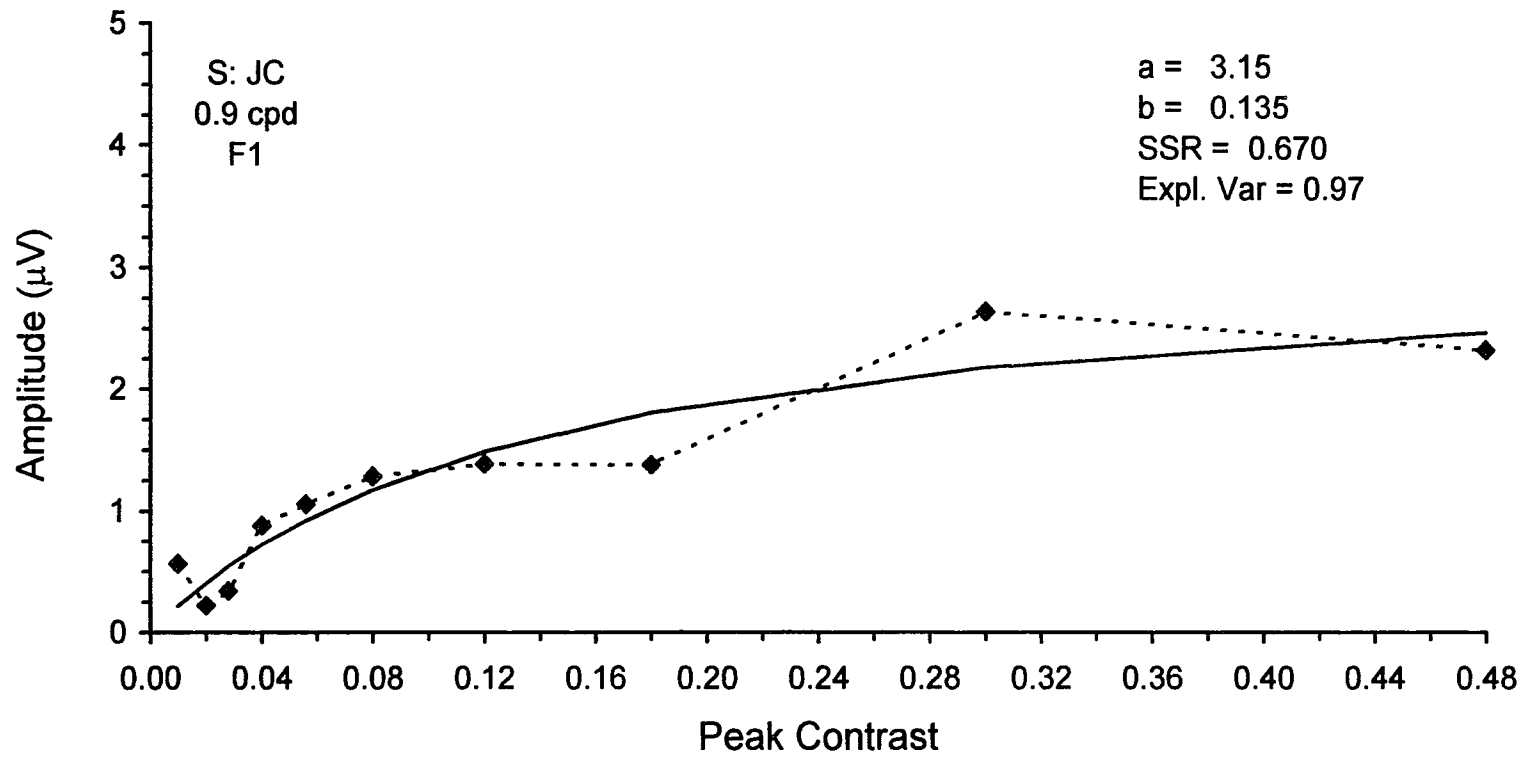


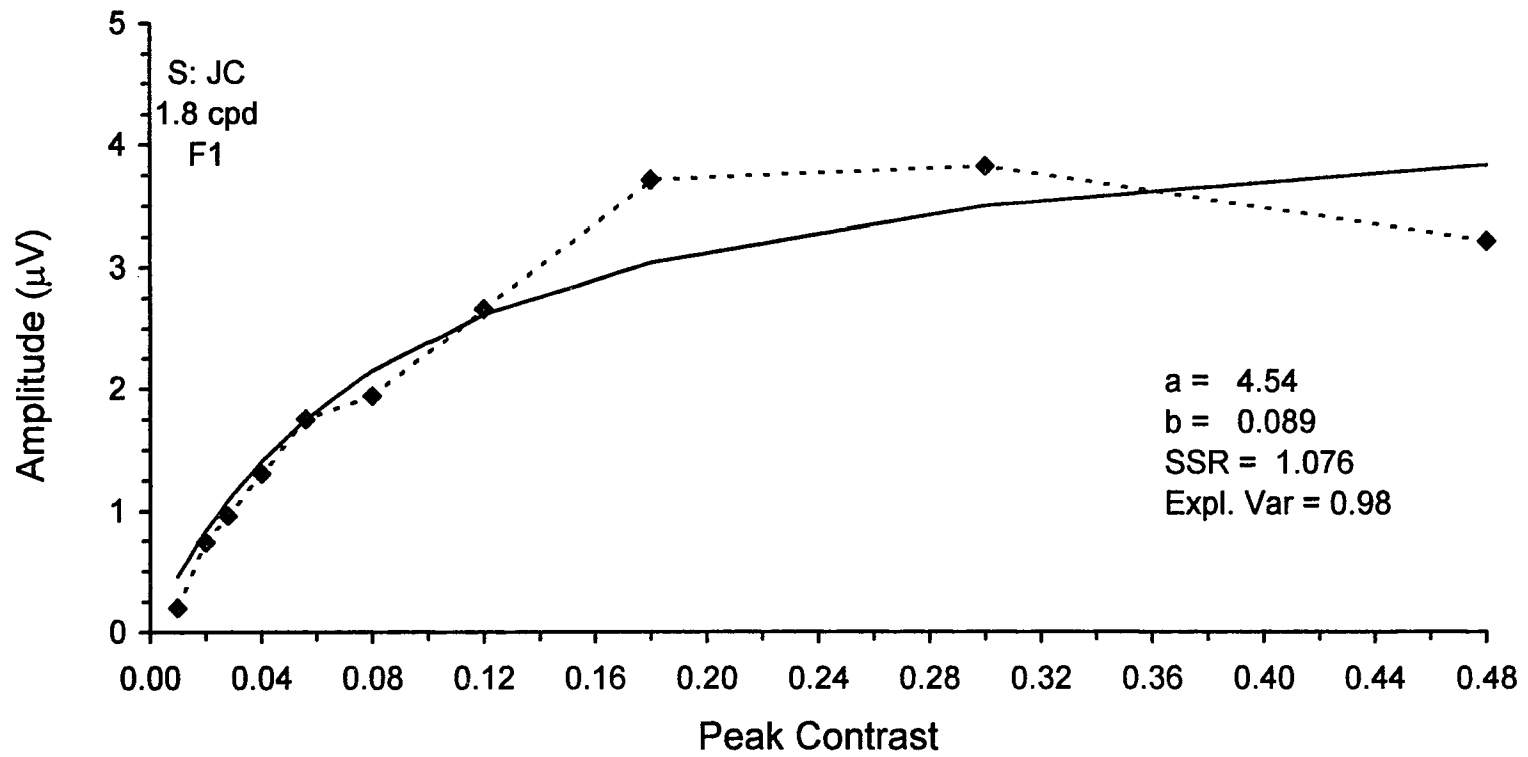


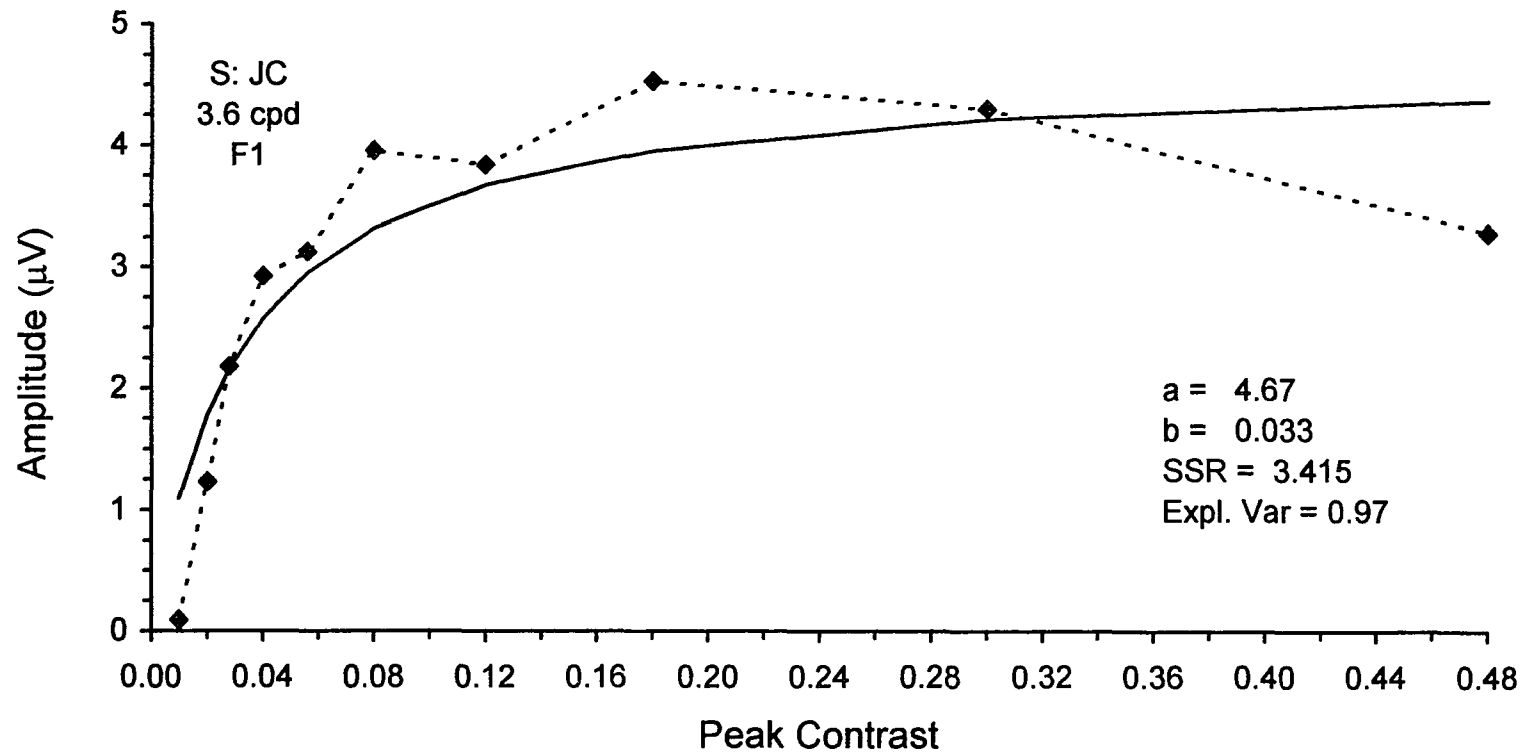


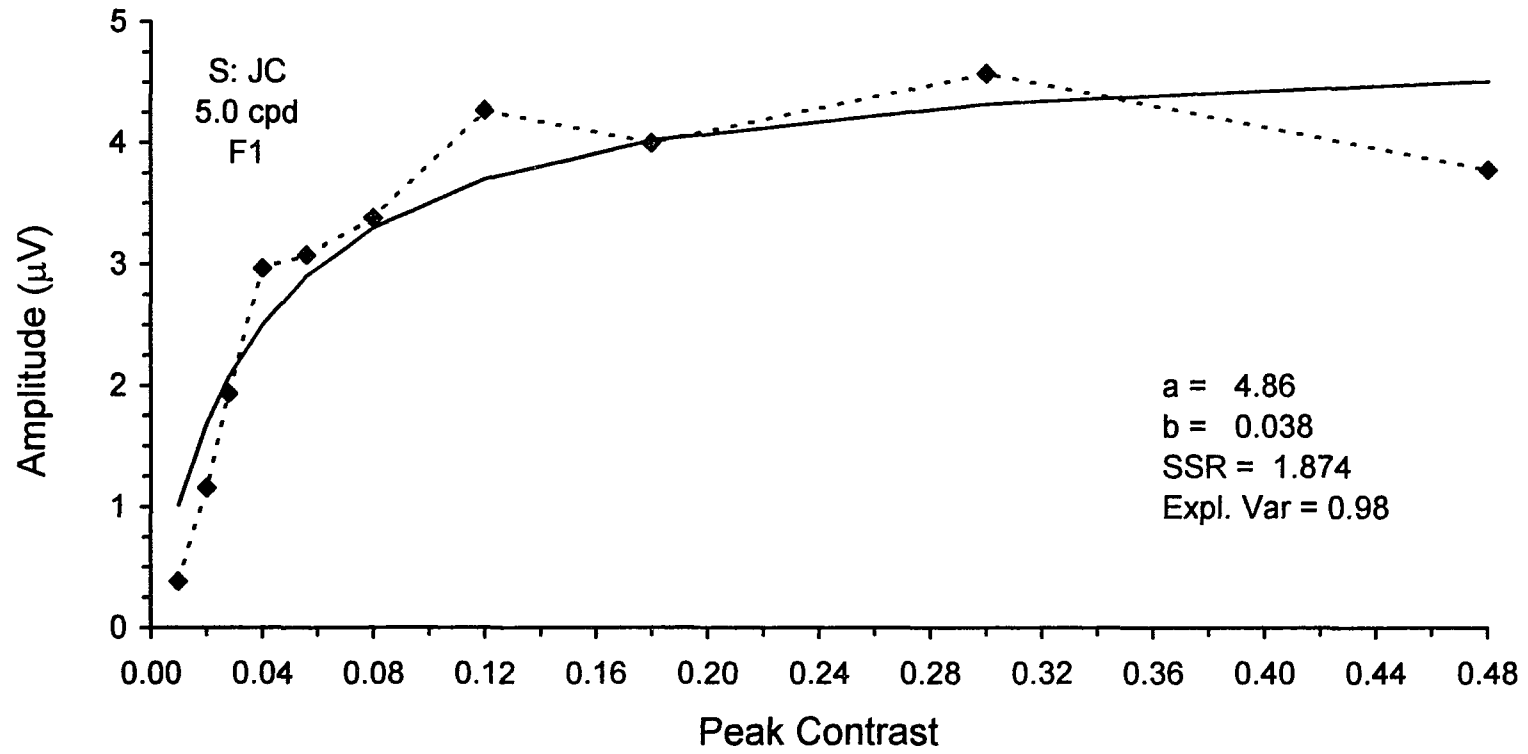


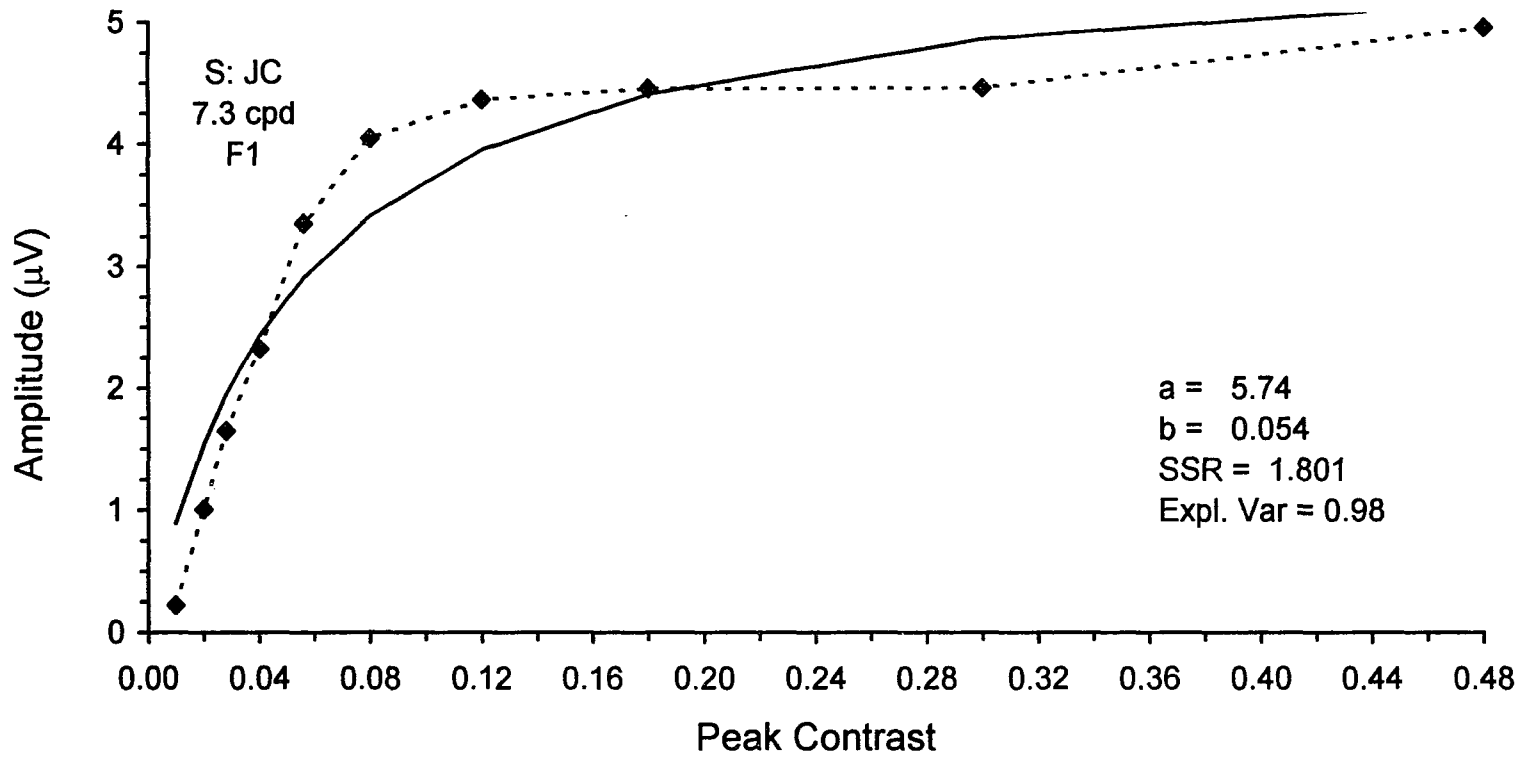


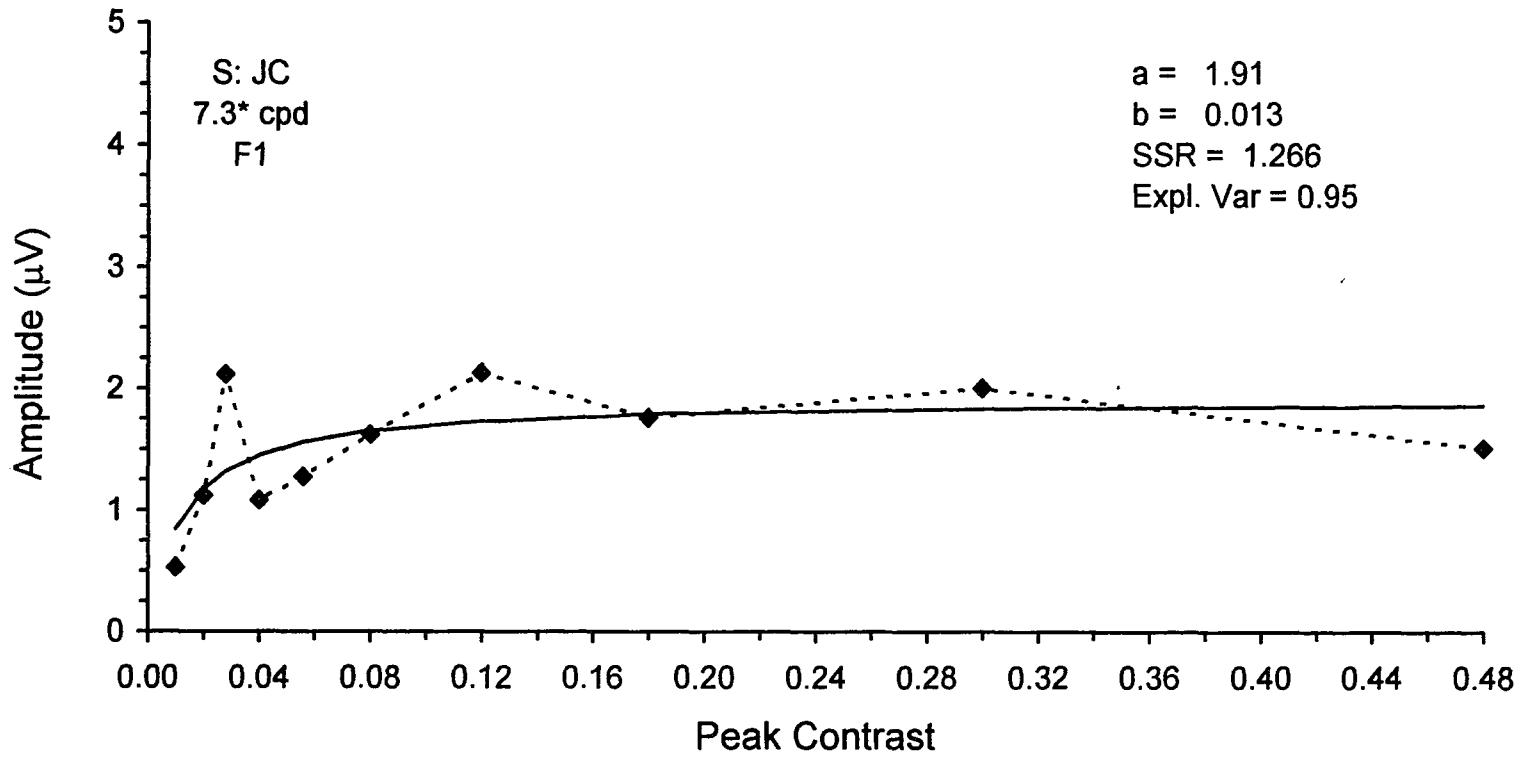


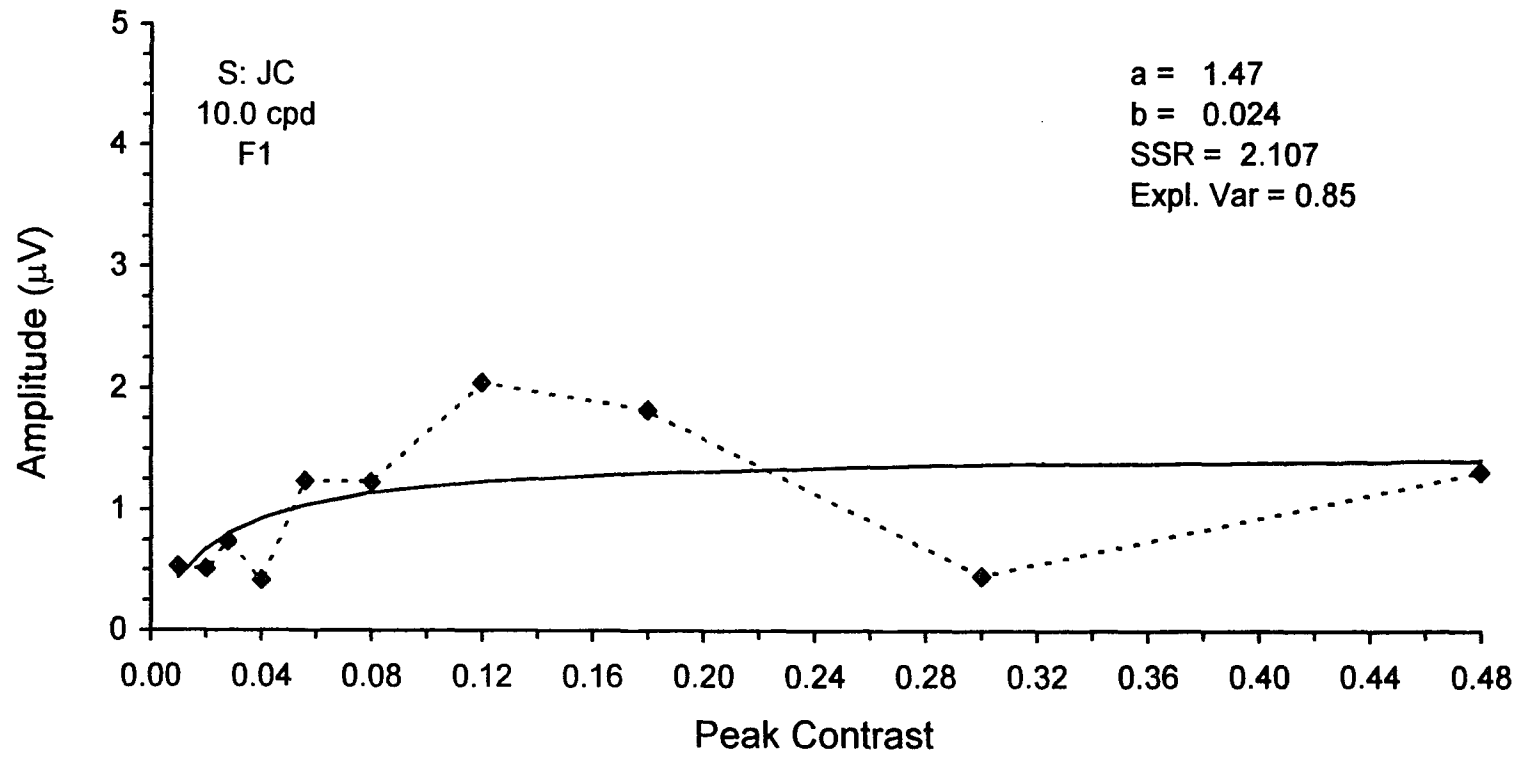


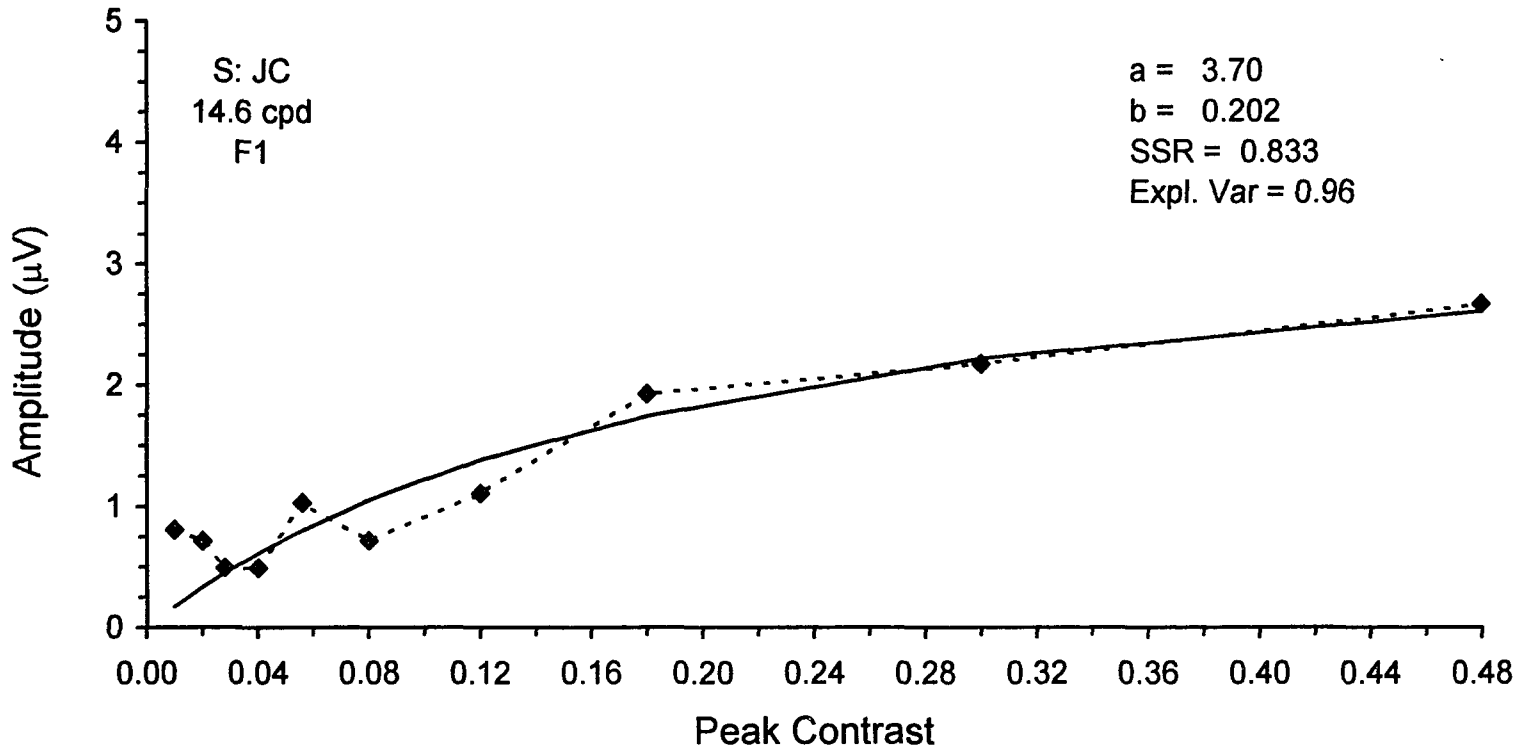


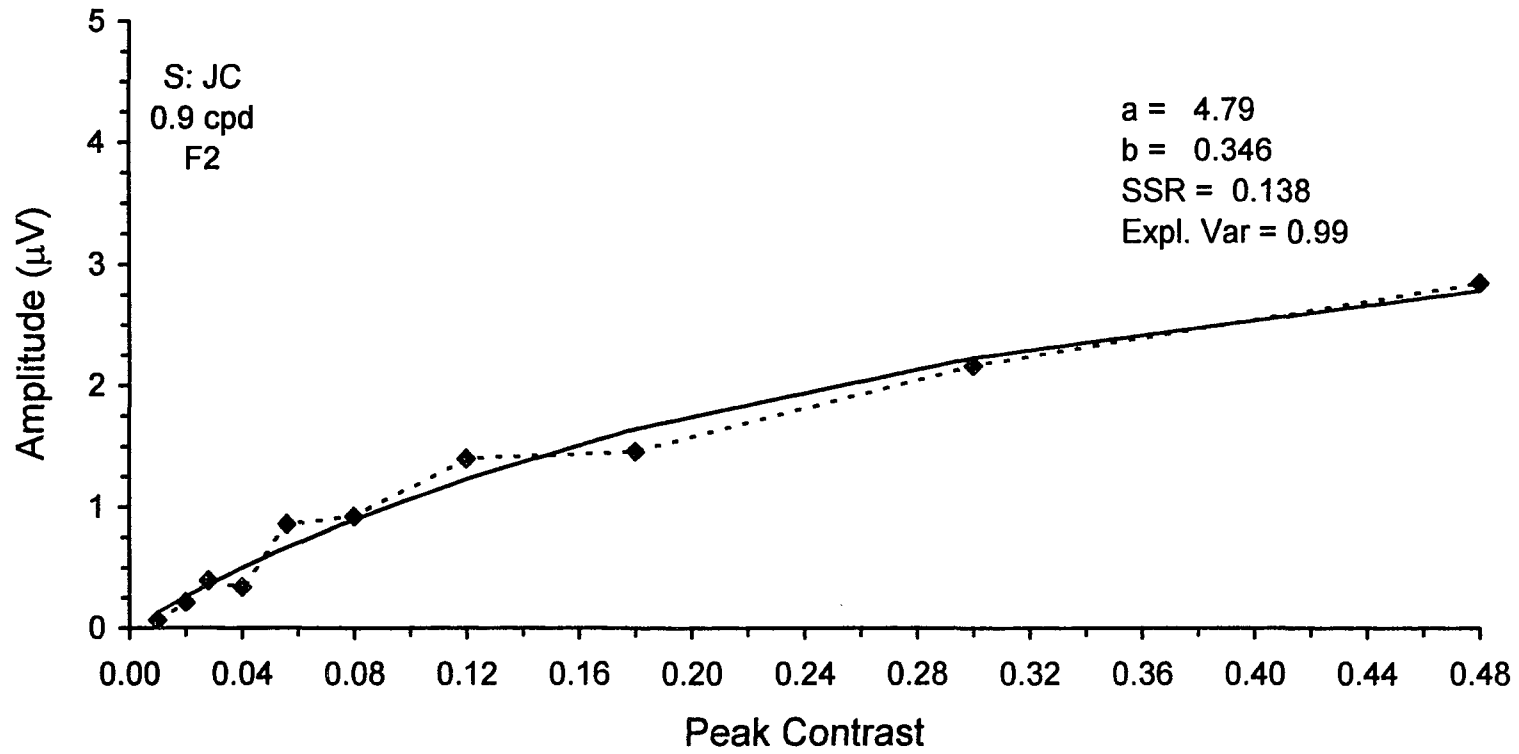


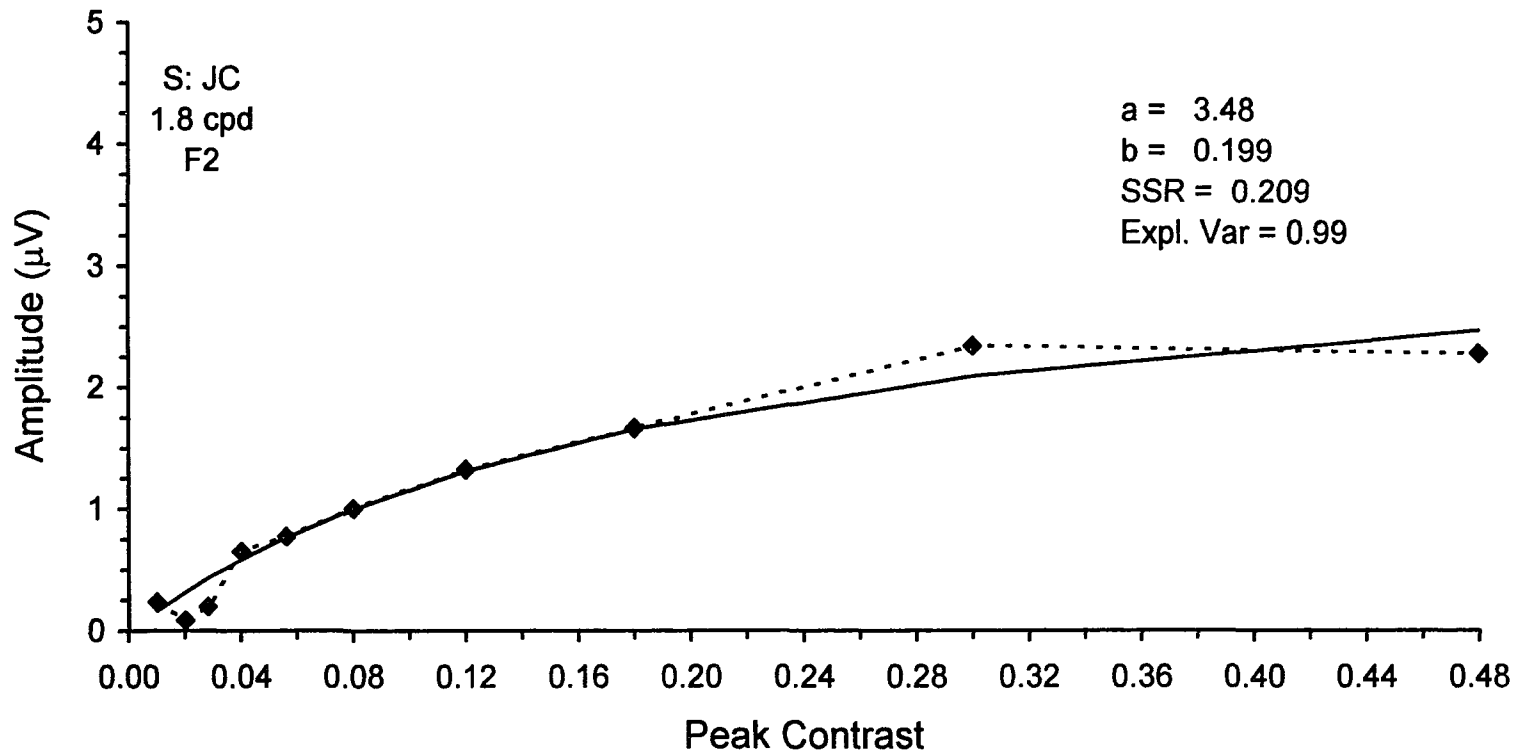


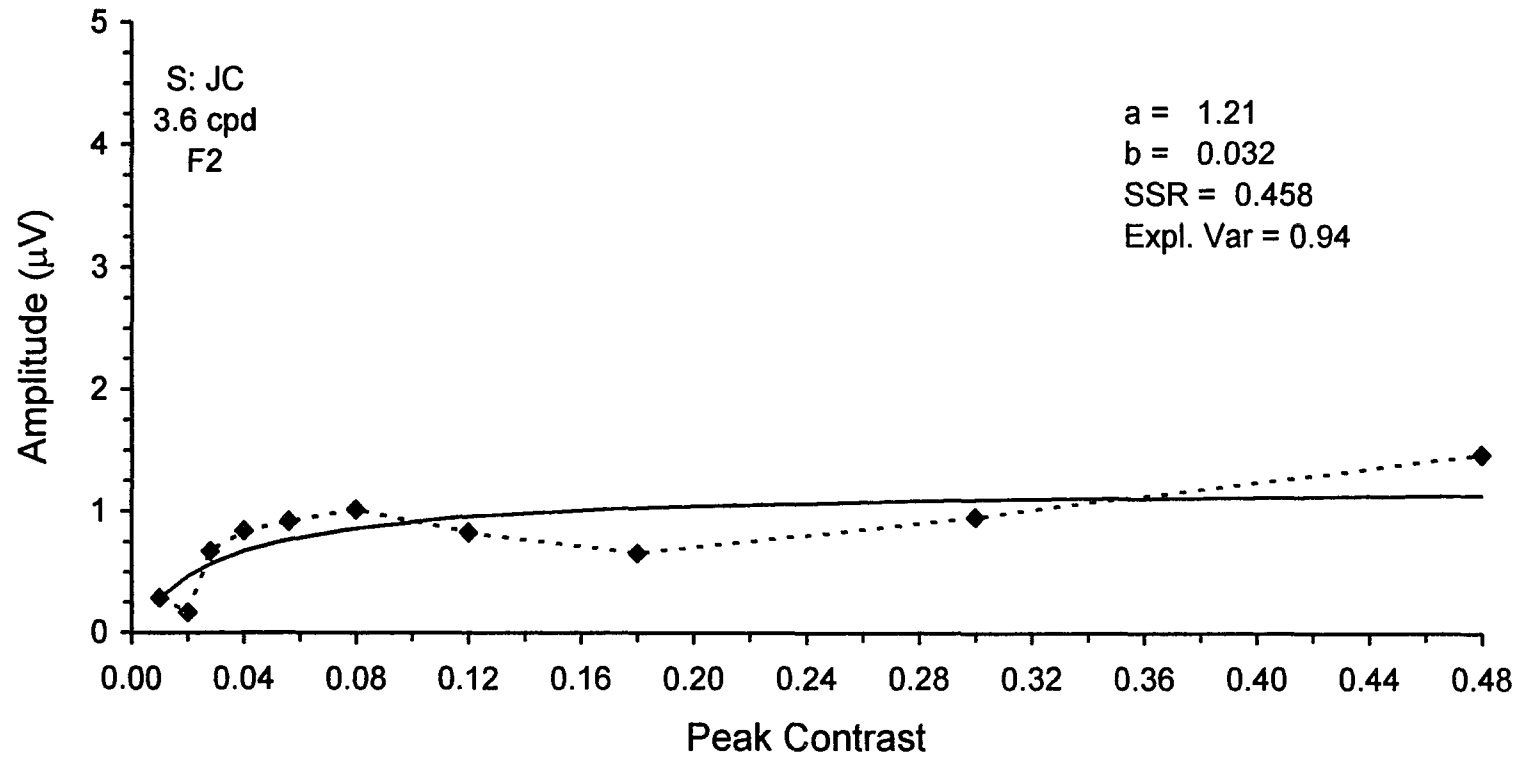


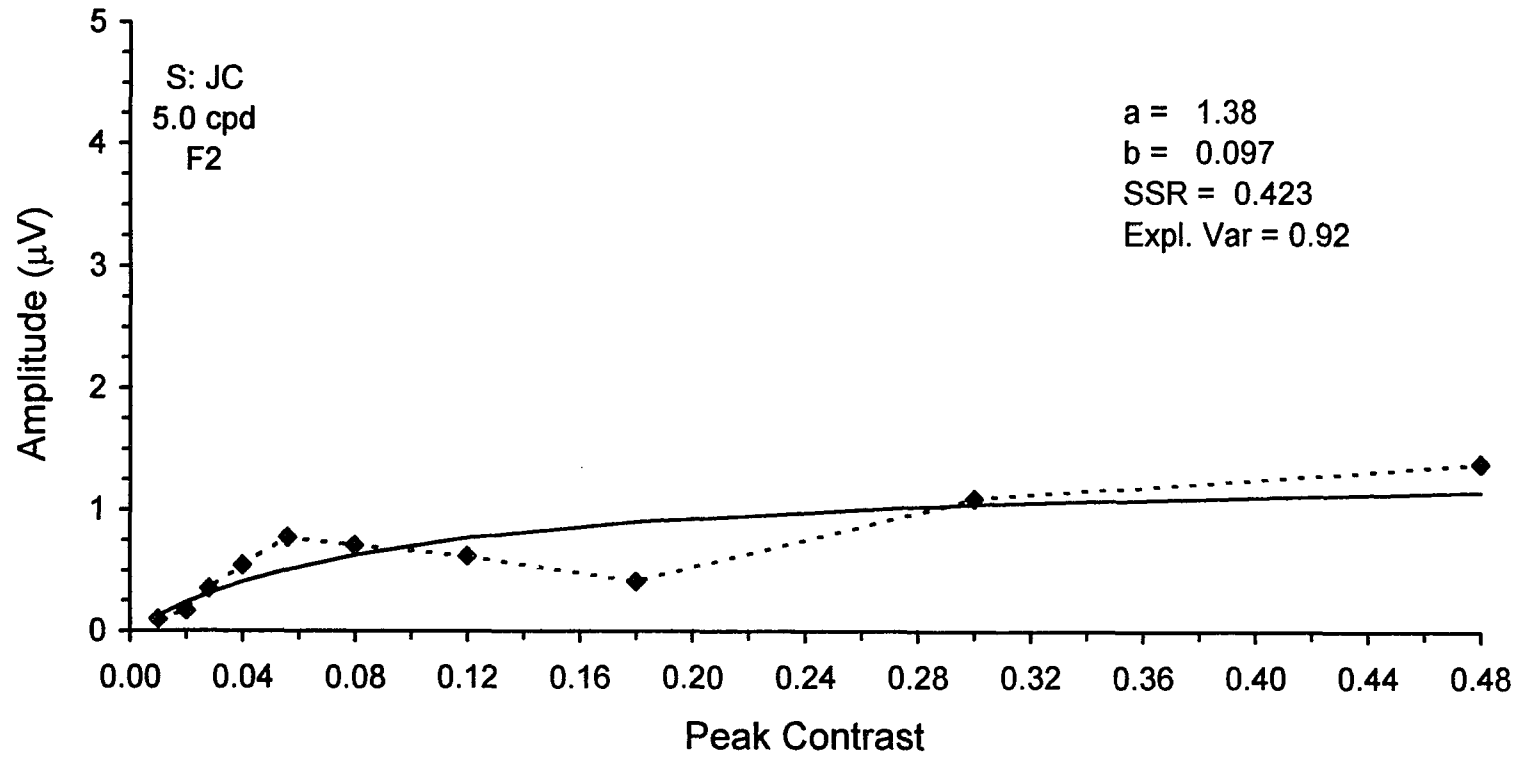


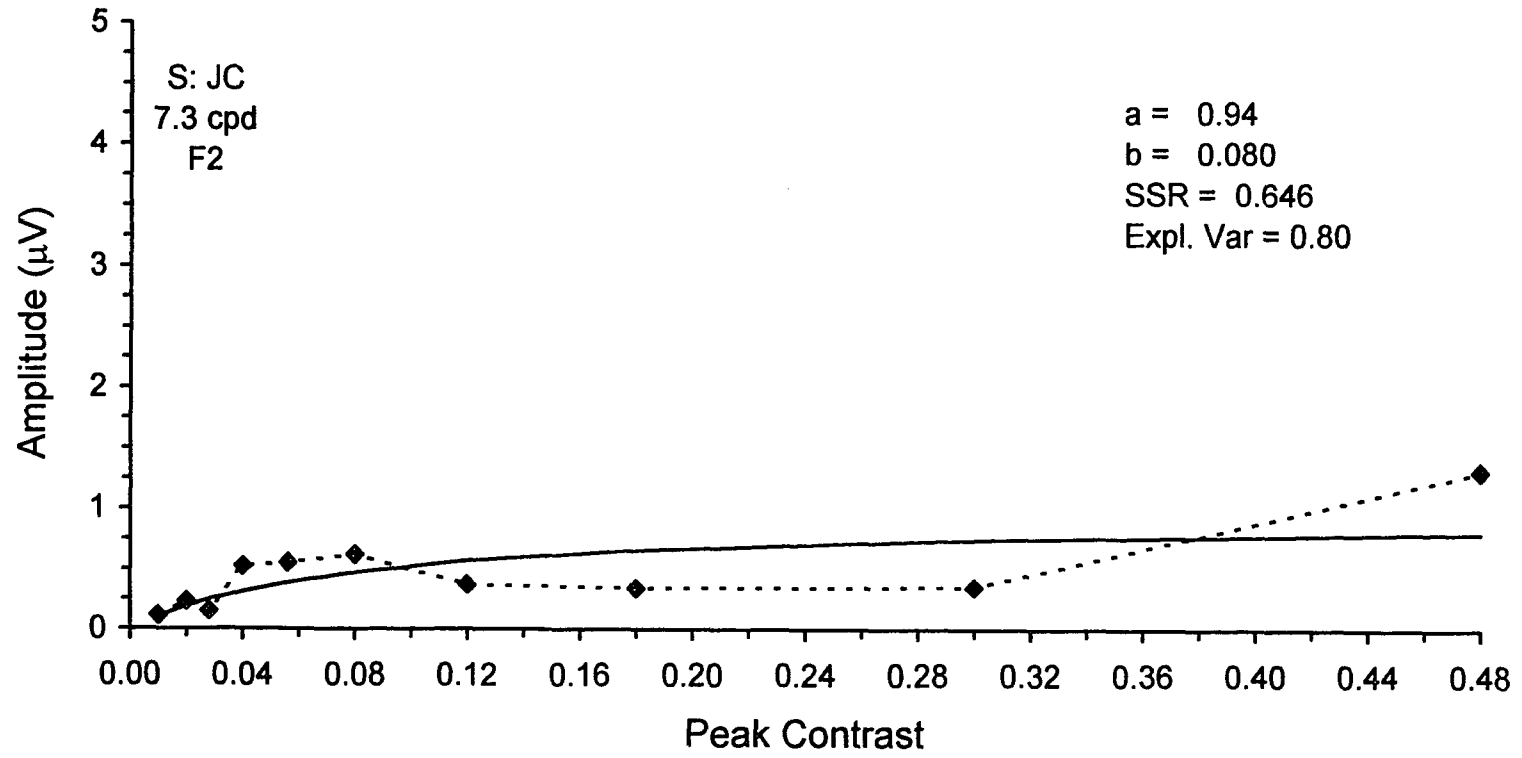


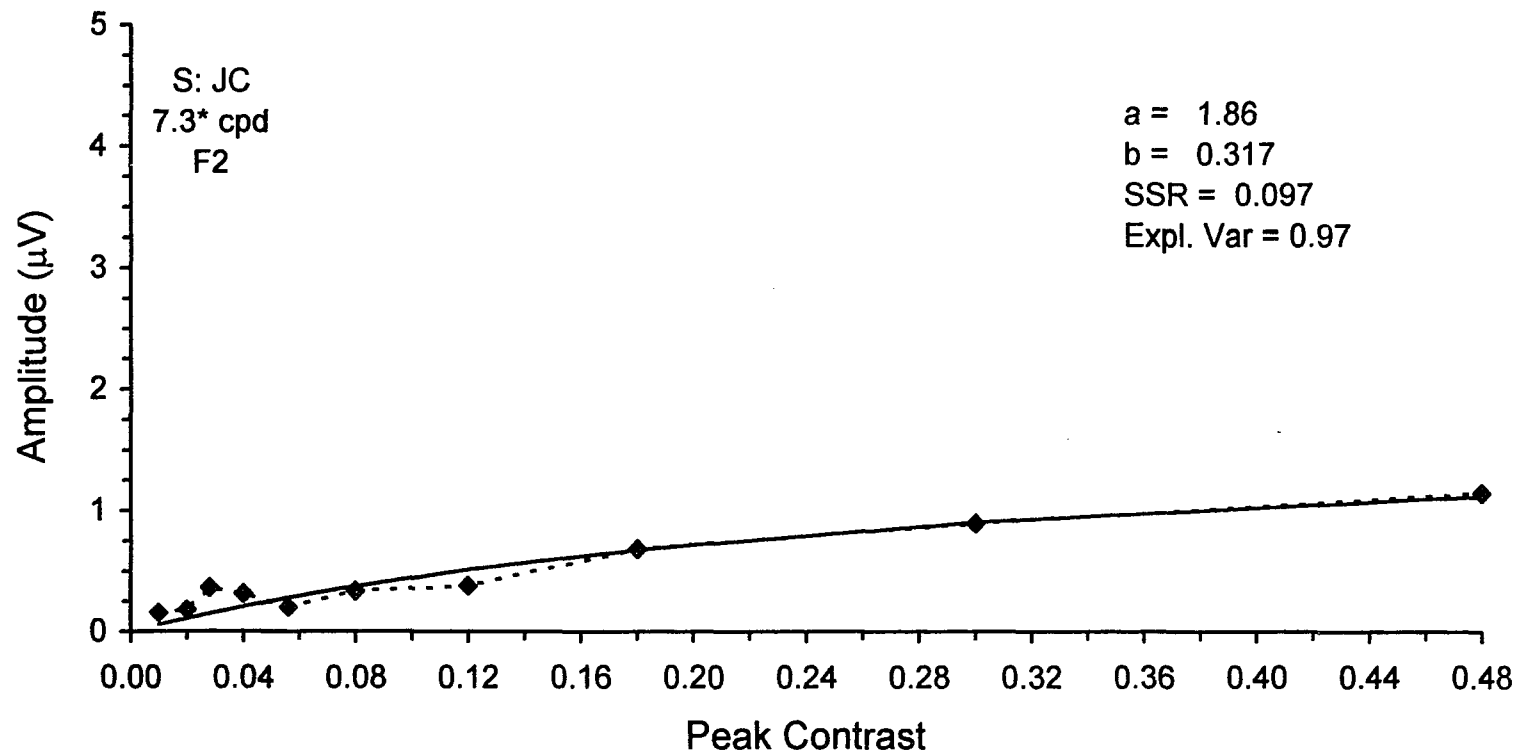


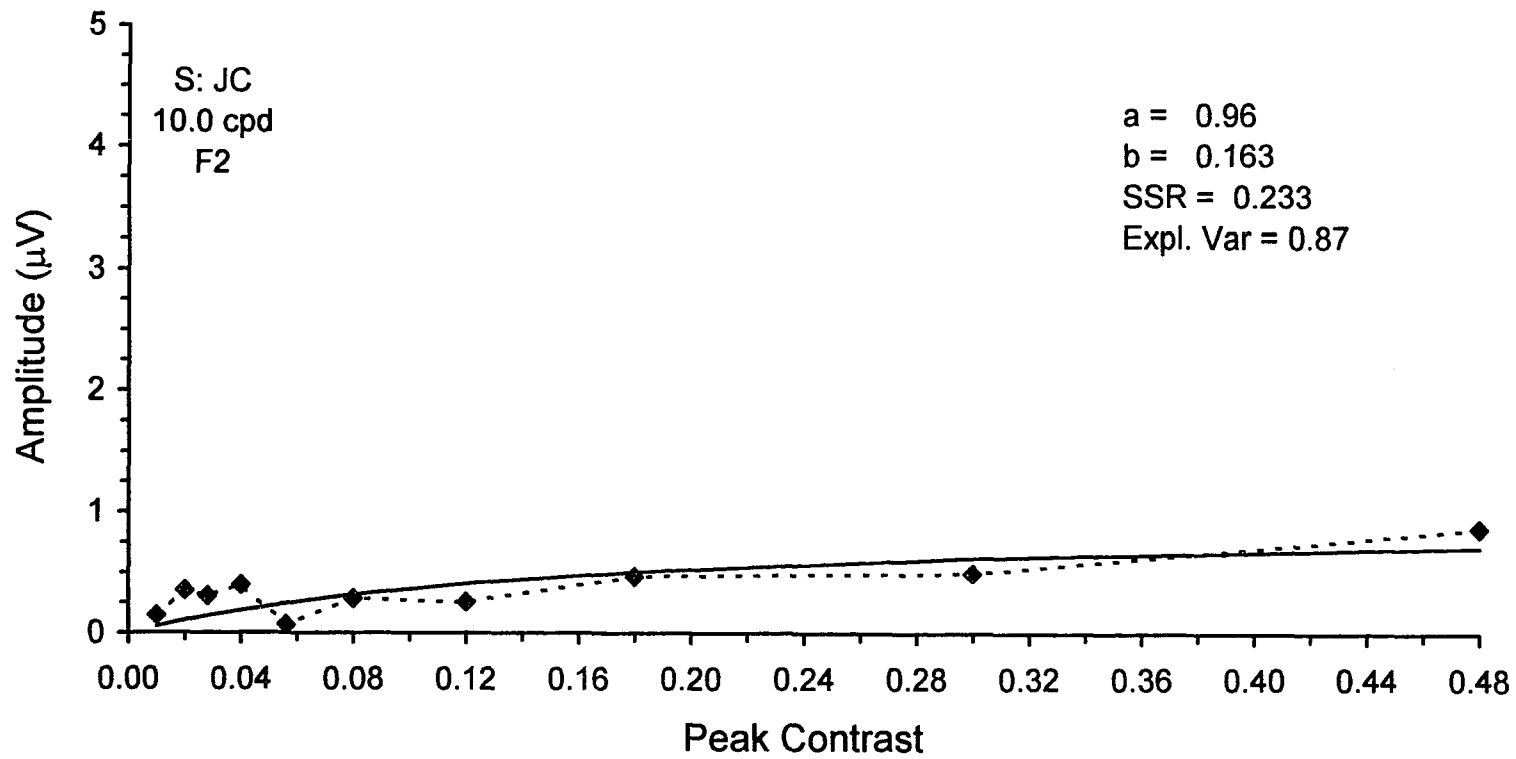


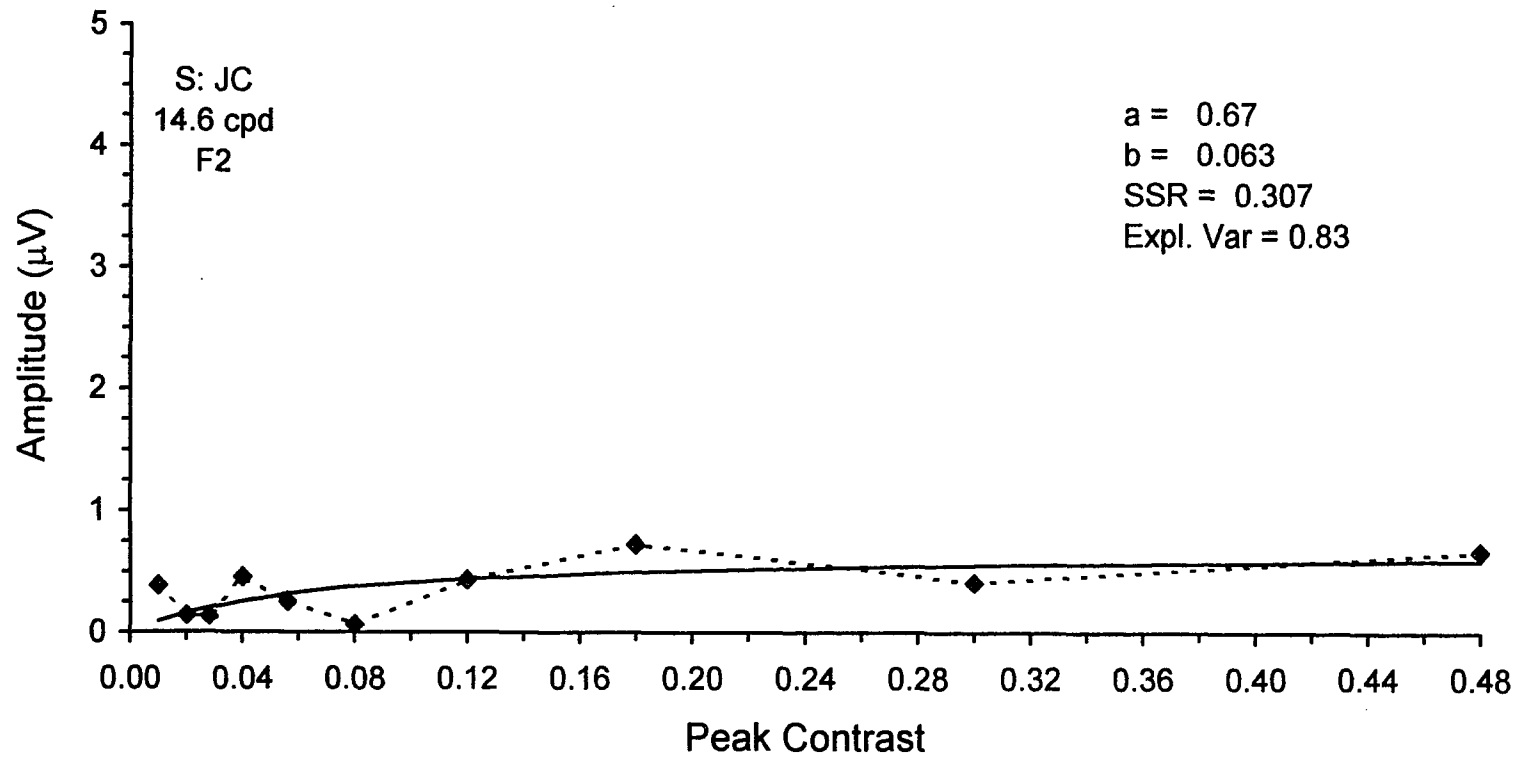


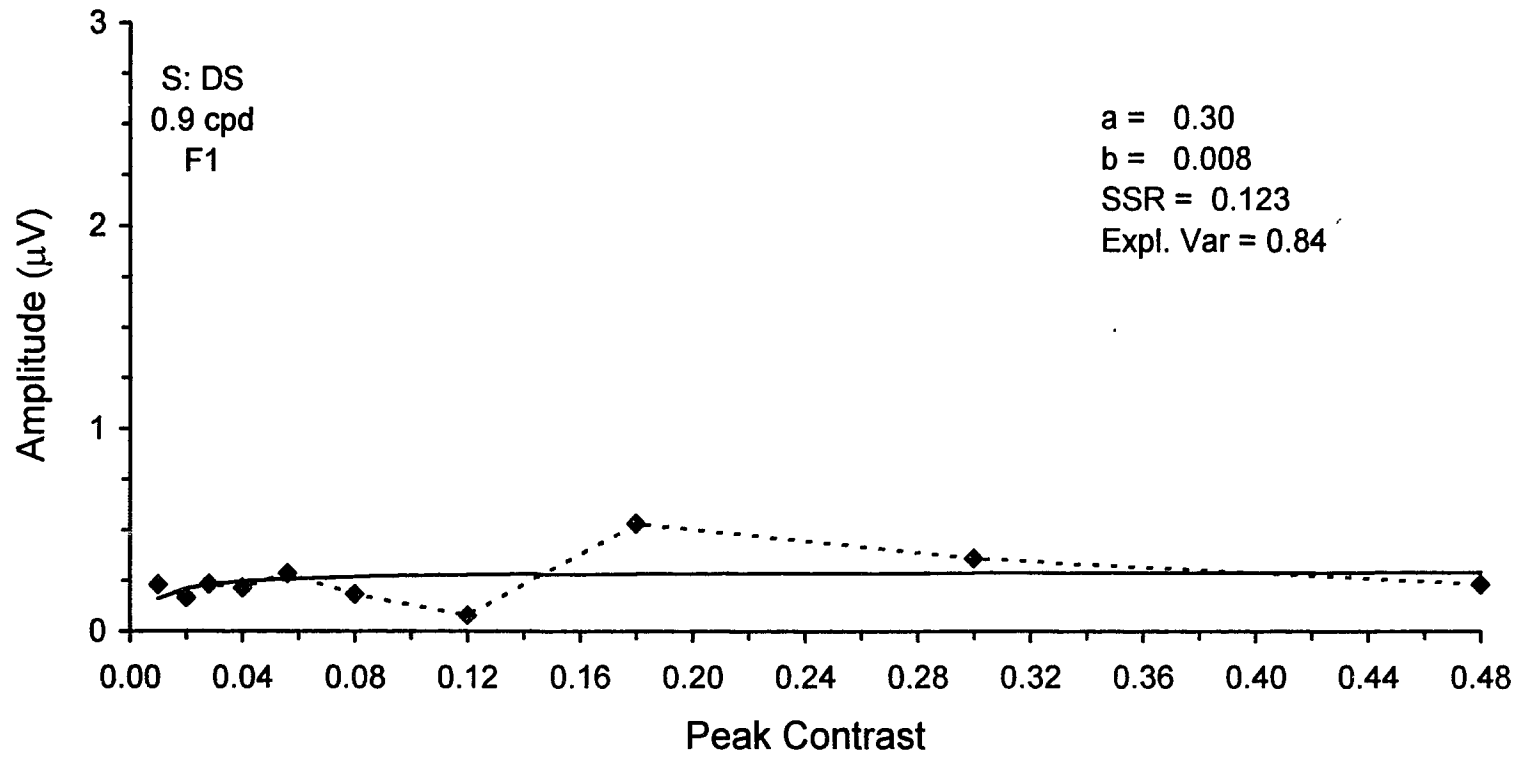


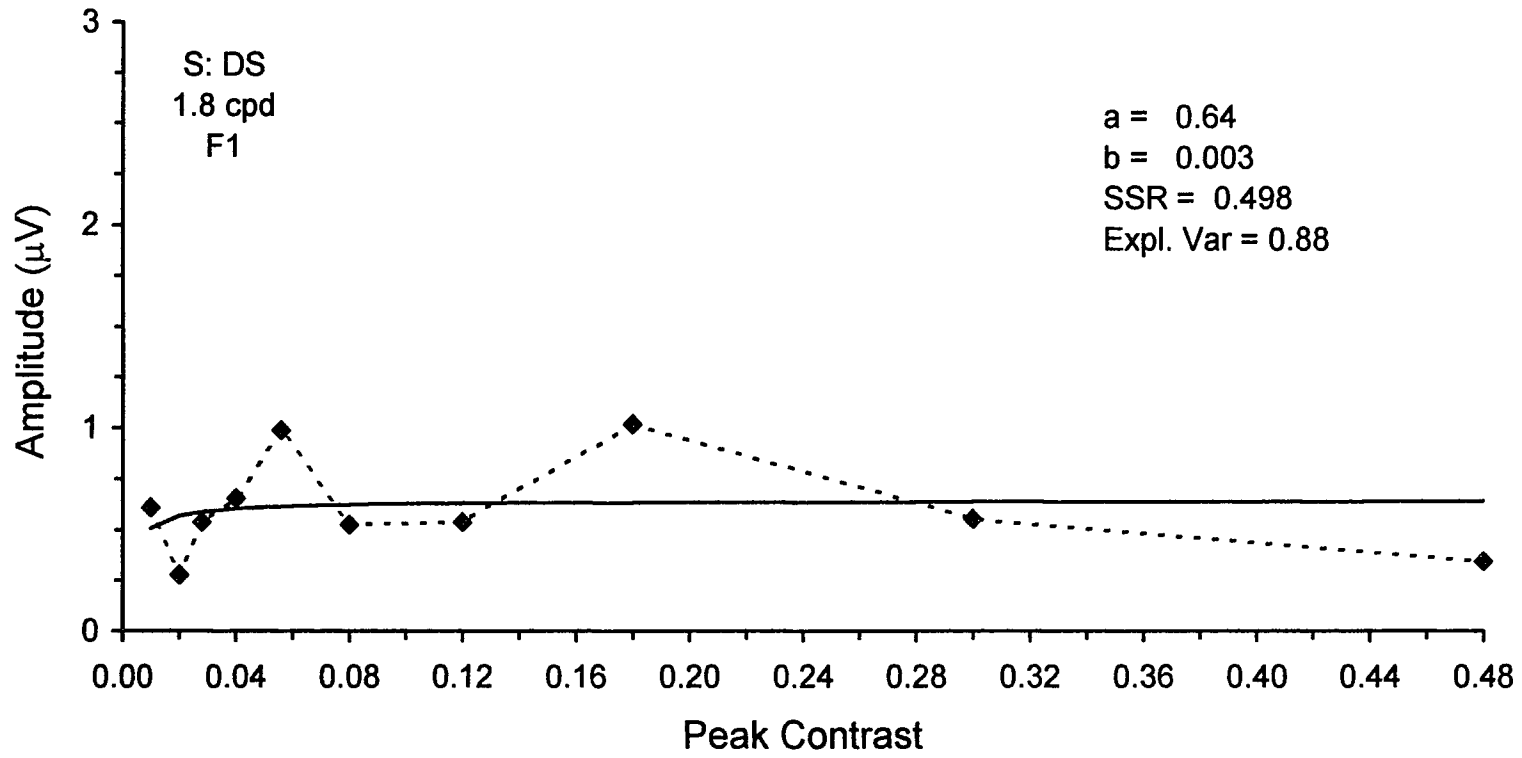


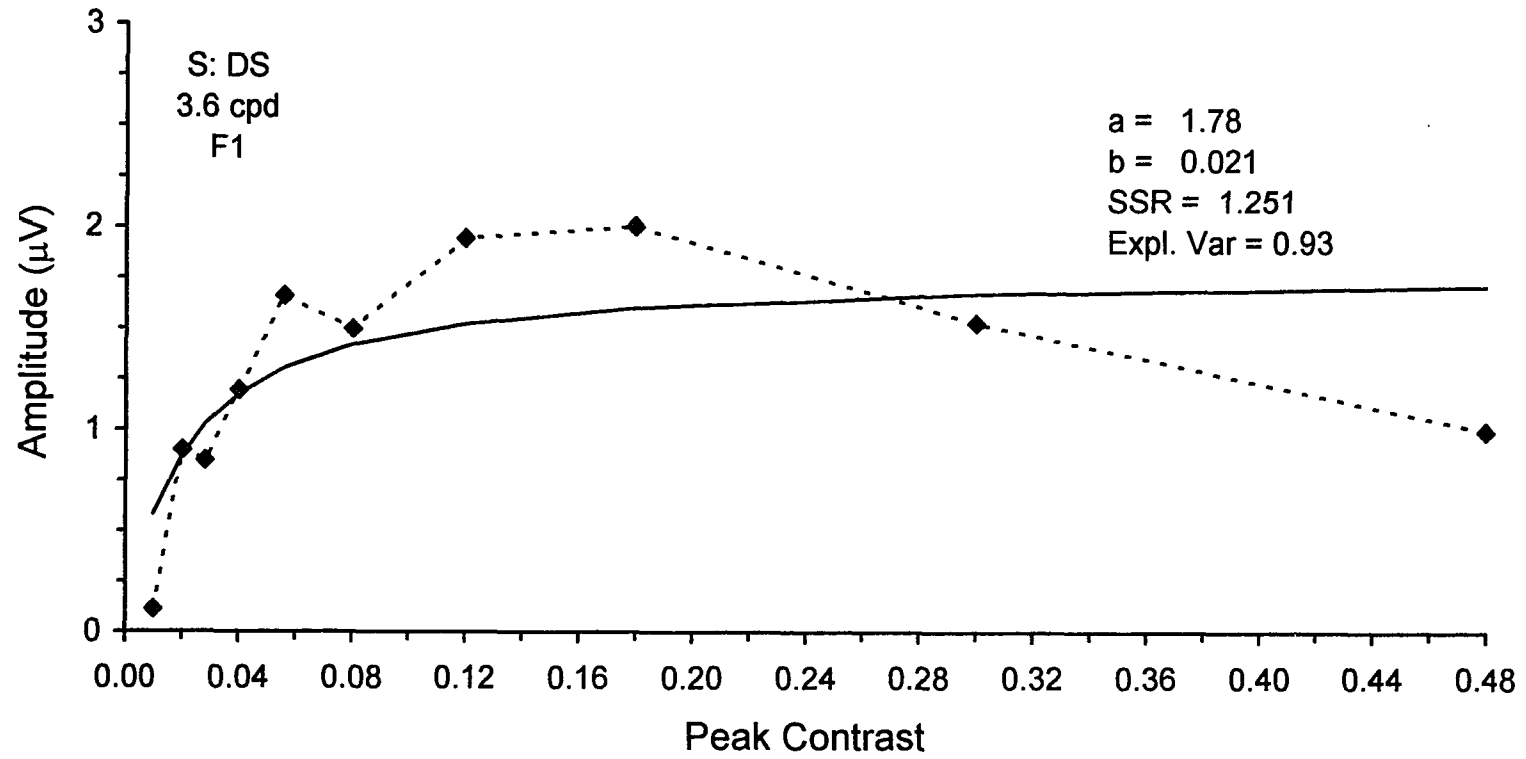


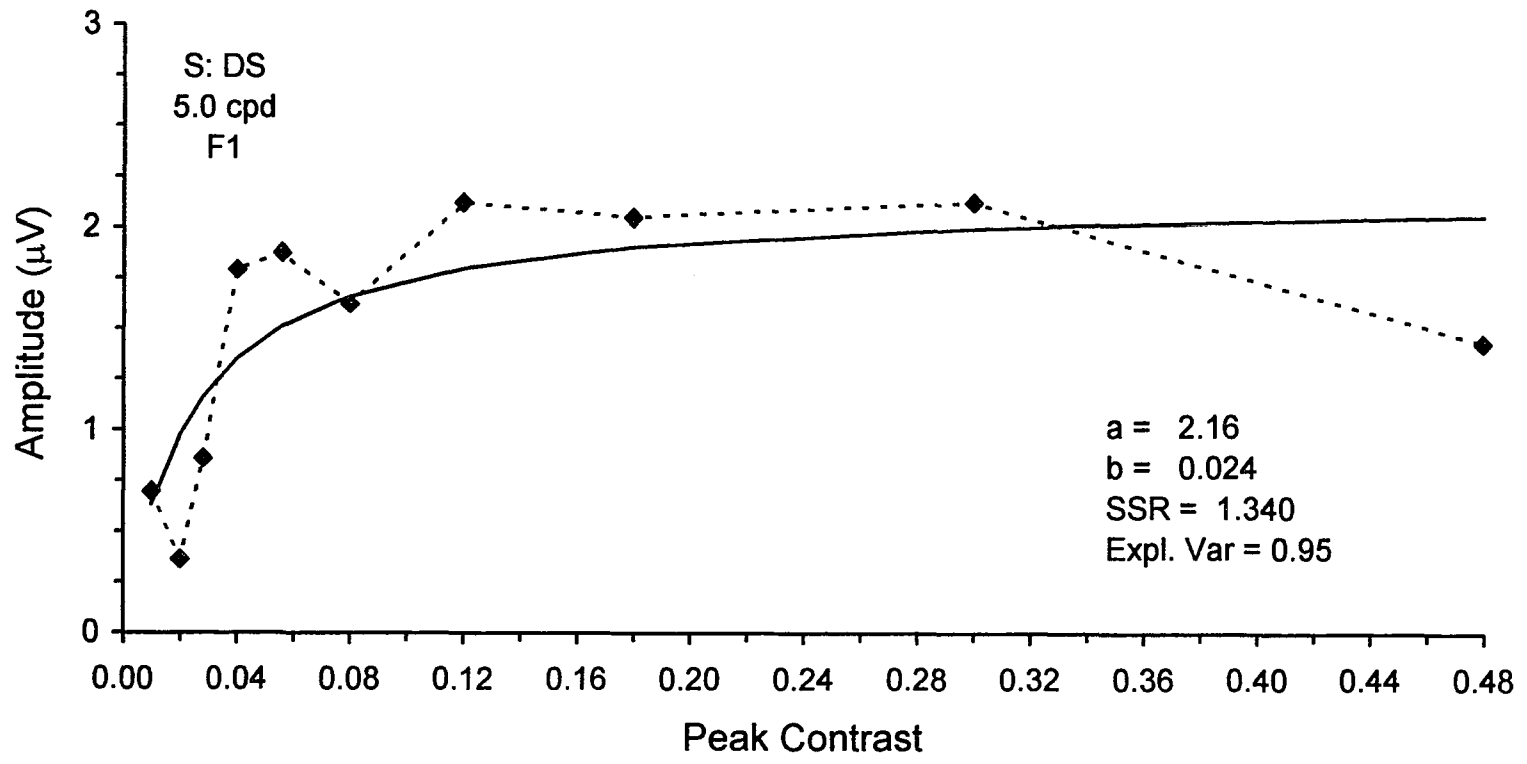


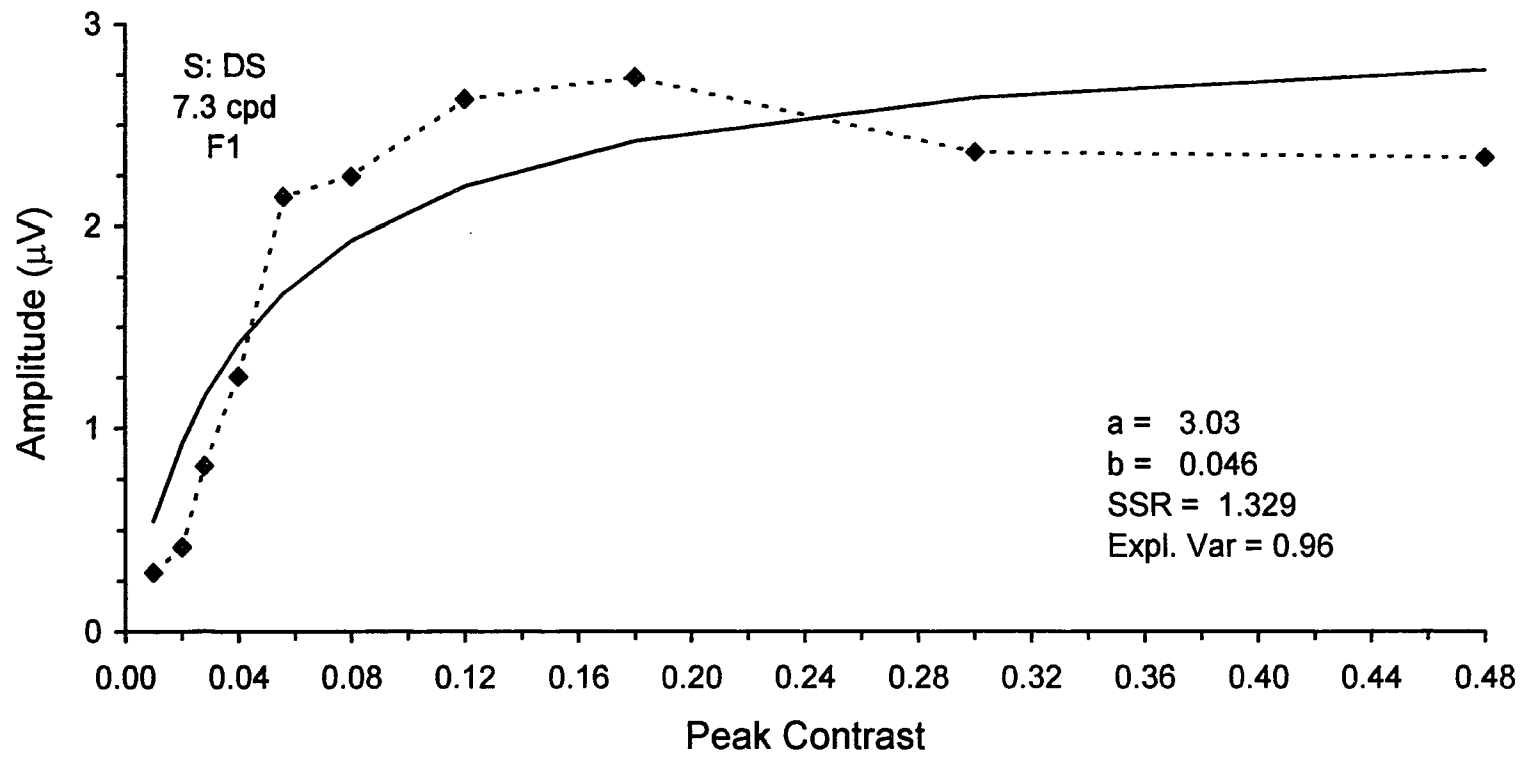


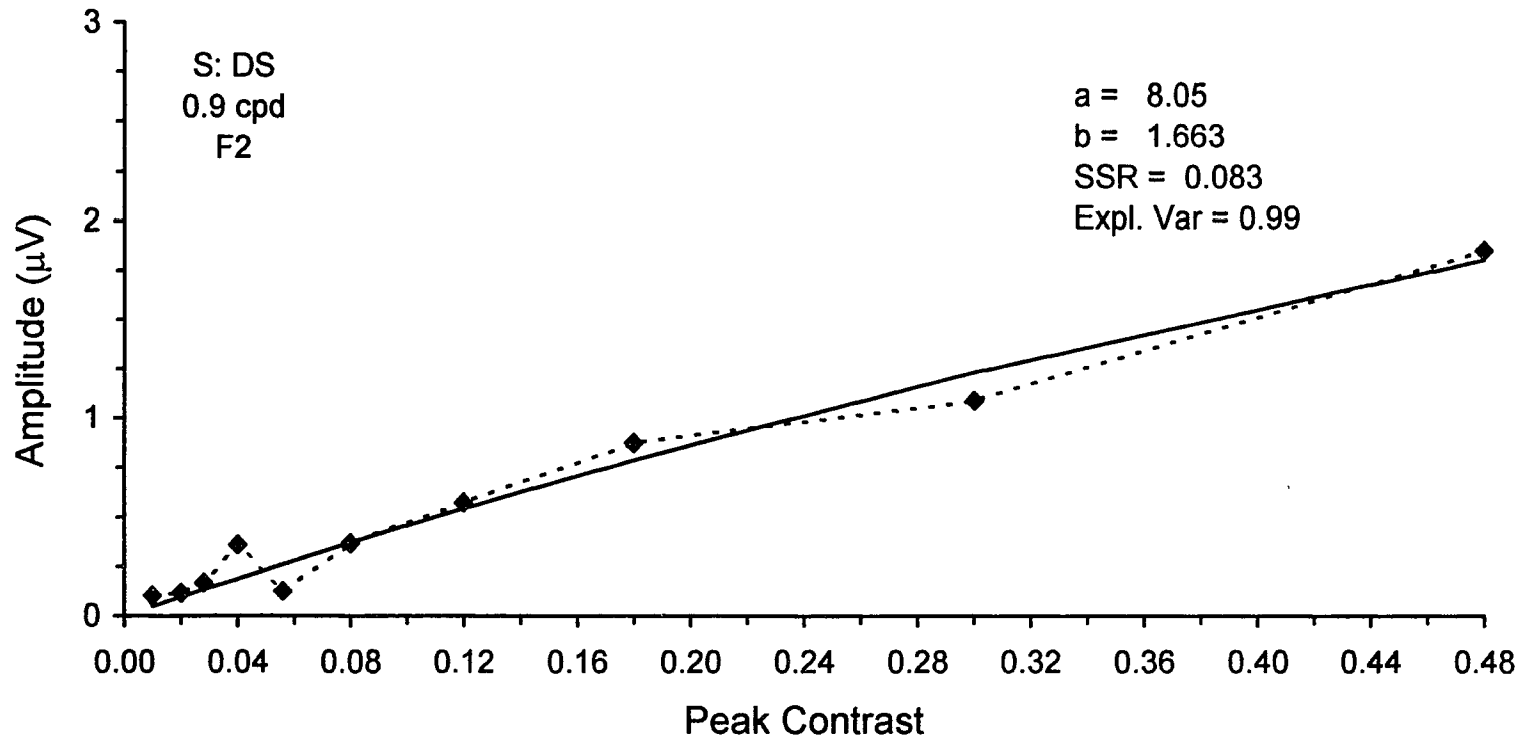


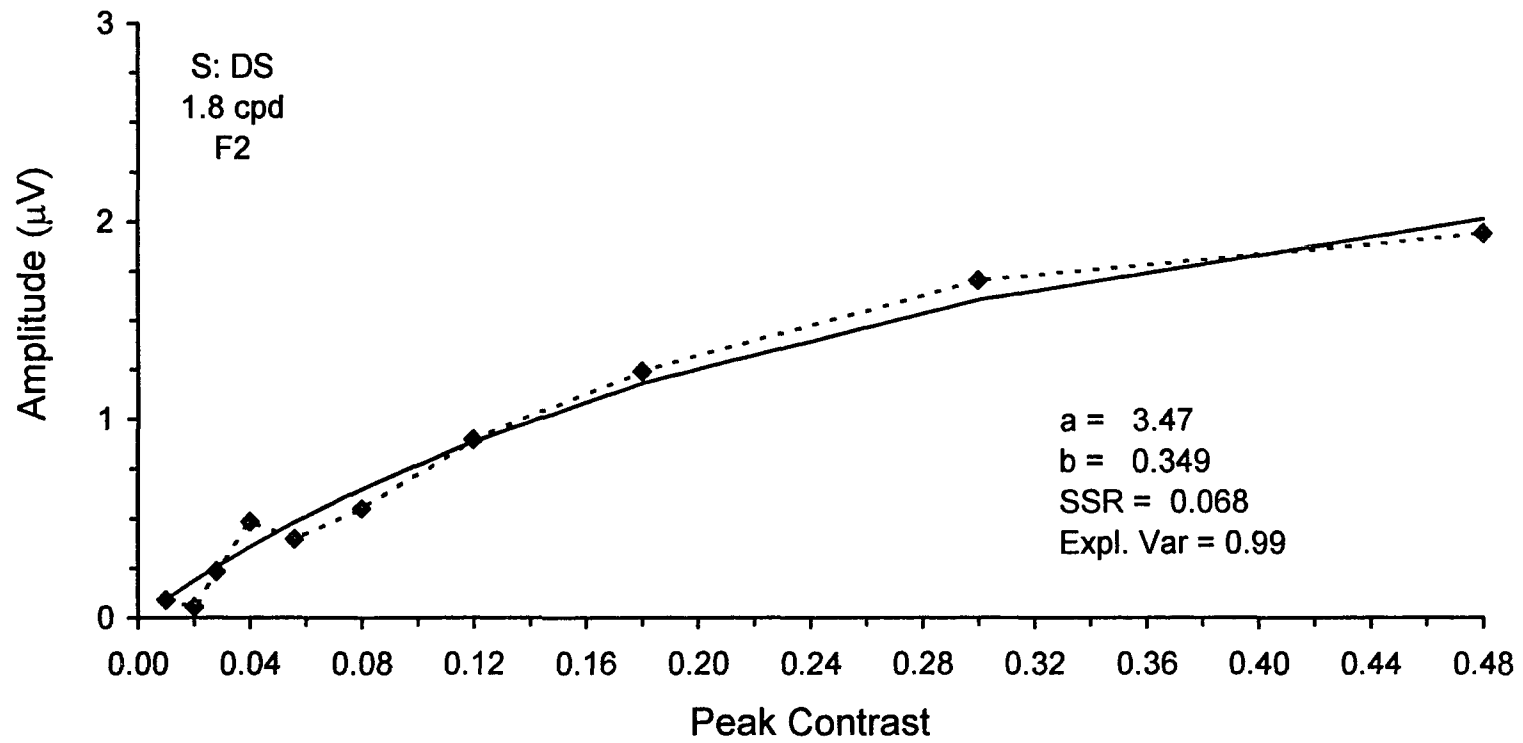


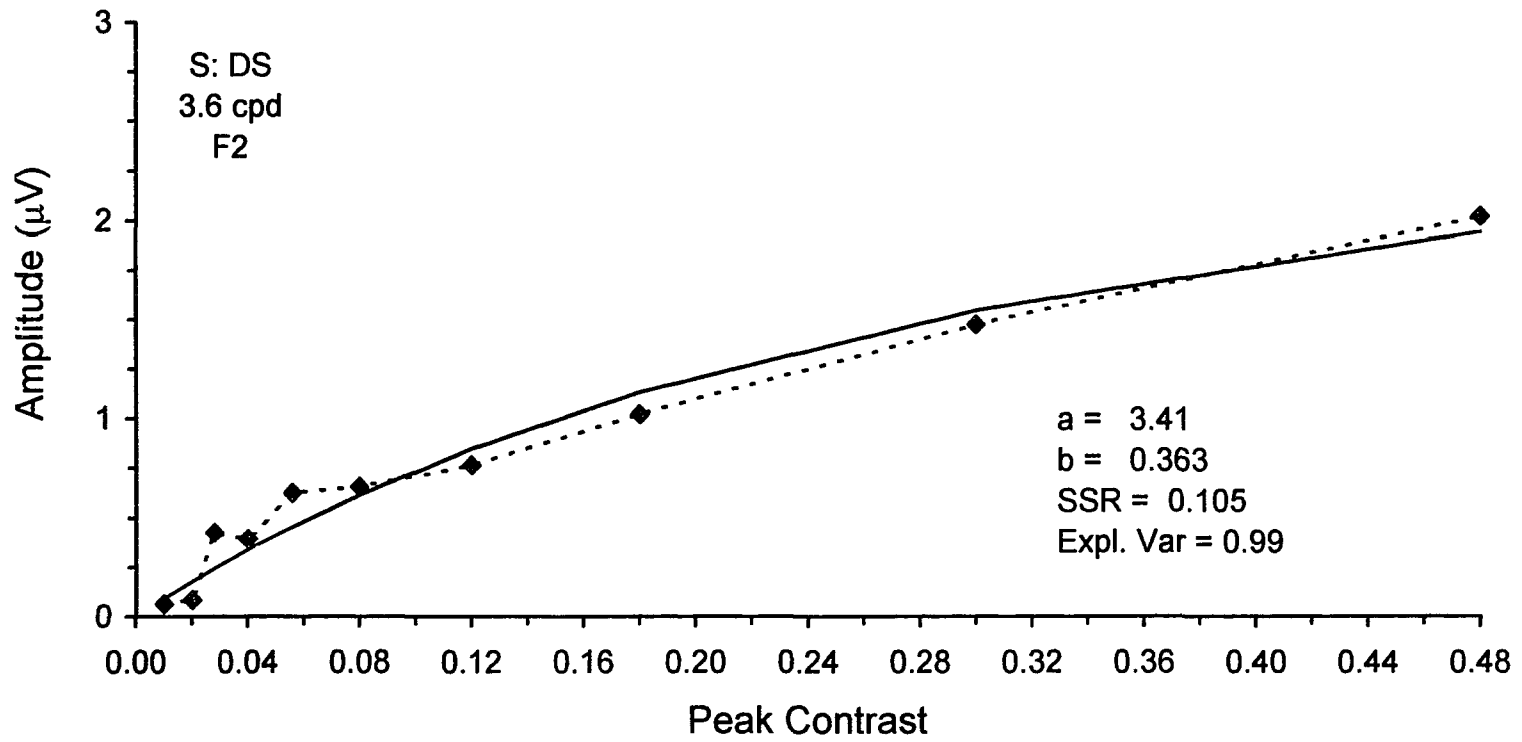


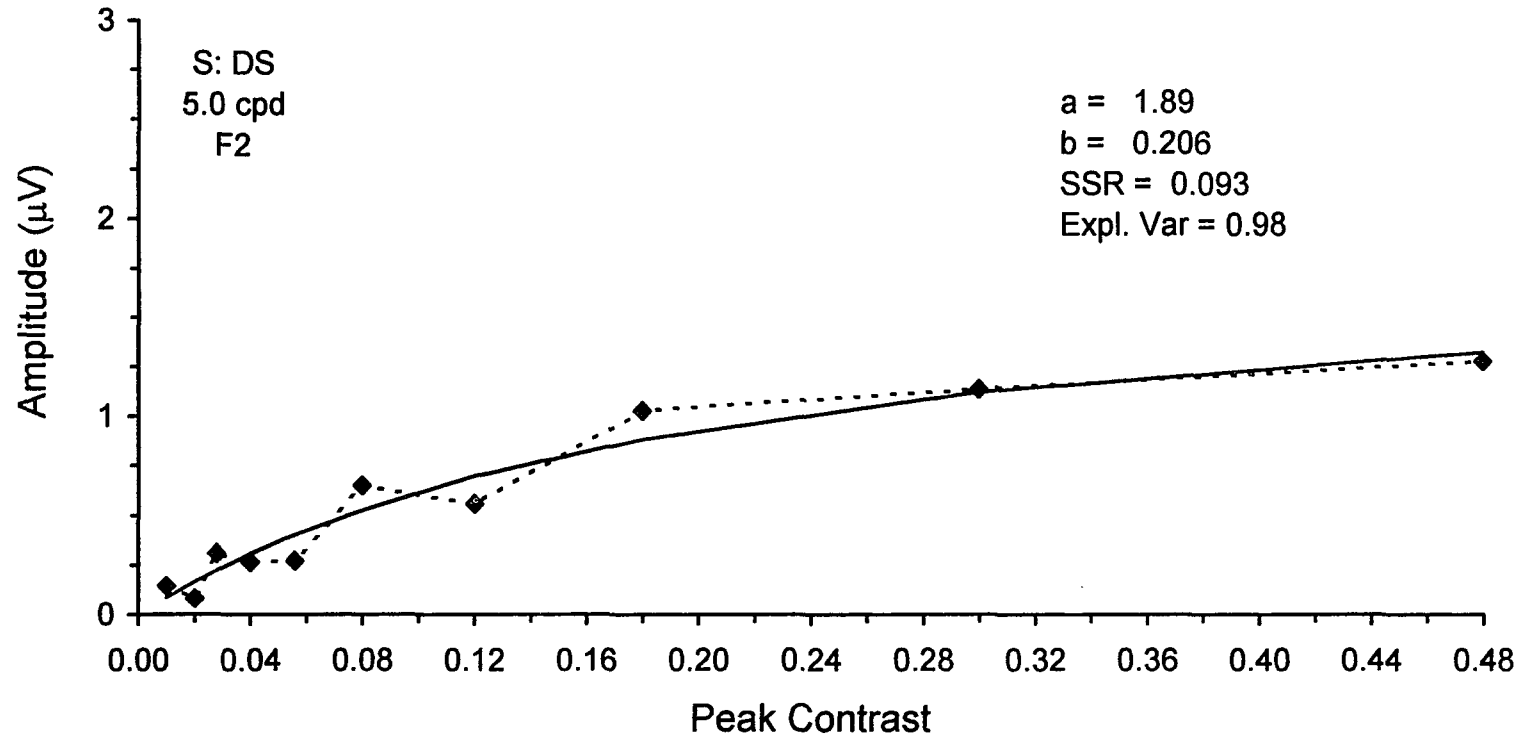


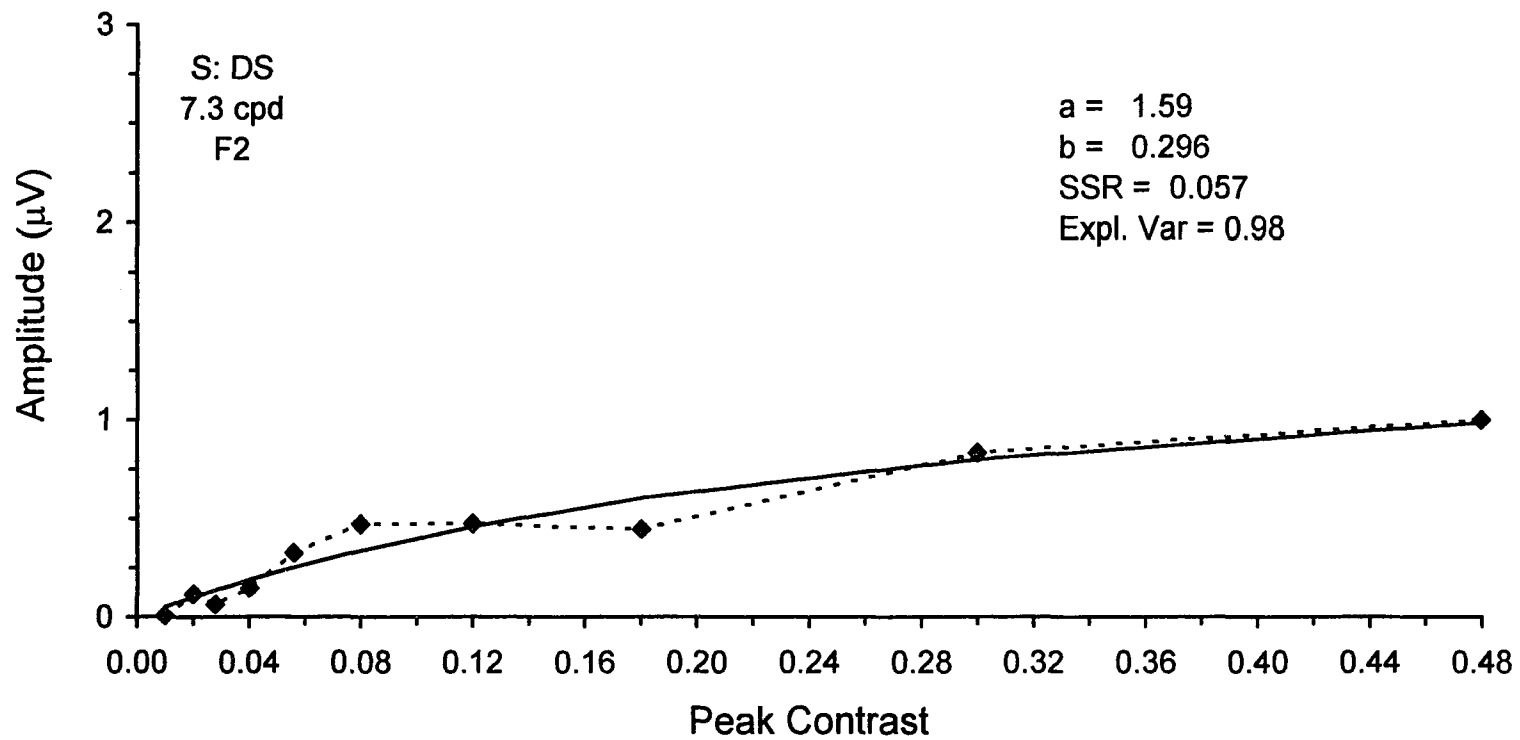












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