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Retino-Geniculate Pathways and the Spatio-Temporal Properties of the Human Visual System in Normal, Aging, and Glaucomatous Vision

Jocelyn Faubert

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Abstract

Retino-Geniculate Pathways and the Spatio-Temporal Properties of the Human Visual System in Normal, Aging, and Glaucomatous Vision

Jocelyn Faubert, Ph.D.
Concordia University, 1991

The series of experiments in this study attempted to determine how changes in the visual system due to aging alone or due to glaucoma can affect selective retino-geniculate pathways as assessed from psychophysical responses. The first experiment evaluated the effect of aging on the spatio-temporal threshold surface under a 70 td illuminance level where both the M and P pathways can respond. The psychophysical procedure used throughout the experiments was such that reaction time, observer biases, criterion shifts, and optical effects such as miosis of the pupil were ruled out as possibly influencing the results. As expected, a loss of sensitivity at the high-spatial-low-temporal and low-spatial-high-temporal regions of the surface were produced by aging. A loss at the middle spatial frequencies and middle temporal frequencies was also found. This was taken as support for the notion of "diffuse" cell loss in the visual system caused by aging.

The second experiment established the effect of aging under a low illuminance condition (0.70 td) which presumably isolates the function of M cells. As expected, very little sensitivity loss was observed for the older group relative to the young normals. This implies that aging does not selectively affect large fibers of the visual system which would have been represented by a large sensitivity decrease of the spatio-temporal threshold surface under this illuminance.

The third experiment assessed the effect of glaucoma and ocular hypertension on the threshold surface obtained in a 70 td illuminance condition.

Globally, glaucoma patients showed a greater loss at the low-spatial-high-temporal region of the surface, demonstrating that glaucoma selectively affects large fibers. Individual data show that three out of five glaucoma observers have a relatively greater loss for the high-temporal and low to medium spatial frequency region of the threshold surface, another subject showed no loss, and the last subject showed some loss for the high spatial frequency region relative to aged matched normal observers. Ocular hypertensive observers did not show significant loss relative to normals. However, they did demonstrate the greatest sensitivity drop at higher temporal rates. In fact, the ocular hypertensive "sensitivity loss" profile was independent of spatial frequency and responded primarily to temporal rates showing suprasensitivity for most conditions with a dramatic sensitivity decrease at the highest temporal rate used (15 Hz). Individual data show that two out of three ocular hypertensive observers have a relatively greater loss at the low-spatial-high-temporal region of the surface.

The fourth experiment assessed the effect of glaucoma and ocular hypertension under a low illuminance condition (0.70 td). As expected, the glaucoma group showed reduced sensitivity throughout the conditions assessed. This is consistent with the hypothesis of large cell loss in glaucoma. The three observers showing a selectively greater loss for the high-temporal and low to medium spatial frequencies have a severe loss of sensitivity relative to normals at 0.7 td. An interesting result was that the ocular hypertensive group still showed suprasensitivity relative to normals with a drop of sensitivity at the highest temporal frequency visible under these conditions (7.5 Hz). One possibility is that this represents two distinct pathophysiological characteristics which, in turn, may be useful in distinguishing between reversible visual dysfunction caused by ocular hypertension and irreversible glaucoma-related

damage. Another possibility is that the ocular hypertensive sensitivity profile observed is a result of early glaucoma-induced damage. The individual data shows only a small loss for the two observers that had some deficit at the high-temporal-low-spatial region of the surface for the 70 td condition.

The results of the experiments, taken together, support the hypothesis that glaucoma causes selective cell loss in some glaucoma observers resulting in psychophysical deficiencies which are predictable from "M cell-like" responses. They also suggest that the study of glaucoma, in early stages of the pathology, may be useful in understanding normal visual processes attributable to different physiological mechanisms. However, the results also demonstrate that the clinical classification of early glaucoma may not in itself represent an instance in which there is a selective cell loss. A careful evaluation of the glaucoma patient with measures such as the ones that were used in this study appear necessary prior to making the assumption of a selective cell loss. The results also suggest that aging alone causes some damage to spatio-temporal sensitivities and that these small losses are probably due to a non-specific loss of cell types when reaction time, observer biases, criterion shifts and optical factors are ruled out.

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Statement of the Problem

In the past several decades much attention has been directed towards the study of the physiological processes of the visual system and their spatio-temporal properties. Most of the attention in this area has addressed the possibility that spatio-temporal and chromatic information are segregated early in the visual system and may not be altered significantly until reaching the primary visual cortex. This "parallel" processing has been under substantial scrutiny by vision researchers. Although there have been controversies in the early reports about the extent of this segregation, dealing mostly with the cat's visual system, there is little doubt at the present time that there are two major and distinct physiological pathways in the higher primates which carry different visual information. The present concerns deal mostly with the specific information that is being transmitted by each physiological mechanism and how distinct they are from each other.

In parallel with the study of spatial properties of the physiological mechanisms, much interest has been directed towards human psychophysics and the study of spatial vision. This interest has come about, to a great extent, with the pioneering work of Hubel and Wiesel (1962, 1968) and the application of Fourier analysis to the waveform properties of stimuli used in physiology (Enroth-Cugell & Robson, 1966) and human visual psychophysics (Campbell & Robson, 1968). In fact, this application has promoted the use of "fundamental" waveforms as stimulus targets for a majority of the research in spatial vision.

Many studies have attempted to determine whether the visual system has separate mechanisms which selectively respond to different size gratings (*i.e.*, spatial channels) and whether these spatial mechanisms have similar or different temporal properties. Thus, sine wave gratings have been modulated in

time to determine whether thresholds differ as a combination of spatial and temporal properties (*i.e.*, spatio-temporal mechanisms). The spatio-temporal properties in question have been assessed for many different stimulus conditions, such as luminance levels, target size, and retinal location. These properties have also been tested using many different psychophysical procedures which, as will be discussed later, can influence the end result. One concern of this study was to assess the spatio-temporal properties of the normal human visual system using a more controlled psychophysical procedure than has generally been utilized. The psychophysical procedure used is believed to be free of criterion shifts or observer biases and is not affected by reaction time, which may influence the response of observers particularly when dealing with inexperienced and/or elderly persons. Further, the stimulus itself was generated so that no visible edges were perceived, other then the intended pattern, thus allowing better control of the stimulus features. The spatio-temporal characteristics of the visual system for inexperienced and elderly observers have not been previously determined under these conditions.

Stemming from the results obtained by the psychophysical and physiological approaches mentioned above, an interest has been expressed by some researchers regarding the extent to which the human visual experience on the whole is segregated early by the parallel pathways and what kind of information is processed in these stages. The next problem is to determine what part of this visual experience is transmitted by each of the two pathways. Clarification of these issues is one of the main attempts of this study. More directly, the main objective of this dissertation was to examine what aspects of the achromatic spatio-temporal thresholds are processed by one pathway as opposed to another. Because it is impossible to eliminate the individual pathways in human subjects, the attempt to isolate the mechanisms was made

indirectly, based on knowledge of physiological responses obtained from single cell recordings and on the pathophysiological evidence of glaucoma.

As described later in detail, there is evidence that one of the physiological mechanism's responses to spatio-temporal properties can be isolated by manipulating luminance levels. Specifically, it is possible to reduce the luminous intensity to a certain degree where one of the mechanisms virtually stops responding and the other still responds adequately (Shapley, 1988). The second way of controlling for physiological mechanisms is by using people with early glaucoma as observers in the experiments. There is growing evidence that one of the physiological mechanisms, characterized by large fibers, is selectively damaged in early glaucoma (Minckler & Odgen, 1987; Quigley, Dunkelberger, & Sanchez, 1987). Thus, by determining which spatio-temporal functions are most affected, one can establish the functions that are under the control of one major mechanism as opposed to another.

Although controlling luminance levels to isolate a mechanism is relatively simple, using individuals with glaucoma involves certain complications. One of the highest risk factors for glaucoma, as for many other visual disorders, is age. It becomes imperative, therefore, that the effect of aging on the psychophysical functions to be determined in these experiments is established. Although there is evidence of cell loss with aging, there are very few reports about whether distinct cell types are more affected by aging. However, there is some evidence showing a tendency for selective losses of large cells with age in the midfrontal, superior temporal, and inferior parietal areas of the cortex (Terry, DeTeresa, & Hansen, 1987).

To summarize, this dissertation was concerned with several issues. First, it examined spatio-temporal characteristics using a technique which eliminates criterion problems and the effect of different reaction times. Further, Gabor

functions were used to control for visible edges and sharp temporal onsets. Second, it determined spatio-temporal thresholds under two very different luminance conditions which are presumed to bias the response of the two main physiological mechanisms in different ways. Third, the effect of early glaucoma on the psychophysical procedures mentioned was assessed. If the pathophysiological data are correct, the sensory losses demonstrated by glaucoma should reflect the reduction in sensitivity as a result of a diminution in the number of cells of the large fiber pathway. Fourth, the effect of aging on the spatio-temporal properties of the visual system was established.

Introduction

Physiological Mechanisms and Parallel Processing

In 1966, Enroth-Cugell and Robson showed that, based on electrophysiological and functional properties, there are distinct cell types among cat retinal ganglion cells which they termed X- and Y-cells. Other researchers soon confirmed these results and extended them to the dorsal lateral geniculate nucleus (LGN) of the thalamus (Cleland, Dubin, & Levick, 1971; Ikeda & Wright, 1972; So & Shapley, 1979; Stone & Hoffman, 1972). Morphological counterparts of these cell types were soon confirmed in the retina (Boycott & Wassle, 1974; Fukuda & Stone, 1974; Fukuda, Hsiao, & Watanabe, 1985; Fukuda, Hsiao, Watanabe, & Ito, 1984) and in the LGN (Fukuda & Stone, 1975; Hoffman, Stone, & Sherman, 1972). It is now known that some of these cell types are found in many different species (Peichl, Ott, & Boycott, 1987; Rodieck & Brenning, 1983). This discovery of parallel cell types in the retinal ganglion cells and the LGN (retino-geniculate pathway or RGP) had great significance for several reasons. First, it demonstrated that, in the mammalian visual system, information is represented differently by different cell types and that this distinction starts at the retina and is maintained up to higher levels, presumably in areas of the primary visual cortex. This can be distinguished from the notion that the retina and the LGN act like a camera as a relay of sequential neural information to the visual cortex.

Briefly, it was found that Y-cells, relative to X-cells, had larger receptive fields (Cleland, Harding, & Tulunay-Keesy, 1979; Linsenmeier, Frishman, Jakiela, & Enroth-Cugell, 1982), larger cell bodies and axon diameters (Boycott & Wassle, 1974; Illing & Wassle, 1981; Leventhal, 1982; Leventhal, Rodieck, & Dreher, 1985), and faster conduction velocities to electrical stimulation

(Cleland, *et al.*, 1971; Fukada, 1971; So & Shapley, 1979; Stone & Hoffmann, 1972), although there is controversy whether this can be generalized to visual stimuli because it is not clear whether differences in conduction velocity contribute to differences in responsiveness to higher temporal frequencies (Lennie, 1980). Further, X-cells respond linearly and Y-cells non-linearly to spatial targets such as sine wave gratings (Enroth-Cugell & Robson, 1966, 1984; Hochstein & Shapley, 1976a, 1976b). Secondly, a direct consequence from this research was the doctrine that these may be underlying mechanisms for processing spatial and temporal properties of visual stimuli, one cell type with better defined spatial properties and the other with better defined temporal properties.

An interesting issue for visual psychophysicists and other behavioral vision researchers is whether spatial and temporal properties in higher primates, such as the monkey and man, are controlled under parallel mechanisms as in the cat. Another question of interest is whether other visual functions, such as sensitivity to colour, are processed in a parallel fashion. There is evidence that the macaque visual cells can also be sorted into cell classes (Blakemore & Vital-Durand, 1981; DeMonasterio, 1978a, 1978b, 1978c; Gouras, 1968; Kaplan & Shapley, 1982; Schiller & Malpeli, 1978).

Cell types in the monkey A large body of evidence suggests that there are two major divisions of cell types in the RGP of the macaque monkey (DeMonasterio, 1978a; Dreher, Fukada, & Rodieck, 1976; Gouras, 1968; Leventhal, Rodieck, & Dreher, 1981; Perry & Cowey, 1981; Perry, Oehler, & Cowey, 1984; Schiller & Malpeli, 1977, 1978). These studies show no substantial differences between the receptive field organization and functional properties of the LGN cells and their respective retinal ganglion cells. For this

reason, a distinction between the LGN cells and their retinal ganglion counterparts will be made in the present context only if there are differences between the two in the characteristics discussed. Both cell groups have circular receptive fields (concentric) and most have a center- surround organization as defined by Kuffler (1953). One group of fibers projects to the four dorsal parvocellular layers of the LGN and the other group to the two ventral magnocellular layers of the LGN (Perry, *et al.*, 1984). The cells projecting to the parvocellular layers are referred to as P cells and those projecting to magnocellular layers are named M cells (Schein & DeMonasterio, 1987; Shapley & Perry, 1986). The M cells have receptive fields which are significantly larger than those of the P cells (DeMonasterio & Gouras, 1975) and the conduction velocity of M cells is much faster (Schiller & Malpeli, 1977). The cells projecting to the parvocellular layers comprise approximately 80% of the total number of fibers leaving the retina (Perry, *et al.*, 1984). The P cells are colour sensitive with strong colour opponencies and respond in a sustained fashion when the light stimulus is at the peak of the cell's spectral sensitivity. They also respond phasically to achromatic light (DeMonasterio, 1978a). M cells have little chromatic opponency; that is, they show little wavelength selectivity. However, recent work by Derrington, Krauskopf, and Lennie (1984) shows that they may receive antagonistic signals from different cones.

Other types of cells have been discovered which are neither P nor M cells but these are rare (DeMonasterio, 1978c; Perry, *et al.*, 1984; Schiller & Malpeli, 1977). These cells, which cannot be classified as either P or M cells, have similar characteristics to the W-cells found in the cat (Cleland & Levick, 1974), are not wavelength selective (DeMonasterio, 1978c; Marroco, 1976), and mainly project to the superior colliculus (Marrocco, 1976; Perry & Cowey, 1984; Schiller & Malpelli, 1977).

Physiological classification One of the first classifications, based on physiological responses demonstrated in the monkey RGP neurons, is presented by Wiesel and Hubel (1966). They separated the P units into three distinct classes based on the chromatic and spatial characteristics of the receptive fields and these were labeled Type I (chromatically opponent) Type II (chromatic opponency but no achromatic opponency), and Type III cells (no antagonistic colour inputs). Recent spatial frequency analysis using both chromatic and achromatic gratings demonstrates that Type I and Type III cells comprise only one group. This is evidenced by data showing that almost all P cells are linear (Blakemore & Vital-Durand, 1981; Kaplan & Shapley, 1986; Shapley, Kaplan, & Soodack, 1981), that achromatic spatio-temporal frequency sensitivities of Type I and Type III cells are identical (Derrington & Lennie, 1984), and that Type III cells actually have chromatically opponent receptive fields (Derrington, *et al.*, 1984; Padmos & Van Norren, 1975).

The magnocellular units were separated into two classes of cells labeled Type III and Type IV by Wiesel and Hubel (1966). The distinction between the magnocellular Type III neurons and the parvocellular Type III neurons are that these two types differ considerably in contrast sensitivity and conduction velocity. In the light of recent evidence, the Type III and Type IV distinction probably does not have any classification value. Kaplan and Shapley (1982) and Derrington and Lennie (1984) demonstrated that these groups are indistinguishable based on achromatic contrast sensitivity and linearity measures. Derrington and his coworkers (1984) also showed that all M cells have weak colour opponency for chromatic gratings.

Several researchers have suggested that the P cells of the monkey are analogous to the X-cells of the cat and that the M units represented the Y-cells

(Dreher, *et al.*, 1976; Schiller & Malpeli, 1978; Sherman, Wilson, Kaas, & Webb, 1976). Recent evidence demonstrates that this is not the case (Derrington & Lennie, 1984; Derrington, *et al.*, 1984; Hicks, Lee, & Vidyasagar, 1983; Kaplan & Shapley, 1982; Kaplan & Shapley, 1986). These studies show that the M cells are more sensitive to contrast than are the P cells while in the cat the X-cells are more sensitive to contrast. Secondly, most M cells show linear responses as opposed to the Y-cells in the cat with only 15-25% of the M cells showing non-linearity typical of Y-cells. Clearly, this demonstrates that there are distinct differences between the M and P cells of the monkey as opposed to the Y- and X- cells of the cat and that the use of this classification for the monkey should not be encouraged since it confuses the issue.

Illuminance levels and their effects on the pathways Shapley (1988) has reported a series of experiments where different luminance levels were used to establish if there were selective effects in relation to the parvocellular and magnocellular pathways. He found that when the mean retinal illuminance is reduced to 1 td or less, the response to contrast for both P and M cells declines. However, although the response level of the M pathway is still relatively strong at these illuminance levels, the response of the P pathway is virtually nonexistent. This implies that the M cells are driven by rods to a substantial degree which is not the case for the P cells. The second implication, which relates to the present study, is that if illuminance in a human psychophysical experiment was reduced to 1 td or lower, an isolation of the M pathway would be obtained. The response of hypothetical M and P cells to illuminance change is demonstrated in Figure 1. The X-axes represent contrast and the Y-axes correspond to the cell response in impulses per second. As demonstrated in

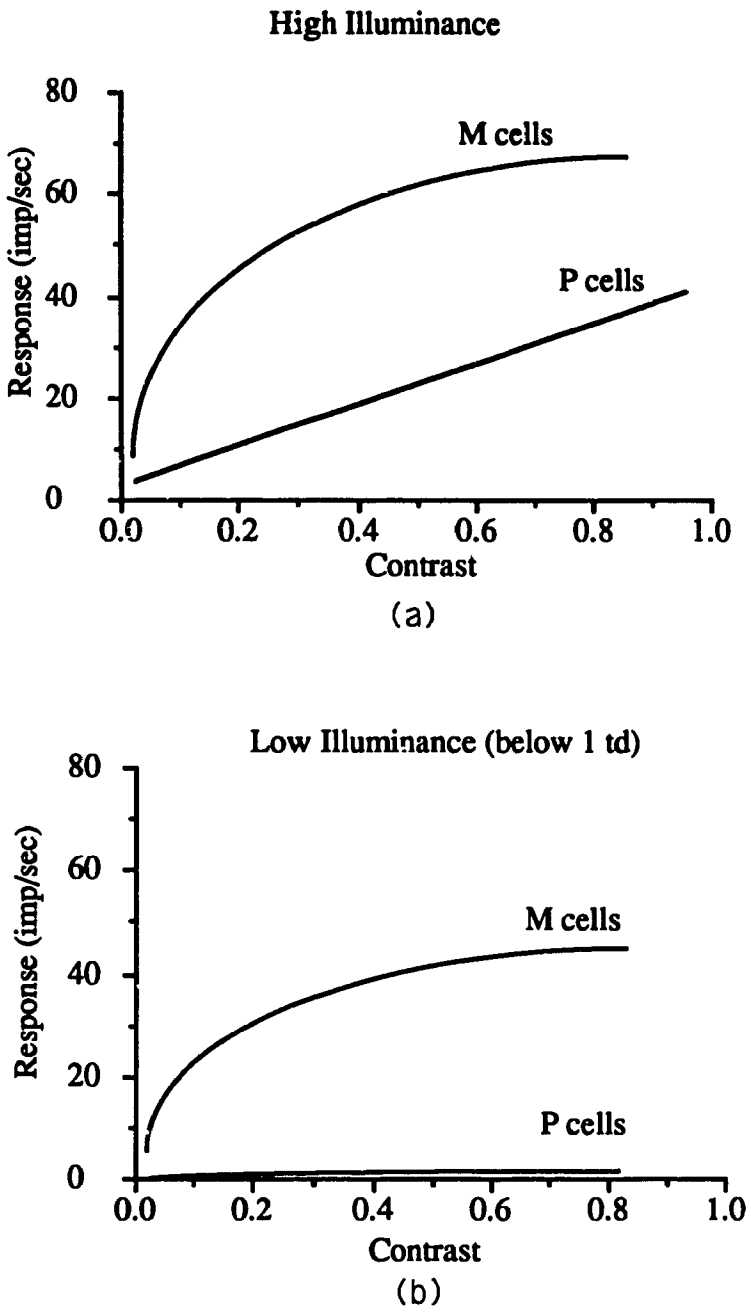


Figure 1. Hypothetical responses of macaque LGN neurons as a function of contrast. Example of responses from M and P cells under high illuminance (a) and low illuminance (b). The graphs do not represent actual data.

Figure 1 (b), the reduction of the illuminance level below 1 td virtually eliminates the response of the P cell while the M cell is still active.

Parvocellular cells and chromatic information One of the first studies, using the method of "neutral points", found that there were two classes of chromatically opponent units of which the specific cone inputs were inferred theoretically from spectral response properties of retinal ganglion cells (DeValois, Abramov, & Jacobs, 1966). These are the red-green (R-G) type receiving antagonistic inputs from the red (R) and green (G) cones and the yellow-blue (Y-B) type receiving opposite inputs from blue (B) cones and either R or G cones (in some cases a combination of the two). However, this study did not demonstrate clearly organized antagonistic properties and some cells of the P layers were not identified as colour opponent. The neutral point technique has been criticized and more recent studies using either the chromatic adaptation technique (DeMonasterio & Gouras, 1975) or the chromatic modulation paradigm (Derrington, Lennie, & Krauskopf, 1983) have demonstrated more rigidly organized chromatic responses in the P cells.

Using the techniques just mentioned, it was found that almost all the P cells received antagonistic inputs from more than one cone type. Clearly, a group of P cells is driven only by R and G cones. In this group, one cone type contributes primarily to one antagonistic mechanism and the other cone type to the other mechanism. The R-G group comprises approximately 80% of all P cells. Most have a clearly defined center-surround organization with one cone type responsible for the center and the other for the surround. DeMonasterio (1978b) and Demonasterio, Gouras, and Tolhurst (1975) have demonstrated that some R-G units can be influenced slightly by B cones under high chromatic adaptation conditions.

Another group of P cells is called the Y-B group and is driven by B cones with the other antagonistic signals coming from some combination of R and G cones. Virtually all cells from this group receive excitatory signals from the blue cones. These cells are much rarer than the R-G units, have poorly defined center surround properties, if any, and generally have larger receptive fields. How much the R or G cones contribute to the Y antagonistic signal of the Y-B group is not clear from the literature. All that can be said at this point is that there is evidence for both R and G cones being involved (Derrington, *et al.*, 1983; DeMonasterio, *et al.*, 1975).

Wiesel and Hubel (1966), along with Blakemore and Vital-Durand (1981), have shown that the R-G cells respond well to achromatic spatial contrast and can respond to very high spatial frequencies in the fovea. It would appear from these data that the majority of P neurons (*i.e.*, R-G) may play an important role in the presumed spatio-temporal achromatic mechanism proposed by psychophysicists and this casts doubt on the role of the M cells in the latter. Further, the M units comprise a very small proportion of the fibers leaving the retina. This complicates the argument which implies that M cells are solely responsible for the achromatic system. Such arguments, among others, have been used by Ingling and Drum (1973) and Ingling and Martinez-Uriegas (1983, 1985) to propose the theory that R-G units are responsible for both colour information and edge detection of higher spatial frequencies observed in human psychophysics of foveal vision. Further analysis of the physiological literature and some pharmacological studies, which will be discussed later, lends support to this notion.

Linearity vs. non-linearity Prior to identifying spatial filtering properties in the monkey RGP, the notion of linearity *vs.* non-linearity requires some

elaboration. In their study of X- and Y-cells in the cat, Hochstein and Shapley (1976a, b) established a non-equivocal classification of linearity/non-linearity now frequently used in physiological studies. This method is based on the cell's response to a stationary sinusoidal grating (now many researchers use counterphase flickering gratings at low temporal frequencies). They found that the amplitude of the modulated response of X-cells was related to the position of the grating on the receptive field. The strongest modulated response was observed when the grating was placed approximately in the center of the unit's receptive field. Using this test, it was possible to identify a "null" position for the X-cells but not the Y-cells. That is, when the grating was shifted to one side or the other, there was a position where the response of the cell was not modulated but, rather, was flat. This effect is assumed to be the result from equally stimulating the antagonistic center and surround areas of the cell's receptive field, causing them to cancel each other's excitatory and inhibitory influences. The Y-cell response remains modulated regardless of the position of the grating. Further analysis of cell responses, using Fourier methods, showed that the X-cell response varied sinusoidally with the fundamental frequency (first harmonic) of the spatial component. Given that X-cells are linear, this was the only frequency component determined in the response. Y-cells showed additional components at twice the frequency of the fundamental (second harmonic), regardless of the position of the grating.

Using this classification, it was found that 80% of the M units have only fundamental frequency components and thus are linear (Blakemore & Vital-Durand, 1981; Kaplan & Shapley, 1982). A few M cells are found to have second harmonic components in their response levels. These differences, however, are found to lie on a continuum which implies that the differences in the linearity response represent two extremes of a continuum in the

magnocellular layers. This is similar to the "linearity" hypothesis of the cat X- and Y-cells proposed by Hochstein (1979). Almost all the P cells that were tested for linearity were found to have primarily fundamental frequency components.

The contrast sensitivity of the monkey RGP cells has been studied substantially in recent years (Derrington & Lennie, 1984; Hicks, *et al.*, 1983; Kaplan & Shapley, 1982; Marroco, McClurkin, & Young, 1982; Schiller & Colby, 1983; Shapley, *et al.*, 1981). All these studies found that M cells are more sensitive to contrast than are P cells. Particularly interesting are the results obtained by Kaplan and Shapley (1986) which concern the "contrast gain" of cells in the RGP. The contrast gain of a cell is its dynamic ability to respond to the depth of modulation of the stimulus from the onset of the stimulus to saturation of the cell's response. A sinusoidal grating at the cell's optimal spatial frequency was presented with the grating temporally modulated at 4 Hz. Contrast levels from 0.02 to 0.64 were tested and it was found, as expected from previous research, that M cells responded more strongly than P cells. It was interesting in the analysis that the M units increased firing rates quite rapidly, started saturating just above the 0.1 level, and almost reached asymptote at the 0.32 level. The cell response of the P cells increased very slowly and steadily as compared to the sharp increase for the M cells (*i.e.*, this is the difference in "contrast gain"). The contrast gain is high when there is a sharp increase in firing rate with little contrast increase form zero modulation and low when when the firing rate increases slightly under the same conditions. Further, the P cells never reached maximum levels and the response curve was linear (see Figure 1a). As discussed earlier, reducing luminances has profound effects on contrast sensitivity of a cell and consequently on the contrast gain. As shown in

Figure 1b, below about 1 td the P pathway stops responding while the M pathway is still relatively responsive.

Cortical levels receiving input from the LGN In discussing parallel processing in the RGP, it is not automatically assumed that the process is continuous at all levels of the central nervous system. As discussed earlier, both colour and achromatic information goes through the P pathway. Therefore, some decision making must occur at higher levels. However, it would appear important that some of the earlier cortical levels, that is, levels which receive input directly from the LGN should maintain the properties which are characteristic of the two separate pathways of the RGP. This has been demonstrated by several experiments examining the properties of layer 4 of the visual cortex which receives direct input from the LGN. More precisely, the 4C-alpha cells receive input directly from the M pathway and the 4A and 4C-beta cells from the P pathway. Research by Blasdel and Fitzpatrick (1984) as well as Hawken and Parker (1984) on these layers demonstrated that these cells have response characteristics to spatial-contrast information which are very similar to the LGN cells which supply their respective input. It was shown that the 4A and 4C-beta cells have generally low contrast sensitivity and small receptive fields and the 4C-alpha cells have larger receptive fields and are very sensitive to contrast, which corresponds well with their LGN counterparts. A summary of the different characteristics of the P and M pathways is given in Table 1.

Pharmacological isolation of cell types Establishing the link between visual physiology and human psychophysics is mostly based on indirect comparison. An ideal situation would be to eliminate one cell class specifically to allow the direct assessment of the other group using conventional, indirect,

Table 1

Summary of the P and M pathway characteristics

	M-cells	P-cells
Relative receptive field size	larger	smaller
Relative axon and soma size	larger	smaller
Relative axonal conduction velocity	faster	slower
Relative dendritic field diameter	larger	smaller
Linear response	no, yes	yes
Colour opponency	no	yes
Chromatic selectivity	no	yes
Respond to luminance	yes	yes
Response to photopic luminance conditions	strong	strong
Response to scotopic luminance conditions	strong	nil
Contrast sensitivity	high	low
Contrast gain	high	low

psychophysical means used in human vision. This could be done only recently when it was demonstrated that acrylamide specifically affects the P cells of the RGP (Eskin, Lapham, Maurissen, & Merigan, 1985; Eskin & Merigan, 1986; Leventhal, *et al.*, 1981; Perry, *et al.*, 1984). Acrylamide produces axonal swelling followed by degeneration and gliosis especially in LGN.

Merigan and his colleagues have studied the effects of acrylamide on psychophysical performances in the monkey (Merigan, Barkdoll, Maurissen, Eskin, & Lapham, 1985; Merigan & Eskin, 1986). Generally, they had monkeys undergo acrylamide intoxication and the psychophysical studies were undertaken at least three months after the last ingestion of the drug to allow recovery (Merigan & Eskin, 1986). They used a forced choice procedure where the monkey had to press one of two buttons corresponding to one of two screens on which the stimulus was presented, and the mean luminance of the screens was 17 cd/m^2.

The spatio-temporal contrast sensitivity, visual acuity, and the flicker fusion frequency of the monkeys were assessed. The spatio-temporal parameters assessed varied in spatial frequency from 0.4 to 23 c/deg and in temporal frequency from 0 (stationary grating) to 10 Hz. A staircase procedure was used with initial contrast above threshold. A psychometric function was established and a 75% response criterion was used as the critical measure. The visual acuity data were obtained in a similar way but the grating was maintained at maximum contrast and the spatial frequencies were varied in 0.18 octave steps. The flicker fusion frequency was also determined using this staircase procedure with maximum contrast and varying frequency in 0.18 octave steps.

Results show that sensitivity to static gratings was severely impaired across all frequencies when compared to data obtained before treatment or to

data from control monkeys. At low temporal frequency (0 and 0.5 Hz) loss of sensitivity of the acrylamide-treated monkeys was also evident for all spatial frequencies. At the medium temporal frequency (2.3 Hz) and the high temporal frequency (10 Hz), the treated animals did not show loss at the lowest spatial frequency. The general sensitivity pattern of the acrylamide treated monkeys is that sensitivity to low spatial frequencies is decreased if they are presented at low temporal frequencies and is not decreased if presented at high temporal rates. Sensitivity to intermediate spatial frequencies is impaired when presented at low to medium temporal frequencies but not high temporal frequencies and, finally, sensitivity to high spatial frequencies is impaired when presented at any temporal frequency. The fusion flicker frequencies for a diffuse non-patterned target was not affected by the loss of P cells.

This study suggests that the P and M layers both play a role in achromatic spatio-temporal vision and that these roles are different. Given that the P layers are destroyed in the acrylamide treated monkeys, it would appear that the spatio-temporal function which remains is performed by the M units. Therefore, these data suggest that the M pathway has band-pass characteristics and is responsible for low-spatial/high-temporal information and the P pathway is a low pass spatial filter and is sensitive to all spatial frequencies at low temporal frequencies and specifically sensitive to high spatial frequencies.

Spatial Vision: Methodological Concerns

Prior to the theoretical discussion of spatio-temporal vision, and its possible implication for the physiological research just mentioned, it is important to understand the stimuli which are used under these conditions. Although the study of spatial vision has used many different stimuli, the present work is only concerned with spatial gratings and the rest of the discussion will focus on this

type of target. For most of the experiments in question, there are three parameters of importance: spatial frequency, luminance (and illuminance), and contrast. The spatial frequency of a target is usually expressed in cycles per degree of visual angle (c/d).

Briefly, luminance can be defined as the stimulus intensity reaching the eye. Illuminance is the stimulus intensity reaching the retina factoring in the pupil size. Luminance often varies in space, so it is commonplace to express luminance for a given spatial area. The most common denotation for luminance is candles per meter squared (cd/m^2). Retinal illuminance is described in trolands and can formally expressed as:

$$T = L * P \qquad (1)$$

where T is the intensity in trolands, L is the luminance in cd/m^2, and P is the pupil area in millimeters squared (mm^2). With the use of sinusoidal gratings, the luminance varies in contrast and is often expressed with the Michelson contrast:

$$\text{Contrast} = \frac{L_{max} - L_{min}}{L_{max} + L_{min}} \qquad (2)$$

The luminance profile can also vary in time, that is, there can be a temporal component to the stimulus. When temporal components are included the luminance can be formally expressed by $L_{x,y,t}$, where the $_{x,y}$ represents the spatial luminance condition and the $_t$ is the time luminance condition. The spatial and temporal components can be factored out where:

$$L_{x,y,t} = L_{x,y}f(t) \quad (3)$$

As mentioned above, the spatial targets are expressed in spatial frequency components. Thus, the luminance profile of vertical sinusoidal gratings can be formally expressed as:

$$L(x,y) = [m * \sin(2\pi f_S x) + 1]L_O \quad (4)$$

where f_S stands for the spatial frequency and L_O is the mean luminance and m is the relative contrast or depth of modulation of the grating. An example of the horizontal luminance profile of a sine wave can be seen in graph (a) of Figure 2. If, for example, counterphase flickering gratings are used the expression can be extended to:

$$L_{x,y,t} = [m * \sin(2\pi f_S x)\sin(2\pi f_t t) + 1]L_O \quad (5)$$

where f_t is the temporal frequency in cycles per second (Hz).

Another stimulus display, though not as frequently used, involves gradually eliminating visible edges of a display by filtering the spatial frequency components with a Gaussian function. The resulting functions are called Gabor functions. To produce such a function one merely has to include a Gaussian expression in formula 4:

$$L_{x,y} = [w(x,y)s(x) + 1] * L_O \quad (6)$$

where

$$w(x,y) = w_1(x)w_2(y)$$

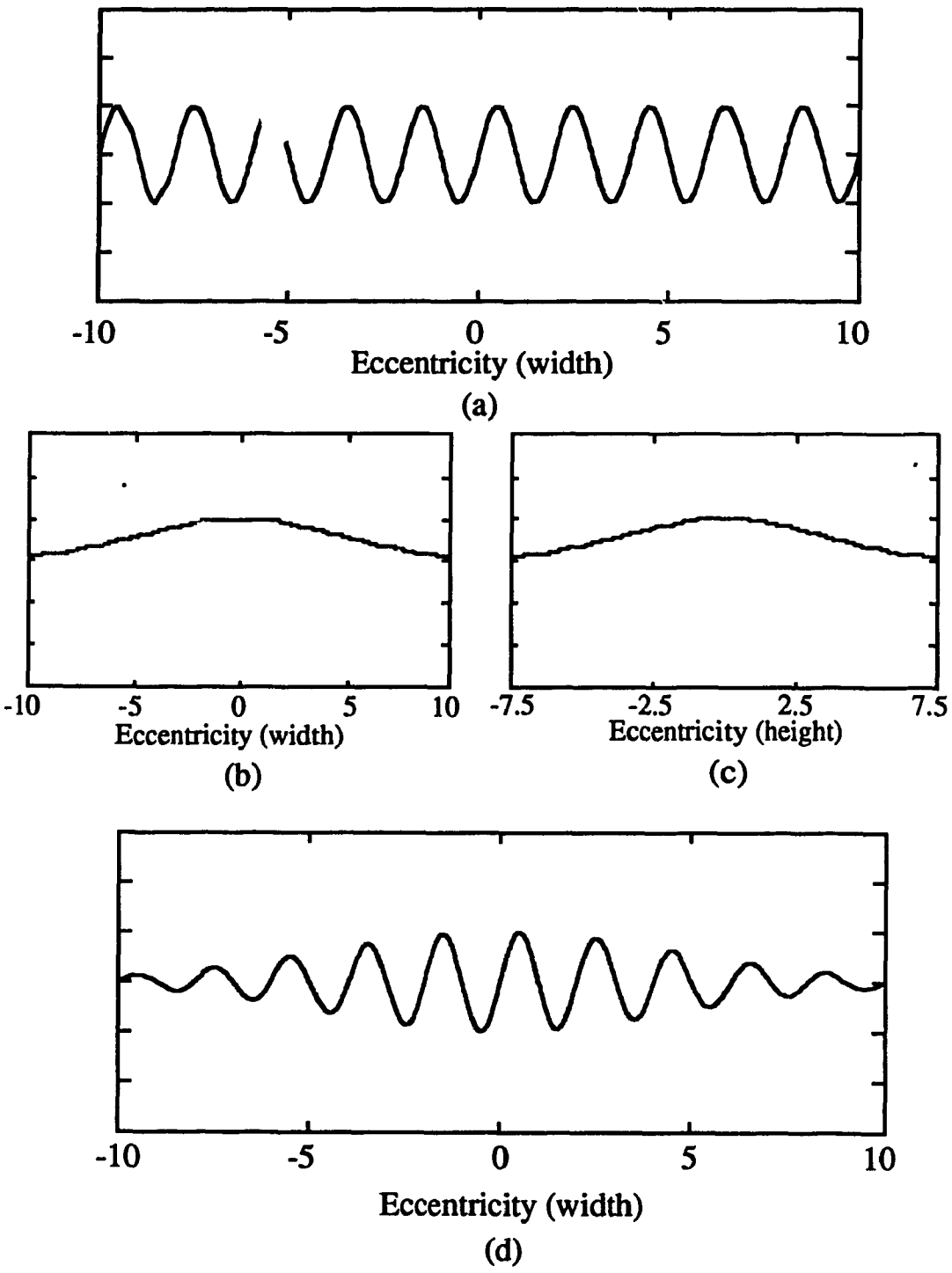


Figure 2. A sine wave function of 0.50 c/d (a), Gaussian functions for screen width (b) and height (c), and a Gabor function (d) obtained as a product of functions (a) and (b). The Y-axes represent the luminance profiles, and the X-axes the retinal eccentricities from fixation point.

$$= \exp[-(x^2/c_x^2 + y^2/c_y^2)] \quad (7)$$

and

$$s(x) = m * \sin(2\pi f_x x) \quad (8)$$

where s(x) is the sinusoidal component on the x axis, w(x,y) stands for weighted functions in space, c_x is the space constant for x and c_y is the space constant for y. The space constants used represent the position from the center (fixation point), to the right or to the left for the x value and up or down for the y value, where the contrast is reduced to 1/e or 37% of the peak contrast. A horizontal luminance profile of the Gabor function can be seen in graph (d) of Figure 2. This is obtained by multiplying the sine wave in (a) by the Gaussian function in (b). A three-dimensional representation of formula (6) can be seen in Figure 3. This was obtained by multiplying graph (a) with (b) (the $w_1(x)$ component) and (c) (the $w_2(y)$ component) in Figure 2.

To complete the picture, if a counterphase flickering Gabor grating is required to increase in contrast in a Gaussian fashion to control for sharp onsets and offsets, the following formula would result:

$$L_{x,y,t} = [w(x,y,t)s(x,t) + 1]L_o \quad (9)$$

where

$$w(x,y,t) = w_1(x)w_2(y)w_3(t)$$
$$= \exp[-(x^2/c_x^2 + y^2/c_y^2)]\exp(-(t^2/c_t^2)) \quad (10)$$

and

$$s(x,t) = m * \sin(2\pi f_x x)\sin(2\pi f_t t) \quad (11)$$

These are the functions that were used to generate the stimuli in this study.

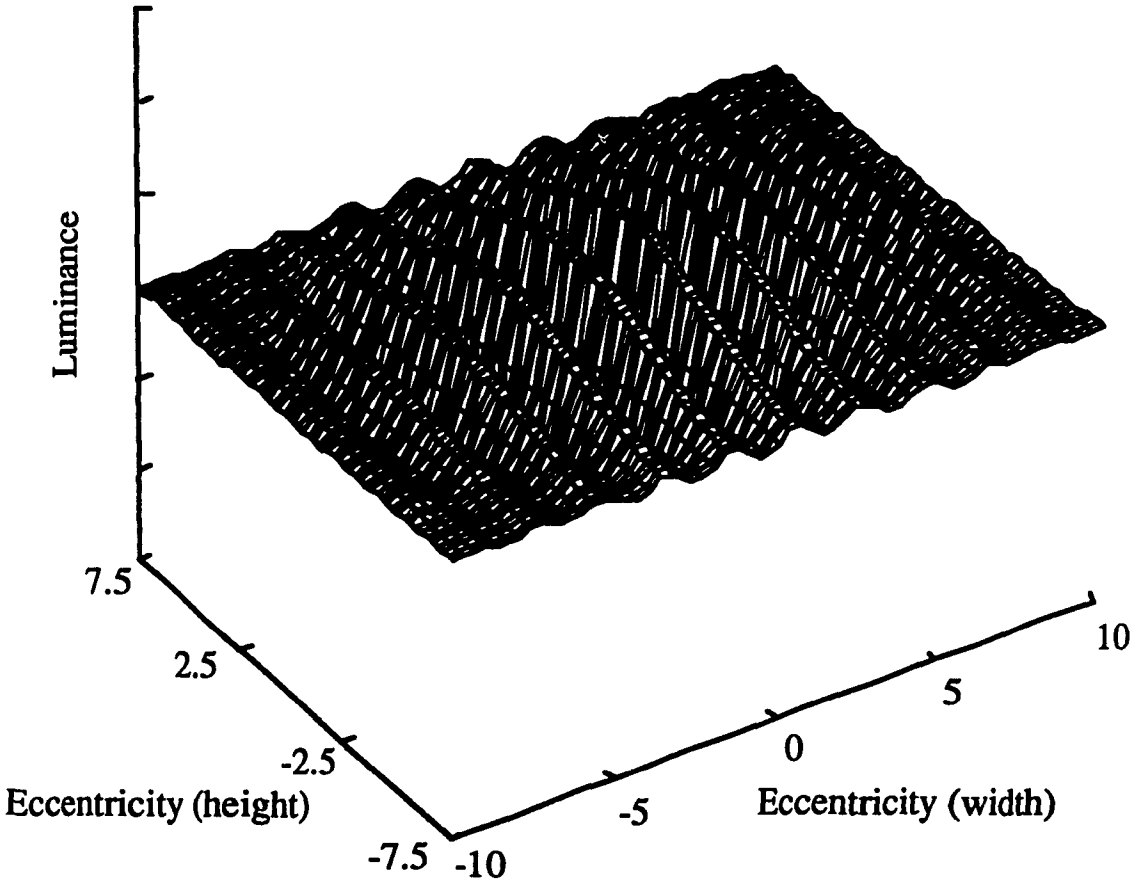


Figure 3. A three-dimensional representation of formula (6) in the text. This is a product of the functions in Figure 2. The X-axis shows the width eccentricities from fixation and the Y-axis the height eccentricities. The Z-axis is the luminance profile of the function.

Detection vs. discrimination The psychophysical procedures used to determine spatial sensitivity generally fall into two main categories, dependent upon what response criterion is required from the observer. In one condition, the observer must indicate whether there is any stimulus at all, and in the other condition, he or she is asked to distinguish between two different stimulus characteristics, such as, spatial and temporal factors or between two different values of a given characteristic, for instance, distinguishing between two spatial frequencies or two temporal frequencies. The first condition is called detection and the second is called discrimination. In discrimination experiments, the observer is often presented with two stimulus patterns and asked if they are the same or different. This method is useful in determining channels or mechanisms, for example, at what point spatial configurations are mutually exclusive. Of particular interest for the present work is the method of detection. In the detection paradigm, the dependent measure is usually contrast sensitivity which is the reciprocal of the contrast measure described earlier.

The method most often used to establish detection thresholds is the method of adjustment. Because it is the most widely used and since there may be some potential problems with it, this technique requires some discussion. In this method the observer adjusts the contrast until the stimulus is barely seen. After several adjustments, the average is taken as the threshold value. One of the major considerations to take into account when using such a method is that the criterion response is never well established and can vary from observer to observer. For instance, if a composite stimulus pattern containing both spatial and temporal components is presented, one observer can establish the spatial configuration as the critical component and another can use the temporal factors. Further, the observer can establish the "just seen" level for a response (liberal response criterion) while another uses a "surely seen" approach

(conservative criterion). In essence, the resulting contrast sensitivity measure in both these cases is sampled on different points of the psychometric function. Another problem with this technique is that there is no assurance that the observer will maintain the same criterion throughout the test sequence. The main advantage for using the adjustment method is that a threshold can be established relatively quickly.

An alternative approach is the forced choice method. In this procedure, the observer is required to determine whether one of several presentations contains the target stimulus as opposed to a uniform field at mean luminance. Some possibilities are that the presentations are shown sequentially (temporal forced choice) or side-by-side (spatial forced choice). Further, the threshold estimation can be determined using a staircase procedure. The advantage of using such a procedure is that of eliminating individual biases by establishing the set criterion through experimental control (Green & Swets, 1966). Thus, one can assess a reliable and predetermined detection threshold. The psychophysical procedure used in this study was a combination of temporal forced choice and a staircase procedure (Graham, Robson, & Nachmias, 1978). The main disadvantage of this procedure is that it is time consuming.

Factors affecting sensitivity There are many other factors which affect the perception of gratings besides psychophysical procedures. Because the method of detection is of particular interest, the present discussion on the consequences of factors such as luminance, stimulus uncertainty, and number of visible cycles will deal, for the most part, with detection experiments.

Research shows that changing the intensity of the stimulus has profound effects on the sensitivity functions of gratings (Campbell & Robson, 1968; van Nes & Bouman, 1967). First, the cutoff frequency, which is the highest

frequency an observer is able to perceive under a given condition, decreases with reduced luminance. Other effects include peak shifts to the left and a change from band-pass functions to low-pass functions as the luminance levels are decreased. The peak sensitivity refers to the highest contrast sensitivity obtained on an observer's sensitivity function. Band-pass functions imply a reduction of sensitivity at either end of the spectrum while the low-pass function refers a sensitivity loss at the higher spatial frequencies but not at the lower spatial frequencies.

In uncertainty experiments, a target grating can be placed in any one of several positions in the visual field. This is known as spatial uncertainty. Another type of uncertainty is frequency uncertainty which occurs when any one of several possible spatial patterns can be presented in a given trial. Research has shown that uncertainty effects, producing reduced sensitivities for a greater number of possible outcomes, *are* present for both spatial and frequency uncertainty (Cohn & Lasley, 1974; Davis, Kramer, & Graham, 1983; Davis & Graham, 1981; Graham, *et al.*, 1978). No effects of contrast uncertainty were found (Davis, *et al.*, 1983; Thomas, 1983).

Stimulus uncertainty is discussed here because a common method of assessing spatial contrast sensitivity involves determining the threshold for one spatial frequency at a time. The methodology in this study involves a randomized staircase procedure where spatial and temporal frequency uncertainty are both present. This has the added advantage of controlling for increased sensitivity with decreasing uncertainty within a block of trials of the same spatial or temporal frequency.

Several reports have shown that the number of visible cycles interacts with luminance to affect sensitivity measures (Campbell & Robson, 1968; Hoekstra, van der Goot, van den Brink, & Bilsen, 1974; Savoy & McCann,

1975). The higher the luminance the larger is the effect of number of visible cycles. For example, at 2 cd/m^2 a minimum of about three visible cycles is required to reach maximum levels, at 25 cd/m^2 about four cycles, and at 165 cd/m^2 about eight cycles, with no change at higher luminance levels. The usual band-pass function observed in contrast sensitivity functions is probably due, in part, to limited stimulus sizes which do not allow an appropriate number of visible cycles at the lower end of the spectrum. When compensated for visible cycles, the sensitivity functions show low-pass characteristics (Hoekstra, *et al.*, 1974). No selective effect of spatial frequency has been found.

Pupillary miosis and lens density Two of the well known effects of aging on the optical properties of the eye are pupillary miosis and increasing density of the lens. Pupillary miosis refers to the fact that the pupil gets progressively smaller with age (Pitts, 1982). Several factors could be responsible for miosis of the pupil some of which include atrophy of the dilator muscle fibers, hyaline substance deposition below the sphincter muscles of the iris, and the loss of retinal receptors responsible for the pupillary neural pathways (Pitts, 1982).

Another effect of aging is increased lens density (Spector, 1982), which refers to the reduction of light transmission through the lens resulting in lower luminance levels at the retina. The main cause of reduced transmission is the yellowing of the lens which is produced by a combination of factors, of which, increased susceptibility to oxidation due to a slowdown of turnover and increased concentration of protein levels are probably major causes (Spector, 1982). Thus, the reduction of light reaching the retina can result from both absorption of the lens and increased scatter.

It is obvious that yellowing of the lens would affect perception at shorter wavelengths (blue spectrum) more than at longer wavelengths (red spectrum);

therefore, colour sensitivity, particularly of blue/green colours would be particularly affected. Verriest and his coworkers have demonstrated this by testing a large sample of observers with the Farnsworth-Munsell 100-hue test (Verriest, van Laethem, & Uvijls, 1982). They found a greater sensitivity loss for the shorter wavelengths with aging. Coren and Girgus (1972), testing 265 individuals using a series of metameric stimuli, have demonstrated a consistent linear decrease in performance to short wavelengths (in this case 490) which they attribute to lens density. They express this sensitivity loss as a lens density factor which can be represented by the following polynomial regression formula.

$$D = 10^{-4} * A + (6 * 10^{-5}) * A^2 + 0.124 \qquad (12)$$

Where D is the lens density and A is age in years. The regression formula accounts for 83 percent of the variance. Clearly, based on these data, lens density increases steadily with age.

Said and Weale (1959) did a series of dark adaptation experiments with a variety of wavelengths ranging from 398 to 680. They found that there is an increase of approximately 0.05 log units in density for each 10 years of age (11% per year). The assumption is that dark adaptation depends on transmittance of the ocular media. They also report a greater effect at shorter wavelengths.

Human Psychophysical Data and Implications for Physiology

It is clear from physiological experiments that P cells do specifically carry colour information. As predicted from the psychophysical literature, these colour cells behave in colour opponent fashion, with a clearly defined R-G

colour opponency and a less clearly defined but present Y-B colour opponency. It is also clear from the physiological literature that the M cells are not wavelength selective. At first glance this would imply that the M cells in the RGP are responsible for the achromatic spatial vision observed psychophysically. As discussed below, this is only partly true.

Spatially tuned mechanisms When light patterns enter the eye, the retinal circuitry structures the pattern of light into receptive fields by which retinal ganglion cells may receive input from many receptors in some cases (mostly rod-driven ganglion cells) and a few receptors in other cases (cone-driven cells in the fovea). Consequently, some retinal ganglion cells respond to a greater area on the retina and others to focus on smaller areas, thus, spatially organizing the stimulation arising from the light into differently sized receptive fields. The theory of spatially tuned mechanisms assumes that this process is responsible, at least in part, for the perception of different spatial frequencies as determined by grating sensitivity.

The evidence for spatially tuned mechanisms in psychophysics comes generally from two different methodologies, namely, studies which assess the interaction between different stimuli, such as masking and adaptation experiments, and discrimination studies described earlier. In the interaction experiments, the assumption is that, in a two-stimuli trial, if these stimuli are independent of one another, the presentation of one stimulus should not affect the sensitivity to the other. Presumably, if there is an effect, the mechanisms responsible for the perception of these stimuli are partially overlapping. In the discrimination experiments, when two stimuli are compared for example, one should be able to tell the difference only when the respective mechanisms are non-overlapping.

Using an adaptation paradigm, Blakemore and Campbell (1969) found that the mechanisms were about one octave apart when the test frequency was above the adapted pattern and two octaves when the test pattern was below the adapted pattern. In other words, if an observer was adapted to a 2 c/d grating, there was no interaction if the test grating was 4 c/d. DeValois (1977) found a small sensitivity increase to test gratings that were larger than two octaves compared to the adapted grating.

Other researchers, using a masking paradigm where filtered noise patterns were used as the mask and gratings as the test stimulus, found that the effect of masking was at half its maximum when the masking stimulus and the test grating were from 0.5 to 0.75 of an octave apart (Henning, Hertz, & Hinton, 1981; Stromeyer & Julesz, 1972). Similar results were found by Legge and Foley (1980) when using gratings for both the test and adaptation stimuli.

Further evidence for spatial tuning comes from summation experiments. In a summation experiment, gratings are superimposed and it is assumed that the spatially tuned mechanisms for the spatial gratings comprising the compound grating are the same when the sensitivity to the compound grating is greater than the sensitivity to either component grating measured independently. Some researchers have shown that only probability summation at chance level is observed when the component gratings are separated by one octave or more, that is, there is no summation effect produced by the gratings alone (Graham & Nachmias. 1971; Sachs, Nachmias, & Robson, 1971). When the gratings differ by less than an octave, the probability summation is greater than chance levels. Other researchers have confirmed this and also found that, when the difference between the component gratings is large, there is an inhibitory effect (Hirsch, Hylton, & Graham, 1982; Olzak & Thomas, 1981).

Finally, discrimination experiments where observers were asked to determine the target stimulus out of several, at low contrast levels, also determined the critical range of spatial tuning at about one octave (Furchner, Thomas, & Campbell, 1977; Nachmias & Weber, 1975; Thomas, Gille, & Barker, 1982). In summary, there is psychophysical evidence to support the notion of separate, spatially tuned, mechanisms which can be roughly estimated at one octave apart. However, this does not necessarily imply that these mechanisms are independent. As the research demonstrates, when stimuli are beyond an octave apart, the mechanisms may have inhibitory-excitatory properties.

Temporally tuned mechanisms Using the same logic as above for spatially tuned mechanisms, temporally tuned mechanisms can also be described. For example, Watson and Robson (1981) used a discrimination paradigm to distinguish between different temporal frequencies. It was suggested that when two temporal frequencies can be discriminated, they represent different temporally tuned mechanisms. Based on their data, they report two temporally tuned mechanisms, as have other investigators (King-Smith & Kulikowski, 1975; Roufs, 1974; Thompson, 1983). However, some researchers report three separate temporal mechanisms (Hess & Plant, 1985; Mandler, 1984; Mandler & Makous, 1984; Plant & Hess, 1985). Plant and Hess suggest that the three mechanisms may have different band-pass characteristics: specifically, that one mechanism has a low pass characteristic and is tuned to lower temporal frequencies, another shows band-pass properties and is tuned to middle temporal frequencies, and the third is also band-pass and responsive to high temporal properties. The third temporal filter, however, is only evident when using a low spatial frequency target. The temporal filters can be said to range from approximately 0 to 4 hz, 4 to 20 Hz,

and 20 to 32 Hz or higher. The 32 Hz frequency was the highest frequency used.

Spatio-temporal interactions It has been proposed by Kelly (1979), based on human psychophysical experiments, that the temporal and spatial properties of the visual process are inseparable. This would imply that only one physiological mechanism controls the achromatic spatial and temporal interactions (Burbeck & Kelly, 1980). Based on the obvious chromatic *vs.* achromatic nature of the P and M cells, one would be inclined to think that the M cells are responsible for achromatic spatial vision.

Spatio-temporal interactions were first observed by Robson (1966) and extended by a number of researchers (Kelly, 1969, 1972; Koenderink & van Doorn, 1979; Kulikowski, 1971; van Nes, Koenderink, Nas, & Bouman, 1967) using gratings flickering at different rates. The general result of these experiments showed that, at high temporal frequencies, there was no selective interaction with spatial frequency. At low temporal frequencies, however, there was a dramatic decrease in sensitivity for the lower spatial frequency gratings. This implies that, at high temporal and spatial frequencies, the sensitivity functions are separable. That is, the sensitivity function can be expressed as the product of the individual spatial and temporal sensitivities. At low frequencies, the sensitivity function reflects interaction.

Later, Kelly (1979) assessed the spatio-temporal interaction using drifting gratings and a stabilized retinal image. An eye tracking device was used to slave the visual stimulus to the observer's eye movements. Based on his results and those of the other researchers mentioned, he suggested the concept of spatio-temporal surface. Basically, this is a three dimensional representation which depicts the spatio-temporal interactions in a global fashion. In the spatio-

temporal interactions, it is generally found that sensitivity to low spatial frequencies is enhanced if presented at high temporal and diminished if presented at low temporal frequencies. Sensitivities for high spatial frequencies are not much affected by temporal rate but seem to prefer slightly lower temporal frequencies. Thus, there exists a band-pass spatial contrast sensitivity function at low temporal frequencies, and a low-pass spatial contrast sensitivity function at high temporal frequencies. The spatio-temporal threshold surface, as suggested by Burbeck and Kelly (1980), implies that these processes are generated by a unique mechanism although it is not clear as to why it should be so. Alternatively, the surface can be interpreted as an envelope of the different spatio-temporal mechanisms.

Evidence that the achromatic spatial mechanism is the M pathway comes from physiological data demonstrating that the M cells have better contrast sensitivity than P cells (Derrington & Lennie, 1984; Derrington, *et al.*, 1984; Hicks, *et al.*, 1983; Kaplan & Shapley, 1982), and have a significantly superior contrast gain (Kaplan & Shapley, 1982; Kaplan & Shapley, 1986). However, this notion is not supported by several reports. Parvocellular R-G opponent cells demonstrate a higher spatial frequency cutoff and respond better to achromatic high spatial frequencies than to chromatic high spatial frequencies (Wiesel & Hubel, 1966). Further, the evidence that the M cells comprise only 10% of all fibers leaving the retina, as opposed to 80% for the P cells (Perry, *et al.*, 1984), argues against the notion that the M pathway is solely responsible for the spatio-temporal surface. It would appear that placing so much function on only 10% of the fibers, which are more highly concentrated in the peripheral retina, is not a good strategy for the visual system. This is counterbalanced to a certain extent by the superiority of the M cells' contrast gain.

The most direct evidence against a unique achromatic pathway comes from the studies by Merigan and his colleagues on acrylamide treated monkeys inducing selective P cell loss (Merigan, *et al.*, 1985; Merigan & Eskin, 1986). Clearly, some achromatic spatio-temporal functions were severely impaired by losing the P fibers. Particularly, the high spatial frequencies (which confirms the Wiesel & Hubel data) were affected, as were some intermediate spatial frequencies but only at low temporal frequencies. Low spatial frequencies were also affected but only when presented at low temporal frequencies. However, some functions were clearly spared, particularly the low spatial-high temporal functions which implies that these are served by the M cells regardless of their small numbers.

From these results, it would appear that the P cells are responsible for the intermediate to high spatial frequencies and the M cells for the low to intermediate frequencies which would certainly correspond to their respective morphologies. However, this is contradicted by Merigan's data which show a loss of low spatial frequencies for static gratings. This is perplexing to the extent that P cells have small receptive fields and have low contrast sensitivity. A possible explanation for this comes from the proposition that probability summation alone could account for increased contrast sensitivity (Watson, 1979), and has been used to explain differential contrast sensitivity for target sizes (Kelly, 1984; Robson & Graham, 1981). Merigan and Eskin (1986) calculated Weibull functions for their data to determine if the slope of the response function was the same for treated and untreated monkeys and found that they were indeed the same. Further, these slopes were similar to those calculated for human psychophysics for summation over 1 to 30,000 neurons (Robson & Graham, 1981). They conclude from this that the loss of sensitivity for low spatial frequencies at very low temporal frequencies can be the result of

loss of P cells based on probability summation and is not a result of M cell loss which has not been identified histologically.

Transient/sustained dichotomy Since the distinction was made for the cat's transient (Y-cells) and sustained (X-cells) properties (Cleland, *et al.*, 1971; Enroth-Cugell & Robson, 1966), many attempts have been made to identify separate transient and sustained mechanisms by psychophysical means in the human visual system. It is important to discuss these implications in the light of more recent physiological evidence in the monkey.

Evidence for such a psychophysical distinction in humans comes from several methodologies. One group of studies has demonstrated that sensitivity for low spatial frequency gratings varies more with stimulus duration than sensitivity to high spatial frequencies and has been interpreted as representing two separate mechanisms (Breitmeyer & Ganz, 1977; Legge, 1978; Spitzberg & Richards, 1975). Similarly, Wilson (1978, 1980) obtained different spatial characteristic responses when testing for line-spread functions if the stimulus was presented in either an abrupt or gradual way. Other evidence stems from work by Breitmeyer, Levi, and Harwerth (1981) and Stromeyer, Zeevi, and Klein (1979). Breitmeyer and his colleagues assessed the sensitivity to gratings which were masked by a uniform field flickering at 6 Hz and found that their frequency response curves were significantly affected by the presence of flicker. The Stromeyer study also used a uniform flicker but assessed its effect on wide and narrow bars. Similarly, Green (1981) had subjects adapt to a uniform flickering field and then assessed the sensitivity to drifting gratings. All these studies found evidence for the notion that uniform fields and lower spatial frequencies are detected by a different mechanism than are high spatial frequencies. Other studies have also found evidence for this dichotomy

(Kulikowski & Tolhurst, 1973; Tolhurst, 1973; Tulunay-Keesy, 1972) but have been challenged on methodological grounds (Burbeck, 1981; Derrington & Henning, 1981).

Generalization from the psychophysical data to the physiological data has been put in doubt by Lennie (1980). However, most of the arguments put forth by Lennie condemn the direct comparison between X- and Y-cells of the cat and the human psychophysical results. Clearly, much physiological data on the monkey has been acquired more recently, so this question must be reconsidered. Further, as was implicit in earlier data and argued explicitly by Kaplan and Shapley (1986), the X- and Y-cells of the cat and the P and M cells of the monkey cannot be equated. Based on filtering properties, the X/Y distinction should rather be regarded as a subset of the M cells representing extremes of a continuum. That is, M cells show responses ranging from linear to non-linear characteristics. The presence or absence of linearity vs. non-linearity was a major distinguishing factor applied to the X- and Y-cells in the cat. Another distinction is that the P pathway and the M pathway are much more clearly distinguished morphologically than are the X- and Y-cells of the cat (Perry, *et al.*, 1984).

One of the arguments made by Lennie (1980) against the notion of separate transient and sustained mechanisms was that the difference in conduction velocities between X- and Y-cells was too small to represent the differences obtained in the psychophysical studies. Although this is true for the cat, the differences between conduction velocities of the P and M cells of the monkey are much greater (Schiller & Malpelli, 1977). Another statement by Lennie was that the X-cells of the cat were not found to be less sensitive to large spatial targets than the Y-cells. M cells in the monkey are not only equally sensitive to lower spatial frequency gratings but it has been shown that they are

even more sensitive to contrast in general (Derrington & Lennie, 1984; Derrington, *et al.*., 1984; Hicks, *et al.*, 1983; Kaplan & Shapley, 1982, 1986). However, given the much greater number of P cells (80% of total fibers leaving retina) as opposed to M cells (only 10%) it has been suggested that, by probability summation alone, one can account for the greater sensitivity of P cells collectively for lower spatial frequencies at low temporal frequencies (Derrington & Lennie, 1984; Merigan & Eskin, 1986).

In addition to the arguments above, evidence that the M cells and the P cells represent the transient and sustained mechanisms, as defined psychophysically, comes from other findings. It has been demonstrated that M cells are tuned for higher temporal frequencies, when using spatial targets, than are P cells (Derrington & Lennie, 1984). Further, it is clear that P cells have a higher spatial frequency cutoff than do M cells (Wiesel & Hubel, 1966). The most direct and powerful argument for this separation comes from the Merigan and Eskin (1986) study with acrylamide-treated monkeys. The fact that flicker fusion frequency and spatial contrast sensitivity for low spatial frequencies presented at high temporal frequencies was not affected by acrylamide treatment is indicative that indeed the M pathway is specifically tuned for low-spatial/high-temporal achromatic targets as would be predicted from the psychophysical data. This can be argued on the basis that the P cells were severely, if not totally, destroyed and that the M cells were spared, as attested by histological examination (Eskin, *et al.*, 1985; Eskin & Merigan, 1986).

Moreover, the contrast sensitivity loss of lower spatial frequency targets presented at low temporal frequencies and the loss of high spatial frequencies presented at any temporal frequency demonstrates that the P cells are specifically tuned for high spatial frequencies and low spatial frequencies at low temporal frequencies. These results corroborate well with the

transient/sustained distinction advanced by the psychophysical literature. However, the transient/sustained nomenclature is not appropriate and is often misleading because there is a tendency to equate the transient and sustained terms of psychophysics with those of physiology or vice versa. The properties of the single cells in the retino-geniculate pathway cannot be taken as directly representing the experience of vision.

The transient distinction in physiology can be taken to represent a rapid burst of firing with a rapid decline. Clearly, this kind of response can be obtained from almost any cell under certain conditions. There is obviously some modulation of visual stimuli which is not obtained at the lowest levels of the visual system and requires further processing at the cortical level. For instance, the notion that P cells carry achromatic and chromatic information (Ingling & Martinez-Uriegas, 1985) requires that an ambiguous message coming from this system is interpreted at higher levels than the RGP. This notion is supported by the data summarized thus far. It is obvious, from what has been reported above, that P cells respond to chromatic parameters. It is also clear, that these cells are responsible for the sensitivity to higher spatial frequencies.

Another interesting concept discussed by Ingling and Martinez-Uriegas (1985) is that the R-G cells, which comprise 80% of P cells, are also sensitive to spatially uniform achromatic flicker, that is, the opponent chromatic inputs become additive instead of subtractive (Gouras & Zrenner, 1979). It is interesting that, although this is the case at the single cell level, it does not translate when tested as a group of cells, as demonstrated by Merigan and Eskin's (1986) data. A possibility is that both are sensitive but one mechanism takes precedence over the other at the decision level. At a level where both mechanisms are equally or similarly stimulated, a particular mechanism's

sensitivity can represent either a positive, negative, or neutral signal to higher cortical levels. That is, there are interactive effects between cell types for a given stimulus pattern which may be the source of the distinction made at higher levels.

It is possible that at certain extremes or under certain conditions, visual information about a given stimulus type is specifically carried by a particular cell group without requiring further processing at higher levels. Chromatic information is evidence of such parallel processing where it is clear that this information is primarily transmitted by the P cells. Further, it is logical to assume that the system would not reinterpret information which has already been segregated at lower levels. For example, if a particular stimulus pattern optimally stimulates the M pathway and does not stimulate the P pathway, this could be a clue to higher cortical levels of what visual information is available. This stimulus pattern could possibly be distinguished from another which optimally stimulates the M pathway but also produces a response in the P pathway.

Aging Vision

Brightness sensitivity and aging Pitts (1982) reports studies which assess brightness contrast differences caused by aging. Three main conclusions can be derived from the data. First, the variability of performance increases with age. Second, an increase of contrast by a factor of 1.17 to 2.51 is needed to maintain the same level of performance between the ages of 20-30 and 60-70. Third, a minimum background luminance of 0.34 cd/m^2 is needed for a 60-70-year age group in order to compare the results with those of younger observers because the differences increase dramatically at lower luminance levels. With a 3 mm artificial pupil, this represents 2.4 td. The

problem with relating these results to the present experiments is that brightness contrast experiments generally use small target sizes on a background. It is possible that lens density is more of a factor with smaller targets as demonstrated with data below on spatial contrast sensitivity.

Spatial and temporal factors in aging vision More relevant to the present research are the reports on spatio-temporal contrast sensitivities of the aging individual. Sekuler and Owsley (1982) tested people ranging from 20 to 90 years of age for contrast sensitivity of sine wave gratings. The spatial frequencies tested were 0.5, 1, 2, 4, 8, and 16 c/d at a mean luminance of 103 cd/m^2. They found no differences in sensitivity for the lower spatial frequencies (0.5 and 1 c/d). Older observers had lower sensitivities starting at about 4 c/d showing greater decrements as they got older. A peak shift was also apparent, where the peak sensitivity was at 2 c/d for 60 year-olds and about 4 c/d for the younger observers. Thus, the loss of spatial contrast sensitivities with age is more evident at middle and high spatial frequencies.

To establish whether the cause of middle and high spatial frequency losses were due to transmittance reduction, Sekuler and Owsley (1982) tested 20-year-old observers under the same conditions but with the addition of a 0.5 neutral density filter which reduced the retinal illuminance to about 1/3 the original value and compared the results with the data of 60 year-old observers. This approach was based on the estimation, made by Weale (1963), that a 60-year-old eye transmits about 1/3 the luminance of a 20-year-old eye. Their results indicate a reduction of sensitivity only for the middle and high spatial frequencies but not for the lower spatial frequencies. However, the loss of sensitivity in the experimental condition did not reach that of the 60-year-old

observers, implying that part of the loss at middle and high spatial frequencies for the latter group is due to factors other than media opacities.

Sekuler and Owsley (1982) also report studies on spatio-temporal sensitivities using a 1 c/d grating drifted at low (0.5 degrees per second) and high (10 degrees per second) temporal rates for young and older observers. The results indicate that young observers were much more sensitive to high temporal rates than older observers. Although there was a difference at low temporal rates, this difference was much smaller. Therefore, aging causes a selective loss of sensitivity to large gratings flickering at high temporal rates but not at low temporal rates. This may represent a selective loss of large fibers which, based on evidence cited earlier, might be responsible for the lower spatial frequencies flickering at high temporal rates.

Aging and neural loss Balazsi and his coworkers counted nerve fibers of the human optic nerve in eyes obtained from people ranging between 3.5 and 82 years-of-age (Balazsi, Rootman, Drance, Schulzer, & Douglas, 1984). They found a significant effect of age on nerve fiber loss and estimated that about 5,637 fibers are lost per year. Repka and Quigley (1988) did not find a significant loss of fibers due to age; however, they did report a small reduction of mean fiber diameter with age. Other researchers, using an image-analysis apparatus, have found a selective loss of large fibers in the three cortical areas examined (Terry, *et al.*, 1987). These areas were the midfrontal, superior temporal, and inferior parietal areas. However, no data were available on the visual cortical areas. Thus, it would appear that aging does cause nerve cell loss but it cannot be determined with assurance that some cell types are more affected than others. A reasonable assumption is that aging causes a diffuse loss of nerve fibers.

Glaucoma

Although there are several types of glaucoma, the most common, and the one of interest here, is open angle glaucoma. Glaucoma is a disease of the eye where there is axonal damage to the optic nerve head. Some pathophysiological data on glaucoma are of particular interest since they demonstrate that glaucoma selectively damages the large fiber cells in early stages of the disease (Minckler & Odgen, 1987; Quigley, *et al.*, 1987). This makes sense in the light of the well known initial visual defects caused by glaucoma, which are expressed by peripheral field losses, and in the fact that the peripheral retina is supplied primarily by large fibers. This study attempted to exploit this effect by testing individuals with early glaucoma and ocular hypertensives. The rationale is that the losses experienced under the different experimental conditions by glaucoma patients and suspects should reflect the loss of the M pathway. This would allow a greater insight as to what role the different mechanisms play in the spatio-temporal properties of the visual system.

Because the clinical symptoms of glaucoma are limited and the diagnosis is often based on the psychophysical procedure of visual field testing, there has been much interest in the spatial and temporal sensitivities of glaucoma patients. A number of reports have shown that glaucoma patients can demonstrate loss of grating sensitivity to static gratings (Faubert, Balazsi, Overbury & Brussell, 1987; Faubert, Brussell, Overbury, Balazsi & Dixon, 1987; Hitchings, Powell, Arden, & Carter, 1981; Stamper, Hsu-Winges, & Sopher, 1982). Although patients who show decreased sensitivity often show losses for all spatial frequencies, some glaucoma patients show only low spatial frequency deficits (Faubert, Brussell, *et al.*, 1987). Other research, using flickering gratings, also demonstrates sensitivity losses in glaucoma (Atkin,

Bodis-Wollner, Wolkstein, Moss & Podos, 1979; Neima, LeBlanc & Regan, 1984; Wolkenstein, Atkin & Bodis-Wollner, 1980). Wolkenstein and coworkers have looked at specific frequency losses and report losses for lower and middle spatial frequencies with flickering gratings (Wolkenstein, *et al.*, 1980).

There have been several reports showing temporal resolution deficits with non-grating targets (Brussell, Muermans, White, Faubert & Balazsi, 1989; Faubert, Balazsi, *et al.*, 1987; Faubert, Brussell, *et al.*, 1987; Faubert, Balazsi, Muermans, Brussell & Kasner, 1989; Tyler, 1981). Some of these studies have used a single luminous target at foveal fixation (Brussell, *et al.*, 1989) and at one point viewed peripherally at 20 deg eccentricity (Tyler, 1981). Others have assessed flicker sensitivity throughout the visual field (Faubert, Balazsi, *et al.*, 1987; Faubert, Brussell, *et al.*, 1987; Faubert, *et al.*, 1989). All these reports show that flicker deficits precede static visual field deficits. The reports by Faubert and his coworkers show that the earlier flicker deficits appear in the periphery. It was also demonstrated that flicker deficits correlated with the neuro-retinal rim area (Faubert, *et al.*, 1989). This implies that the observed flicker deficits may represent neural damage identified anatomically.

Present study

In a series of experiments, the present study attempted to elucidate several issues. First, it examined the spatio-temporal characteristics of the human visual system using a technique which controls for visible edges, response criterion, and reaction time. This was done by using a two-alternative temporal forced-choice staircase procedure and by Gaussian filtering the spatial and temporal components of the stimuli.

Second, the effect of aging under these conditions was established. Based on the literature review, a loss of higher spatial frequency sensitivity was

to be expected, as well as a loss of sensitivity for low spatial frequencies flickered at high temporal rates.

Third, the effect of early glaucoma on spatio-temporal properties was assessed. It was expected that the sensitivity loss due to glaucoma would not be significantly greater for high spatial frequencies or low spatial frequencies at low temporal rates. However, a loss of sensitivity for large gratings flickered at high temporal rates was expected to be significantly different from the age-matched normal control group as a consequence of the selective large fiber loss. This allowed the determination of which spatio-temporal properties under the present conditions are under the control of one physiological mechanism as opposed to the other.

Finally, in another condition, the illuminance level was reduced to approximately 0.70 td so that isolation of the M pathway would be possible. This was done for all the groups and established, for the normals, the function of the M pathway. It was expected that the glaucoma group would show sensitivity loss for all visible combinations under this condition. In turn, this would be further evidence that large fibers are selectively affected in glaucoma. If such results were obtained, this would establish that the use of glaucoma could be a good experimental control in the understanding of visual mechanisms by presumably eliminating the M pathway. Consequently, it would allow the determination of the selective role of the M and P pathways in the photopic spatio-temporal properties of the human visual system.

Experiment 1

A major objective of this experiment was to determine whether the spatio-temporal threshold surface reported in previous research for achromatic/photopic luminances can also be obtained for similar luminance levels but under different experimental conditions. A forced-choice staircase procedure was used with Gaussian filtering of the spatial and temporal stimulus properties to control for spatial edges and sharp temporal onset. Another objective was to determine the effect of aging on the spatio-temporal threshold surface when controlling for observer biases, criterion shifts, and reaction time.

Method

Subjects Ten eyes of 10 different observers were used in this study. Five observers were between 23 and 33 and another five between 58 and 65 years of age. All participants had 6/7.5 (20/25) or better corrected visual acuity. The observers underwent an ophthalmological exam and were free of visual pathology. A list of individual ages and acuities along with other relevant information for the subjects used in this study are listed in Appendix A.

Apparatus Sine wave gratings counterphased at several temporal frequencies were presented on a 40x30 cm RGB monitor, equipped with a P22 phosphor (Gigatek - 1931CC) interfaced with graphics boards (Matrox - PG641) under the control of a 386 IBM AT compatible computer. The monitor had a 120 Hz noninterlaced full-screen refresh rate. A joystick was used to record the responses and a chin rest to maintain constant viewing distance. Observers were required to wear their own distance correction over a 3 mm artificial pupil during testing.

Procedure The psychophysical thresholds of 12 different spatial and temporal frequency combinations were assessed for all observers. Sine wave gratings of three spatial frequencies were paired with four different temporal frequencies. The temporal component consisted of counterphase flickering gratings with a sinusoidal temporal function. The three spatial frequencies were 0.50, 2.0, and 8 c/d and the four temporal frequencies were 0.0, 3.75, 7.5, and 15 Hz. The window size was 20 degrees of visual angle wide and 15 degrees high at 114.3 cm viewing distance. The temporal and spatial waveforms were Gaussian filtered, thus producing a three-dimensional Gabor function (the two spatial dimensions and the temporal dimension).

The entire spatio-temporal, three-dimensional, Gabor function is represented by Formula 11. The target area, that is, the area containing one space constant (37% contrast and higher) to the right and left of fixation and one space constant above and below fixation (Formula 7) subtended 10 degrees in height and 13.3 degrees in width. This allowed for a minimum of six complete cycles within the target area. The target stimulus resulted in an oval shape. Luminance was maintained at 10 cd/m^2 and a 3 mm artificial pupil was used. Thus, the retinal illuminance was maintained constant throughout testing at 70 td.

The stimulus was achromatic using a D_{65} white as defined by the u',v' 1976 chromaticity coordinates (u' = .198; v' = .456). A fixation point was located in the center of the screen. With the stimulus functions used, a node is present in the center of the display where the fixation point was located. The node is defined here as the junction point between the sine and cosine portions of the spatial sinusoidal functions. Within a counterphase flickering paradigm, the mean luminance always remains the same at this particular point. Thus, by

fixating directly at the node, the eyes have less of a tendency to follow the movement of the grating.

Each trial consisted of a set of two consecutive presentations of 3 seconds. The temporal constant used was 750 milliseconds so that for 1.5 seconds the stimulus was presented above 37% of the contrast being evaluated. The other 1.5 seconds of the presentation consisted of the rise time up to the 37% level (750 milliseconds) and fall time from the 37 % level (750 milliseconds). The first presentation was preceded by one beep, and the second by two beeps. Only one of the presentations contained the stimulus pattern. The observer responded by moving the joystick to the left if the stimulus pattern was in the first presentation and to the right if the pattern was presented in the second interval. Feedback was given for every response in the form of a tone to indicate whether the response was correct or incorrect. The correct response was followed by a high pitched tone and the incorrect response by a low pitched tone.

A temporal two-alternative forced choice staircase procedure with five reversals was used to determine the thresholds. Contrast was initially set above threshold, based on values predetermined from pilot data. The average of the five reversals was taken as the threshold level for the particular spatio-temporal combination. The contrast was decreased by 0.175 log units until the observer responded incorrectly. When the first incorrect response had been made, the contrast was raised 0.175 log units and the five reversals used to estimate the threshold started only at this point. Four trials were performed at this contrast level. This constituted one step in the staircase. The contrast changed by +4, +3, +2, +1, or -1 units. This change depended on whether the observer made zero, one, two, three, or four correct responses respectively. After each step of four trials the contrast unit changed in the same manner. That

is, the contrast unit after zero, one, two, three, or four reversals would be changed to 0.175, 0.125, 0.0875, 0.0625, or 0.05 log units.

Results

Figure 4 shows the group data obtained from this experiment for both young and older subjects. The individual graphs represent the different spatial frequencies. Graphs (a), (b), and (c) in Figure 4 show the data for 0.50, 2.0, and 8.0 c/d stimuli respectively. Log contrast sensitivity is plotted as a function of the four temporal rates. The two functions in each graph correspond to the mean values for the young observers, and the older group.

The data for the 0.50 c/d stimuli show a band-pass temporal function for both groups with the highest sensitivity at the medium temporal rates (3.75 Hz and 7.5 Hz). The young group has the lowest sensitivity for the 0 Hz condition while the older group has a similar sensitivity for the 0 Hz and the 15 Hz conditions. The function is generally lower for the older group except for the static condition where the values overlap. The greatest difference between the young and the older group, for the 0.50 c/d gratings, appears when these gratings are counterphase flickered at 15 Hz. The functions obtained from the two groups are virtually identical under the 2.0 c/d degree condition except for the 3.75 Hz temporal rate where the older group has lower sensitivities than the younger group (Graph (b)). The younger observers show a band-pass temporal function with a peak sensitivity at 3.75 Hz while the older group has a low-pass temporal function with a peak sensitivity at 0 Hz. Figure 4 (c) shows a clear difference between the young and older observers for the 8.0 c/d gratings. This difference is evident for the three lowest temporal rates but not for the 15 Hz stimuli. Low-pass temporal functions are observed for the two groups.

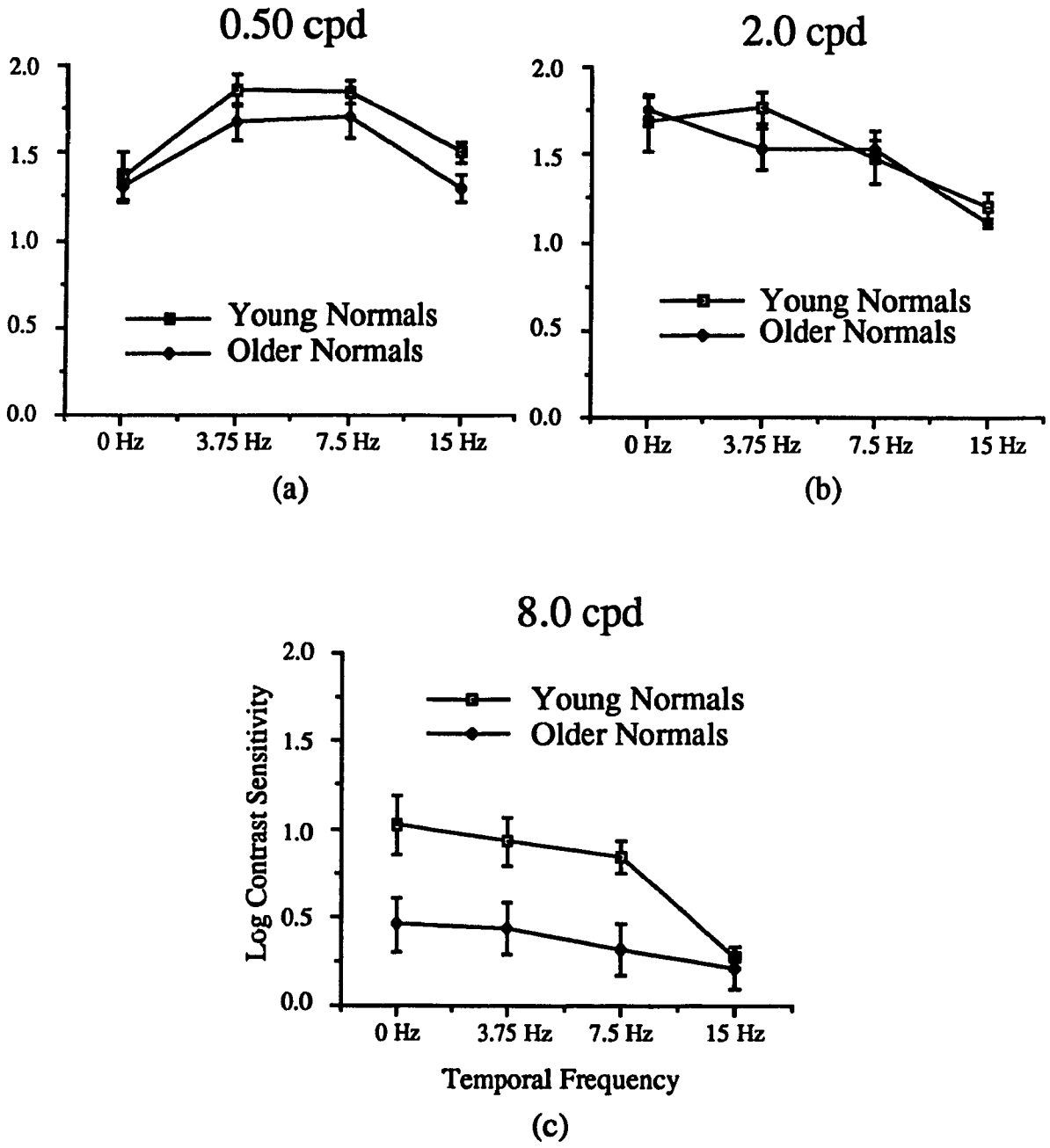


Figure 4. Contrast sensitivity as a function of temporal frequency for the 0.50 c/d (a), 2.0 c/d (b), and 8.0 c/d (c) stimuli of young and older observers obtained using a 70 td illuminance condition.

Both groups have low-pass spatial functions for all temporal rates except for the 0 Hz condition showing a spatial band-pass function with a peak sensitivity at 2.0 c/d. The interrelationship between spatial and temporal components is shown by the three-dimensional spatio-temporal threshold surface for the young observers in Figure 5 graph (a), and the threshold surface for the older observers in graph (b). For Figure 5, the z-axis represents the log contrast sensitivity, the y-axis represents spatial frequencies on a log scale, and the x-axis represents temporal frequency on a log scale. Interpolations of the data for the three-dimensional plots were obtained using a least squares method by McLain (1974). Examples of the threshold surface obtained for a young and older observer are shown in Figure 6. These graphs show a spatial band-pass function at lower temporal frequencies changing to spatial low-pass functions when moving towards high temporal frequencies. We can also observe a temporal low-pass function changing to a temporal band-pass function when moving from high to low spatial frequencies. Individual data for all the observers can be seen in Appendix B.

A 2x3x4 ANOVA with one between factor (age category) and two within factors (spatial x temporal) was calculated on the data. The ANOVA table obtained from the analysis is shown in Appendix C. The overall main effect of groups was not significant at the preset alpha requirements of 0.05, F (1, 8) = 4.27, p = 0.073. As expected, the overall main effects of spatial frequency, F (2, 16) = 97.31, $p < 0.001$, and temporal frequency, F (3, 24) = 51.05, $p < 0.001$, and the temporal by spatial interaction, F (6, 48) = 13.13, $p < 0.001$, were significant. The group by spatial frequency and the group by temporal frequency interactions were not significant. However, the group by temporal by spatial interaction was significant, F (6, 48) = 3.52, p = 0.006. *Post hoc* pairwise comparisons using the Tukey test show a significant difference between groups

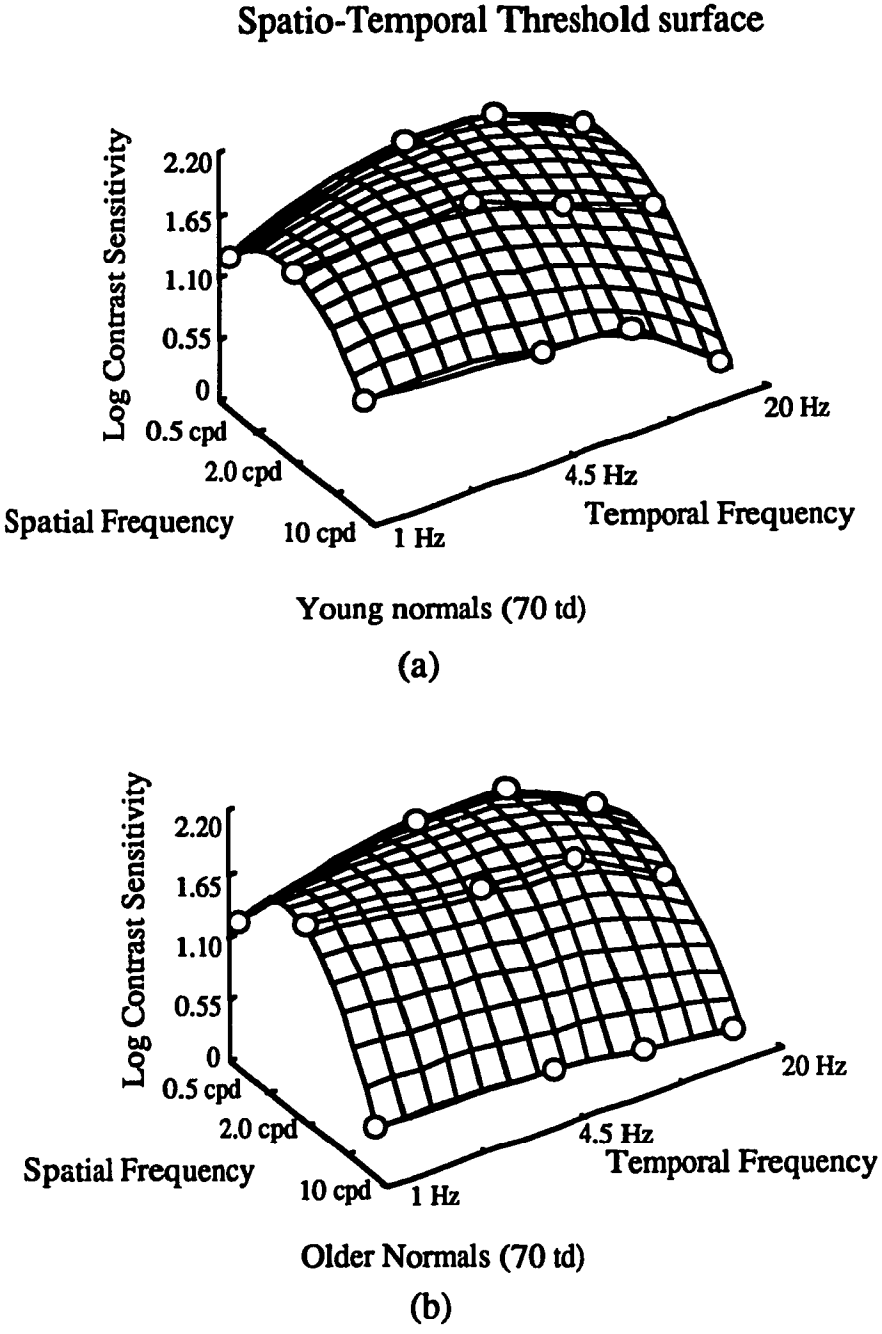
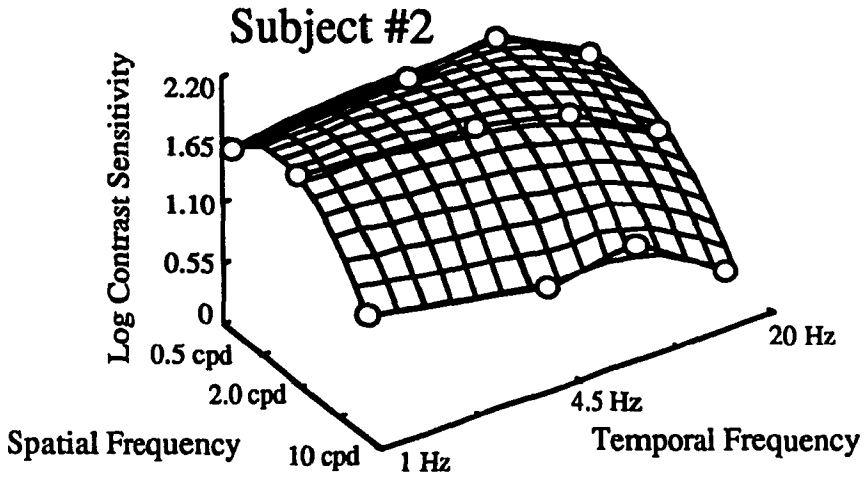


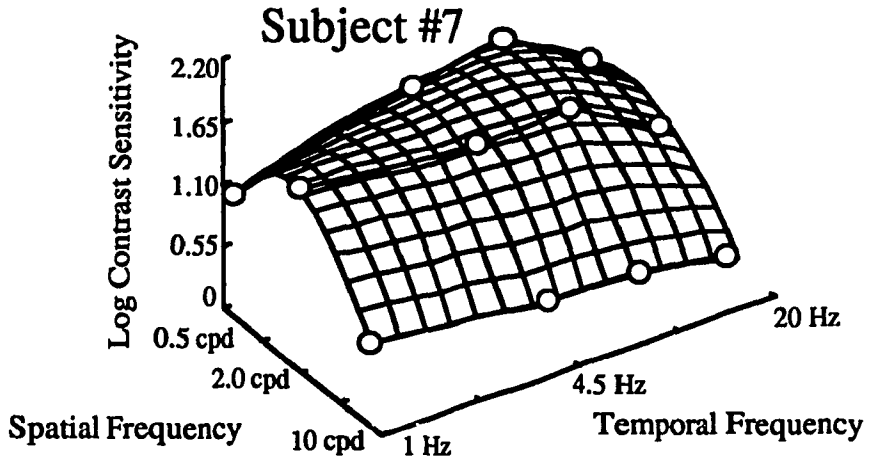
Figure 5. Spatio-temporal threshold surface for the young (a) and older (b) observers obtained for a 70 td illuminance condition.

Individual Threshold Surfaces: examples



Young normal (70 td)

(a)



Older Normal (70 td)

(b)

Figure 6. Spatio-temporal threshold surface for a 23 (a) and 60-year-old (b) observer obtained under a 70 td illuminance condition.

for the three lower temporal frequencies at 8.0 c/d, for the 0.50 c/d grating flickered at 15 Hz, and for the 2.0 c/d gratings flickered at 3.75 Hz with the older group showing lower sensitivities. These five significant pairwise comparisons can easily be identified from graphs (a), (b), and (c) in Figure 4 by the fact that they are the five points where the standard error bars of the two groups do not overlap showing lower sensitivities for the older observers.

Discussion

Figure 5 graph (a) demonstrates the interaction which occurs between the spatial and temporal frequency components on modulation sensitivities of young observers. The transition from a low-pass to a band-pass spatial frequency function with decreasing temporal frequency and from a low-pass to a band-pass temporal function as a result of decreasing spatial frequency are typical of previous findings (Kelly, 1969, 1972; Koenderink & van Doorn, 1979; Kulikowski, 1971; Robson, 1966; van Nes, Koenderink, Nas, & Bouman, 1967). Therefore, although these studies have used a variety of techniques which were different from the one presently employed, the data generally demonstrate the same form. This is evidence that the psychophysical technique used presently did measure the appropriate detection threshold. The data of previous research were obtained from a few experienced observers who were probably aware of the criterion shift and observer bias issues and, thus, consciously controlled for it. Graph (b) in Figure 5, which displays the data for the older group, also has the same general form, regardless of the fact that these observers were not experienced psychophysical observers and were unaware of what was being assessed. However, it was observed from the statistical analysis that a significant loss was apparent at the higher spatial frequency (8.0 c/d) flickered at the lower three temporal frequencies (0 Hz, 3.75 Hz, & 7.5 Hz) and for the

lower spatial frequency only when the latter was flickered at a high temporal rate (15 Hz). These results imply that there was no selective large fiber loss. If the latter were the case, one would primarily expect the sensitivity to large targets flickered at high temporal rates to be affected. On the other hand, these results exclude the purely optical explanation for reduced sensitivity due to aging. This argument cannot explain the loss of sensitivity for the 0.5 c/d-15 Hz and the 2.0 c/d-3.75 Hz targets.

The results support previous research by Sekuler and Owsley (1982) showing a sensitivity loss for high spatial frequencies and large moving targets and extend their work. What was not determined by them, but is shown here, is the fact that this loss of higher spatial frequencies due to aging spans a range of temporal frequencies.

Experiment 2

One primary purpose of this experiment was to establish the spatio-temporal threshold surface under relatively low luminance levels. The aim was to isolate and establish the magnocellular pathway contribution to the spatio-temporal characteristics obtained psychophysically under low illuminance conditions. Another objective was to determine the effect of aging on the psychophysical thresholds established under these conditions and, thus, to determine the effect of aging on the specific visual pathway.

Method

Subjects The same 10 eyes of the 10 observers were used for this study.

Apparatus The same setup was used for this experiment as in Experiment 1 with the addition of a 2.00 log unit Kodak Wratten gelatin neutral density filter (#96).

Procedure The two-alternative forced choice paradigm used in the first experiment was also used in this experiment. The luminance was reduced from 10 cd/m^2 to 0.10 cd/m^2 by using a 2.00 Log unit neutral density filter. Therefore, with an artificial pupil, 3 mm in diameter, the illuminance level was maintained at 0.70 td. Given the low luminance levels used in this experiment, the observers were dark adapted for a 30-minute period before the testing procedure. Two spatial frequencies and four temporal frequencies were assessed. The spatial frequencies were 0.5 c/d and 2.0 c/d, and the temporal frequencies were 0 Hz, 3.75 Hz, 7.5 Hz, and 15 Hz.

Results

Figure 7 shows the group means obtained for the 0.50 c/d (a) and 2.0 c/d conditions (b). Log contrast sensitivity is plotted as a function of temporal frequency.

The results show that the functions obtained from the young group and those obtained from the older group overlap for the most part, except at the 0 Hz condition. The low-pass temporal functions tend to part from one another only when the gratings are static. Figure 8 shows the same data in the form of a spatio-temporal threshold surface. Graph (a) of Figure 8 is the threshold surface for the younger observers and graph (b) is the surface for the older observers. The axes represent the same variables as in Figure 5. In the present graphs, the data show both spatial low-pass functions and temporal low-pass functions within the visible portion of the spatio-temporal threshold surface. This is true for both young and older observers. The striking difference between these data and those obtained in Experiment 1, besides the obvious loss of sensitivities at high spatial and temporal rates and the general reduction in sensitivity, is the disappearance of the spatial band-pass function under static temporal conditions. The data also show that sensitivity to the lower spatial frequencies is generally higher than for high spatial frequencies. Examples of a threshold surface for a young and older observer obtained under this condition is given in Figure 9. Three young observers were tested for 8 c/d gratings and show no sensitivity for this frequency under the 0.7 td condition. Individual data are shown in Appendix B.

A 2x2x3 between-within ANOVA with one between factor (groups) and two within factors (spatial x temporal) was performed on the data. The data obtained for the 15 Hz condition were excluded from the statistical analysis because most of the observers from both groups did not see these stimuli.

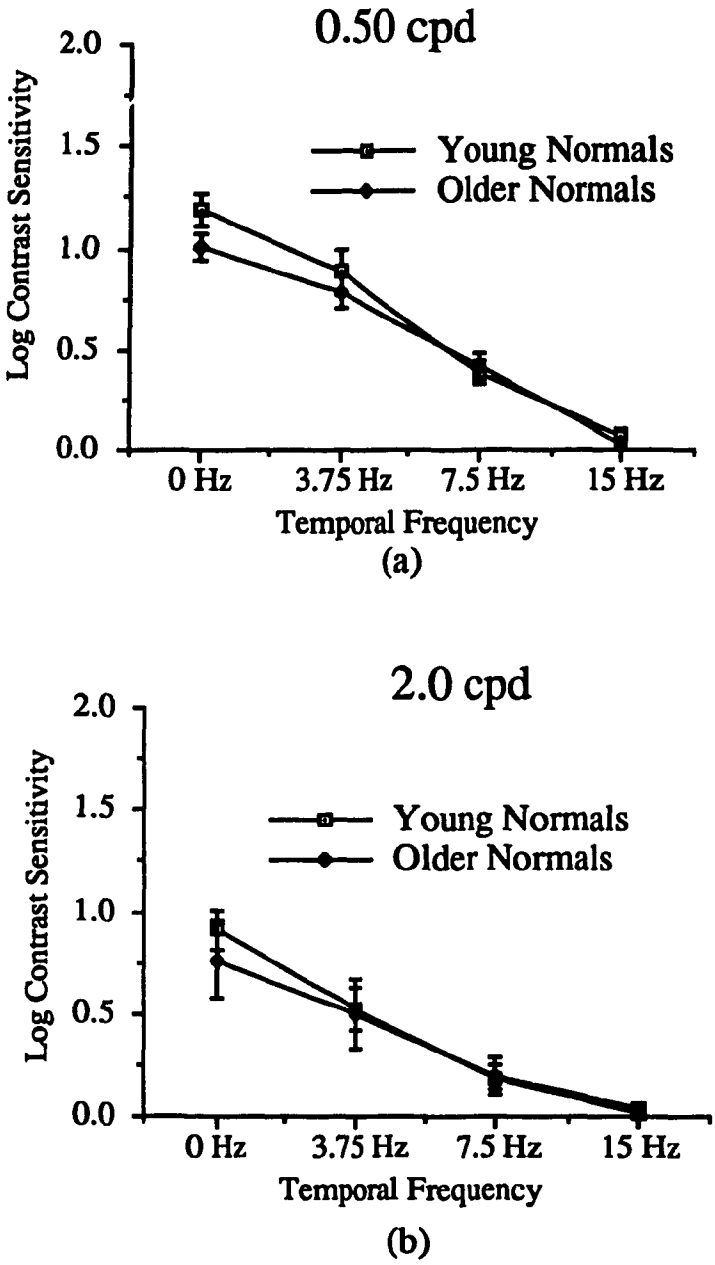


Figure 7. Contrast sensitivity as a function of temporal frequency for the 0.50 c/d (a) and 2.0 c/d (b) stimuli of the young and older observers obtained using a 0.70 td illuminance level.

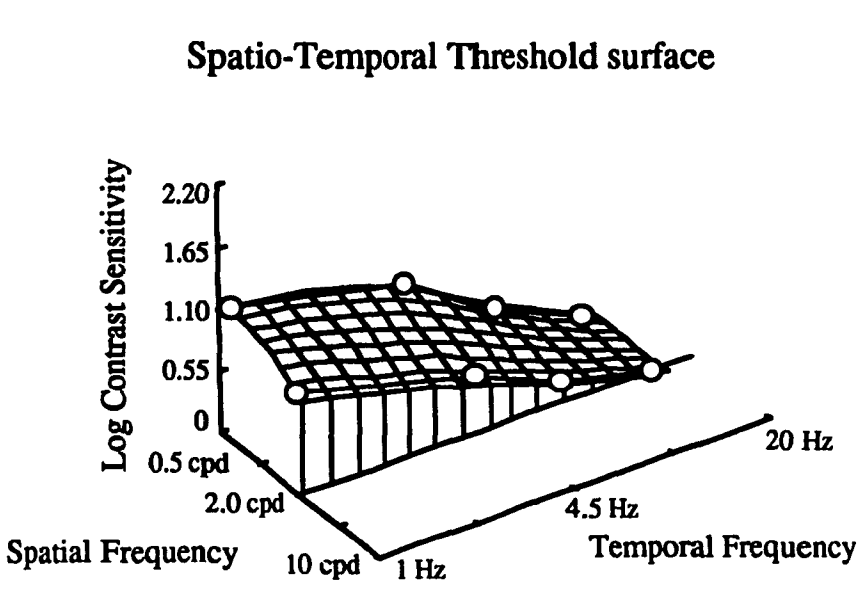
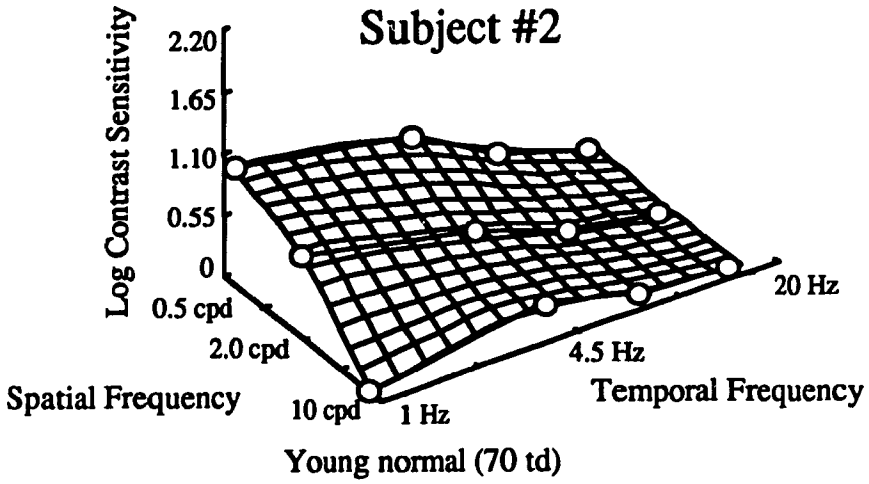


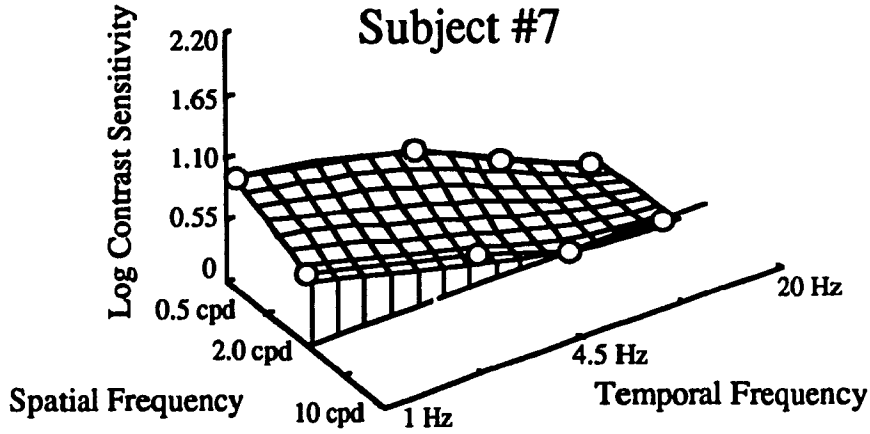
Figure 8. Spatio-temporal threshold surface for the young (a) and older (b) observers obtained for a 0.70 td illuminance condition.

Individual Threshold Surfaces: examples



Young normal (70 td)

(a)



Older Normal (70 td)

(b)

Figure 9. Spatio-temporal threshold surface for a 23 (a) and 60-year-old (b) observer obtained under a 0.7 td illuminance condition.

Appendix C contains the ANOVA table obtained from the analysis. No significant main effect was found for the between-groups factor. As expected, significant main effects were found for the spatial frequency factor, $F(1, 8) = 29.83$, $p = .001$, and the temporal frequency factor, $F(1, 8) = 112.27$, $p < .001$. No significant interactions were found.

Discussion

These results corroborate well with previous data showing a decreased sensitivity to higher spatial frequencies (Campbell & Robson, 1968; van Nes & Bouman, 1967) and higher temporal frequencies (Faubert, 1991; Tyler & Hamer, 1990) as a consequence of reducing luminance. Faubert (1991) found that the stimuli most affected by reducing luminance were small flickering targets. The current results demonstrate that this effect is present for both the young and older group. The results imply that aging does not have a significant effect on the M pathway when the latter is isolated by reducing illuminance levels. It is interesting, however, that the group means virtually overlap when the gratings are counterphase flickered but tend to separate for the static conditions, with the young observers having better sensitivity. The results clearly demonstrate that the visual system becomes more sustained as the luminance levels are reduced.

Experiment 3

This experiment assessed the performance of observers with glaucoma and those who have elevated intraocular pressures on spatio-temporal thresholds under photopic luminances. This attempted to establish whether glaucoma affects specific spatio-temporal conditions. Several assumptions were made for this experiment. The first assumption was that the human visual system is segregated into P and M pathways, analogous to the macaque monkey. The second assumption follows from the first , that is, if large fibers are affected in glaucoma then this should represent a loss of M cells and consequently of "M cell-like" spatio-temporal responses. As mentioned earlier, this should represent the low-spatial-high-temporal characteristics of the achromatic spatio-temporal threshold surface.

Methods

Subjects Fifteen eyes of 15 observers were used for this study. Five observers were diagnosed as having early glaucoma and five as being ocular hypertensives. The performances of these 10 participants were compared with the results of the normal observers of, the same age category who had participated in Experiment 1 and 2.

The glaucoma patients and ocular hypertensives had intraocular pressures greater than 21 mm Hg. Glaucoma patients were categorized on the basis of early visual field defects as determined by the Humphrey 30-2 program and/or disc cup abnormalities as established by any of the three referring glaucoma specialists. Ocular hypertensives showed no signs of visual field or optic disc cup abnormalities.

Apparatus The apparatus was the same as used in Experiment 1.

Procedure The psychophysical procedure was the same as in Experiment 1.

Results

Figure 10 shows the group data for the glaucoma patients and the ocular hypertensives along with the data from the age-matched normal observers obtained in Experiment 1. The individual graphs represent the different spatial frequencies. Graphs (a), (b), and (c) show the data for 0.50, 2.0, and 8.0 c/d stimuli, respectively.

The graphs show that the glaucoma group consistently shows lower sensitivities than the normal or ocular hypertensive groups. The glaucoma group also shows greater variability than do the other two groups. Figure 11 represents the "magnitude of loss" of sensitivities for the glaucoma group (a) and the suspect group (b). The "magnitude of loss" was calculated by subtracting the normal data from the group data of interest. The positive values were replaced with a zero and the absolute value of the negative scores was used. The results of these calculations are shown in Figure 11 producing a "magnitude of loss" spatio-temporal threshold surface (MLS). The MLS is plotted in log units on the z-axis. The y-axis represents spatial frequencies and the x-axis shows temporal frequencies, both presented on a log scale.

Graph (a) of Figure 11 demonstrates the pattern of sensitivity loss for the glaucoma group relative to normal observers of the same age category. It is evident from this graph that a sensitivity loss is present throughout the surface but at different levels. A greater loss is apparent under high temporal frequency conditions for middle to lower spatial frequencies. Other than at the high-spatial-high-temporal end of the scale where sensitivity is depressed for all observers and, therefore, no sensitivity difference is expected, the region of the

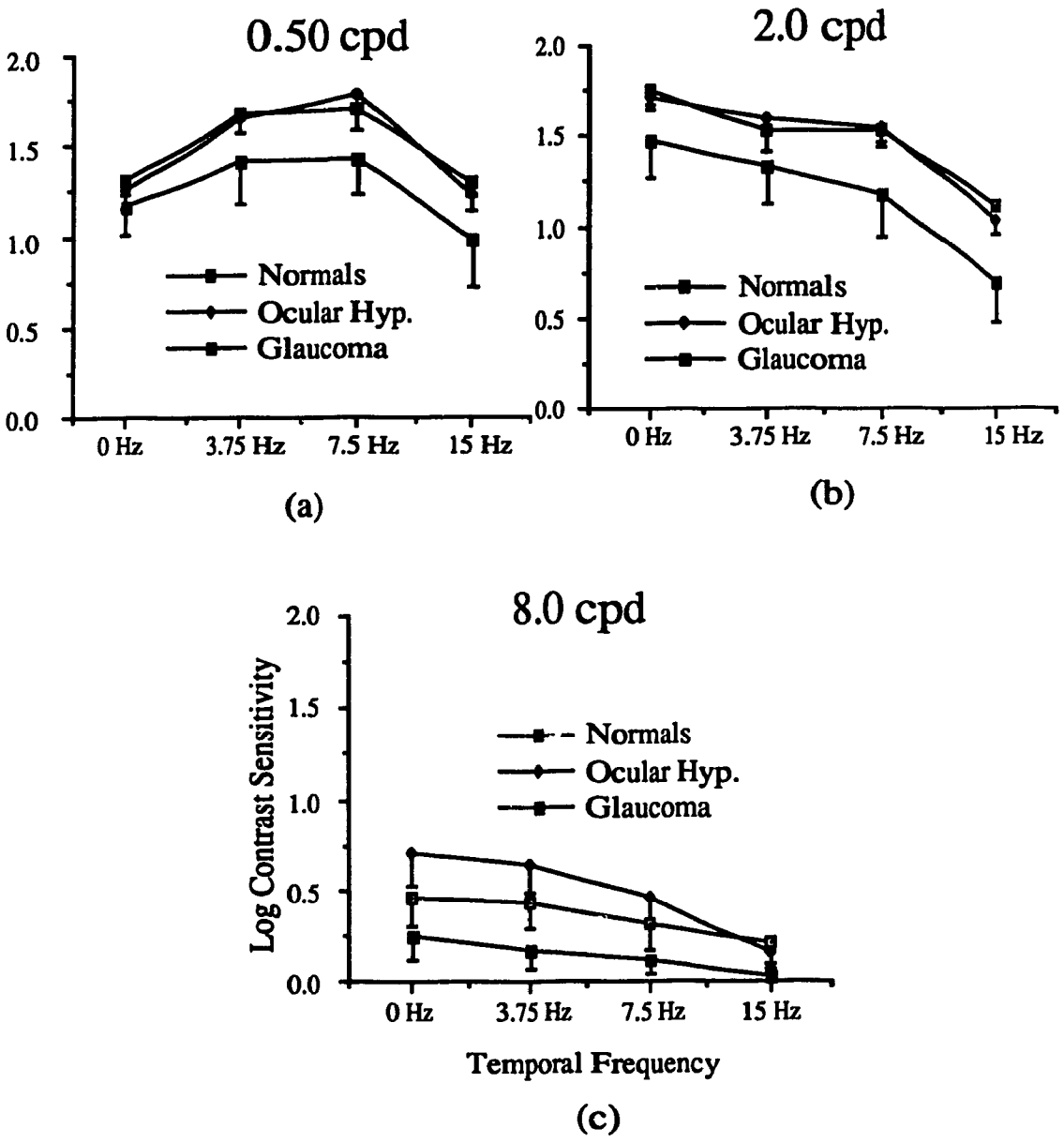


Figure 10. Contrast sensitivity as a function of temporal frequency for the 0.50 c/d (a), 2.0 c/d (b), and 8.0 c/d (c) stimuli of normal, ocular hypertensive, and glaucomatous observers obtained under a 70 td illuminance level.

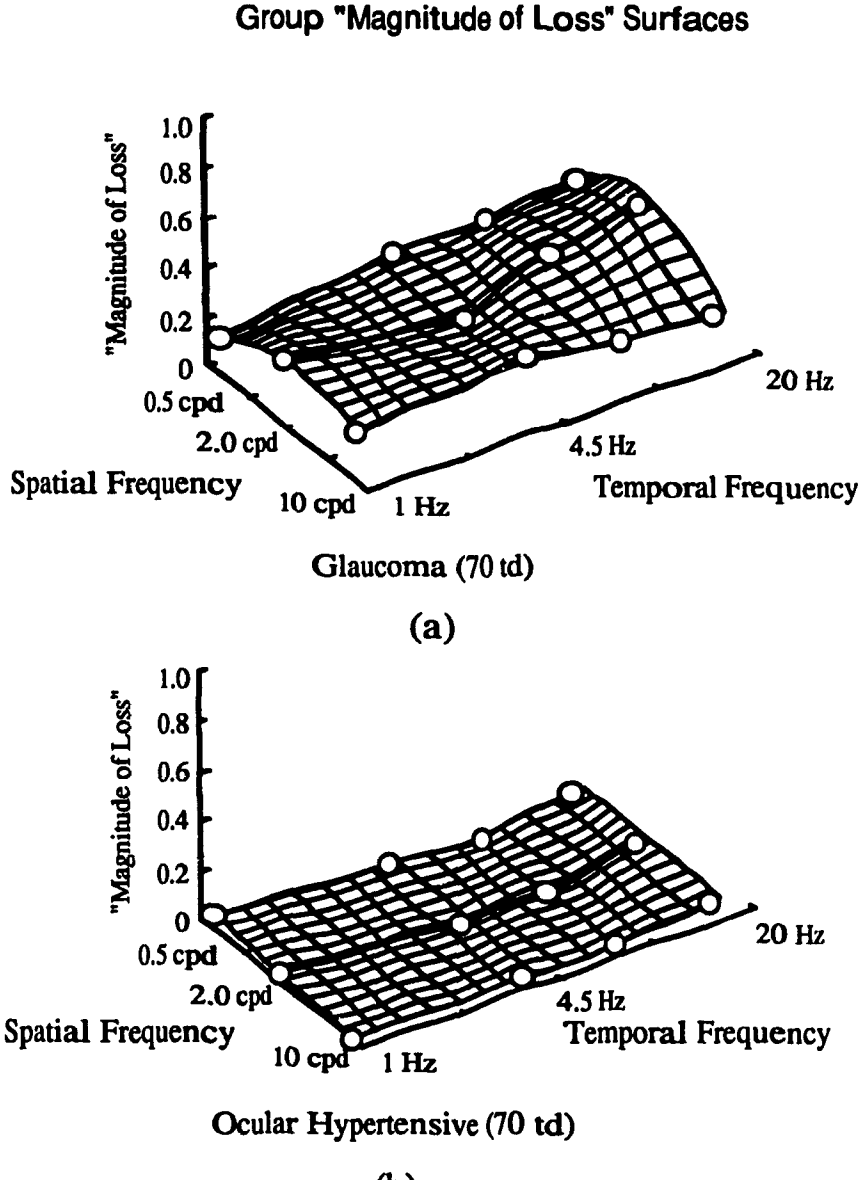


Figure 11. "Magnitude of Loss" spatio-temporal threshold surface (MLS) for glaucoma (a) and ocular hypertensive (b) observers under a 70 td condition. The Z axis arbitrarily portrays only positive sensitivity differences.

surface that is least affected by glaucoma is the mid-spatial-mid-temporal region. The ocular hypertensive group's MLS (b) shows very little loss compared to the normals, with some loss only at the higher temporal rates.

Individual MLS plots are shown in Figure 12 for the glaucoma observers and Figure 13 for the ocular hypertensives. The data show that three of five glaucoma observers have reduced sensitivities for the high-temporal and mid to low spatial frequency region of the surface. For the glaucoma observers, subject 19 shows no loss throughout the surface and subject 17 shows loss only at higher spatial frequencies. Only observers 11 and 12 of the ocular hypertensives show loss relative to normals with the loss generally observed in the low-spatial-high-temporal region of the surface.

A 3x3x4 ANOVA with two between factor (patient category) and two within factors (spatial x temporal) was calculated on the data. The ANOVA table obtained from the analysis is shown in Appendix C. No significant main effect between groups was found. As expected a significant main effect for the spatial factor, $F(2, 24) = 138.94$, $p < 0.001$, and the temporal factor, $F(3, 36) = 222.49$, $p < 0.001$, was found. The group by spatial and the group by spatial by temporal interactions were not significant, while the spatial by temporal interaction, $F(6, 72) = 30.33$, $p < 0.001$, was significant. The most interesting result comes from the group by temporal interaction which was significant, $F(6, 36) = 2.82$, $p = 0.024$.

Figure 14 represents the sensitivity loss relative to normals when collapsed across all spatial frequencies. Means for the three groups were calculated for the four temporal rates across all the spatial frequencies. The means from the normal group were subtracted from the means of the ocular hypertensives and the glaucoma patients. The result is a graph which displays the amount of sensitivity loss, in log units, produced by the respective

"Magnitude of Loss" Surfaces: Early Glaucoma Observers

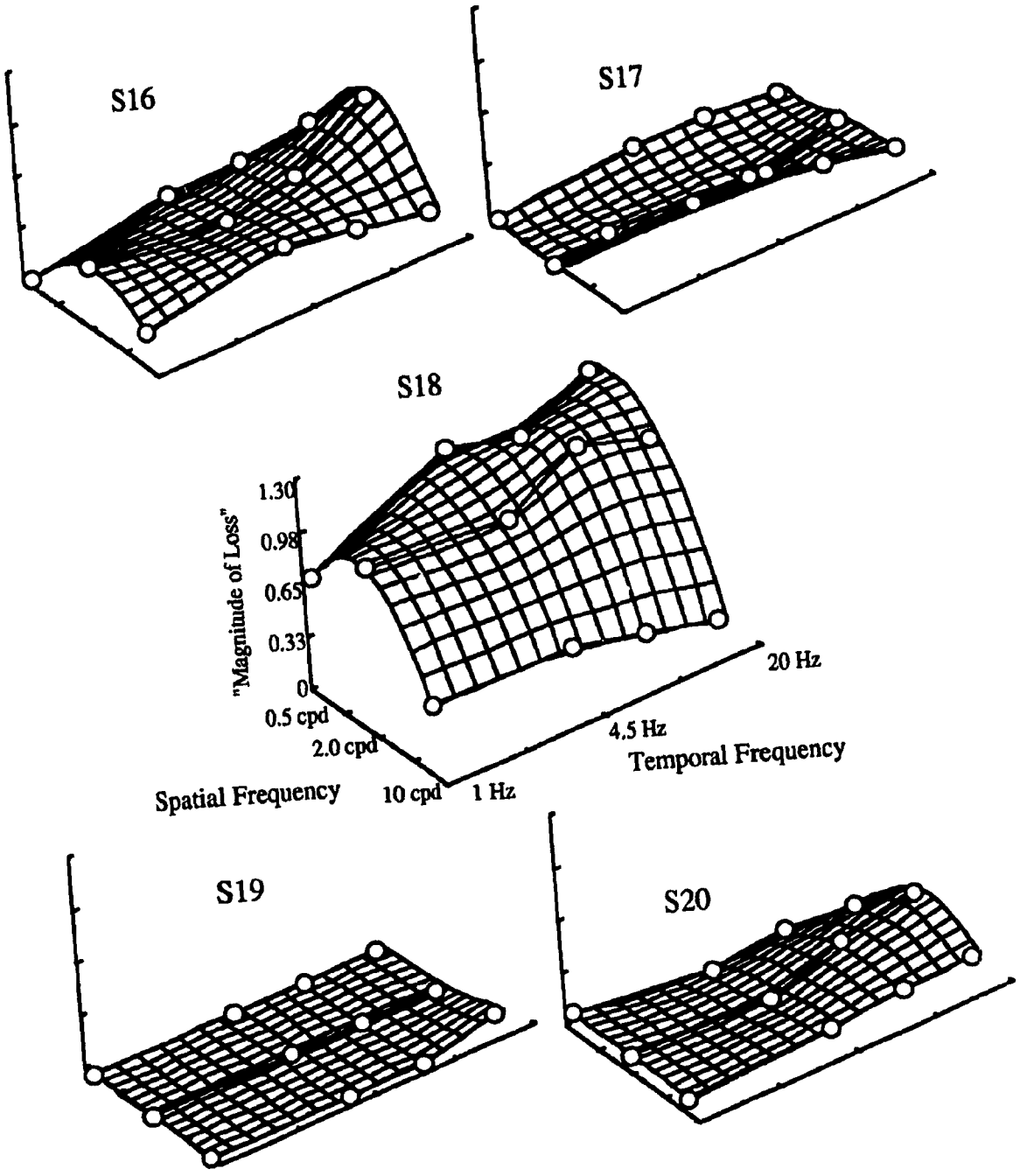


Figure 12. MLS for early glaucoma observers (subjects 16 to 20) obtained under a 70 td illuminance condition.

"Magnitude of Loss" Surfaces: Ocular Hypertensive Observers

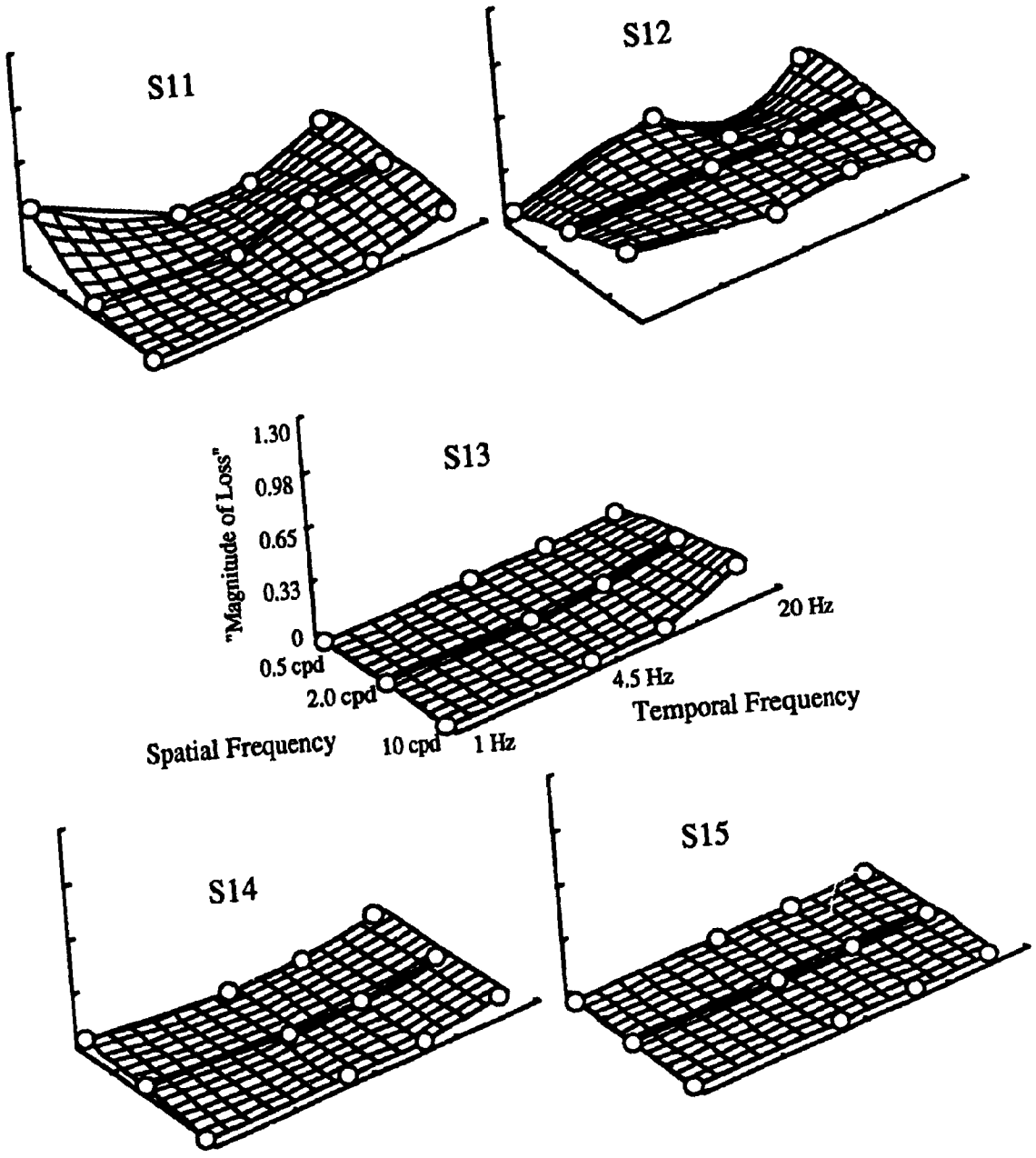


Figure 13. MLS for ocular hypertensive observers (subjects 11 to 15) obtained under a 70 td illuminance condition.

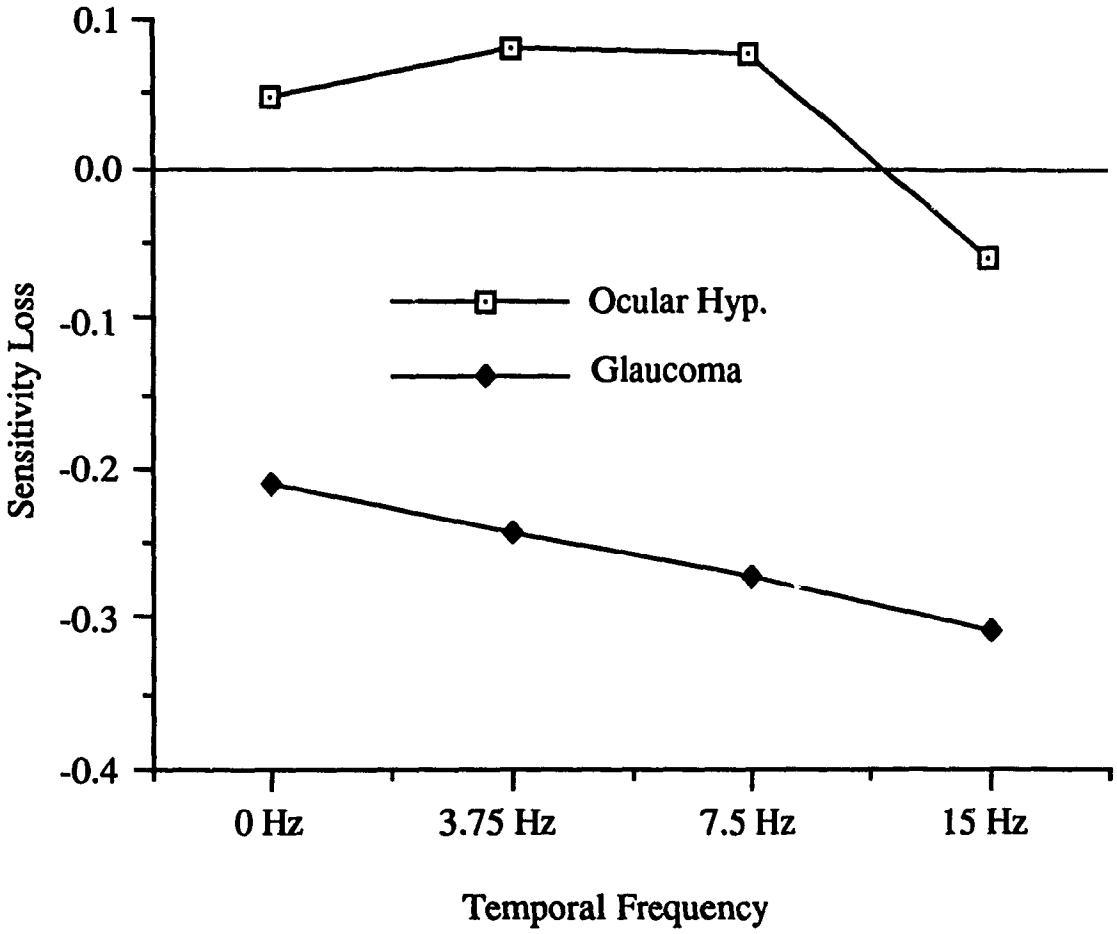


Figure 14. Visuogram of the data collapsed across spatial frequencies as a function of temporal frequency for the glaucoma and ocular hypertensive groups obtained for a 70 td illuminance level.

categories. This kind of graphical representation has been termed a "visuogram" (Bodis-Wollner, 1972). The y-axis represents the sensitivity loss relative to normals and the temporal frequencies are shown on the x-axis. The straight line drawn perpendicular to 0 log units on the ordinate represents the value obtained when subtracting the normal data from themselves. Figure 14 demonstrates the obtained temporal frequency by group interaction. The ocular hypertensives generally show better sensitivity than the normals except for the highest temporal frequency. The glaucoma group is worse than the normals for all temporal rates and this difference consistently increases with the glaucoma group getting progressively worse as the temporal frequency increases. *Post hoc* pairwise comparisons using the Tukey test show that the difference between the glaucoma group and the control group is statistically significant at all temporal frequencies. The difference between the ocular hypertensives and the normals is not statistically significant. However, the drop of sensitivity from the three slower temporal rates to the 15 Hz condition is greater for the ocular hypertensives than it is for the normals or the glaucoma patients. This can be seen in Figure 14 where the relative sensitivity of the ocular hypertensives drops sharply at 15 Hz while the glaucoma group shows a monotonic function.

Discussion

The results show that three of the five glaucoma observers , regardless of the normal acuity levels for their age, have sensitivity losses relative to normals which would be consistent with the notion of a selective large cell loss. However, the results also show that the most important factor in determining glaucoma related loss is the temporal component. Emphasis on temporal components of centrally fixated targets in the evaluation of glaucoma has been suggested by several researchers for grating stimuli (Atkin, *et al.*, 1979;

Wolkenstein, *et al.*, 1980) and uniform targets (Brussell, *et al.*, 1989). Others have emphasized the role of temporal components for both central and peripheral targets for gratings (Neima, *et al.*, 1984) and uniform targets (Faubert, Balazsi, *et al.*, 1987; Faubert, Brussell, *et al.*, 1987; Faubert, *et al.*, 1989; Tyler, 1981). Generally, the research dealing with grating stimuli has been limited to a few spatio-temporal combinations. The 12 spatio-temporal combinations utilized in this study allow a better determination of the selective effects of glaucoma on the spatio-temporal threshold surface. The graph in Figure 11 (a) shows the selective loss of the surface due to glaucoma. This graph shows that some loss is apparent throughout the surface except for high-spatial-high-temporal combinations where sensitivity levels are down for normals. The greatest loss is apparent for middle to high temporal frequencies presented in combination with middle to low spatial frequencies. These results support the notion that primarily large fibers are affected in early glaucoma.

Figure 14 is particularly suggestive of what happens with ocular hypertensives. For data collapsed across spatial frequencies, a drastic drop of sensitivity occurs at 15 Hz, although this particular suspect group generally showed better sensitivities for the slower temporal rates. These results and those from the glaucoma group support Tyler's results using uniform targets, that glaucoma loss is most evident with increased temporal frequency up to about 40 Hz (Tyler, 1981). From the results obtained thus far, one could argue that the sensitivity profiles obtained from the glaucoma and ocular hypertensive groups are consistent with the theory that glaucoma primarily affects large fibers for some but not all observers. However, the observers which do not show this pattern have no loss or very little loss relative to normals which suggests that these individuals probably have not incurred glaucoma related damage.

Further, it suggests that in very early stages, the component of the surface that is affected primarily is temporal in nature.

Experiment 4

This experiment assessed the spatio-temporal thresholds of glaucomatous vision at relatively low illuminance levels. As suggested by Shapley (1988), under low illuminance levels (below about 1 td or less), the parvocellular pathway is not active (see Figure 1). Thus, it is possible to observe the effect of glaucoma, which is thought to selectively destroy large fibres, on the M cells responding under these conditions.

Methods

Subjects The same 15 subjects who participated in Experiment 3 were tested in this experiment.

Apparatus The apparatus used in this experiment was identical to that used in Experiment 2.

Procedure The same psychophysical procedure was used as in Experiment 2.

Results

Figure 15 shows the group means obtained for the 0.50 c/d and 2.0 c/d conditions. As in the previous experiment, the glaucoma group consistently shows lower sensitivity levels than does the normal group. As seen in Figure 15, the difference is greater for the 0.50 c/d conditions than the 2.0 c/d conditions.

Figure 16 shows the "magnitude of loss" of sensitivities for the glaucoma group and the suspect group. The "magnitude of loss" is plotted in log units on the z-axis. The y-axis represents spatial frequencies and the x-axis temporal frequencies both presented on a log scale. One can observe from graph (a) of

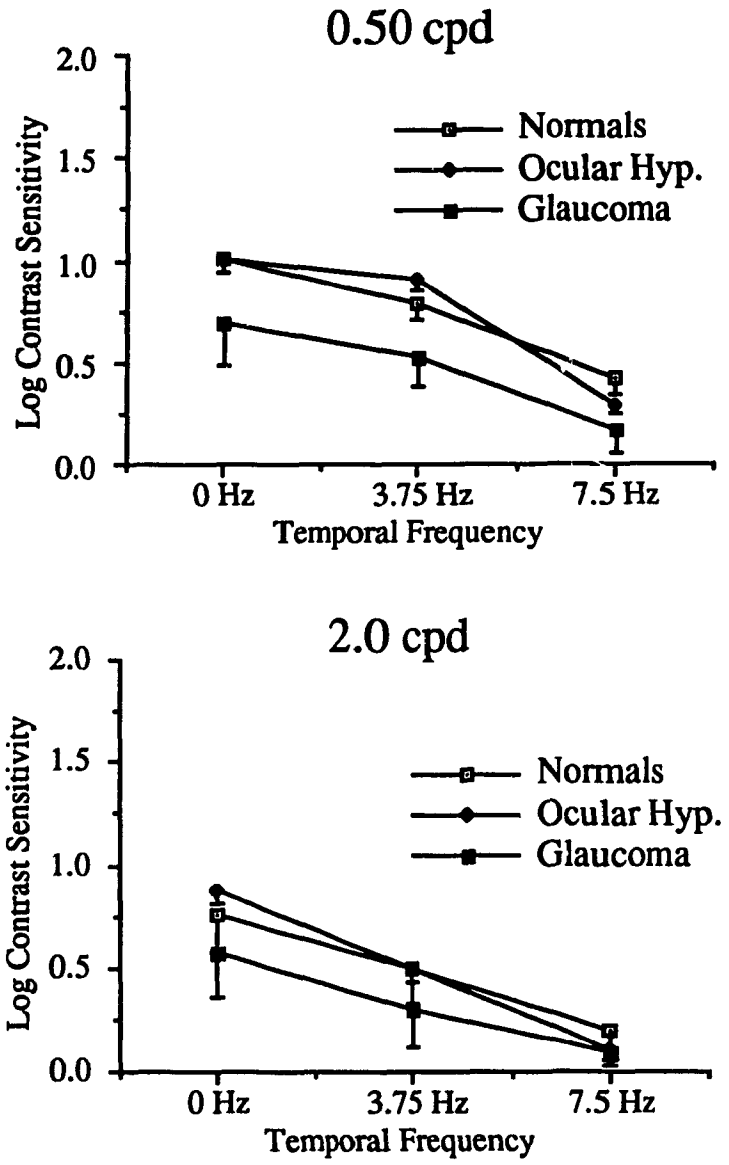


Figure 15. Contrast sensitivity as a function of temporal frequency for the 0.50 c/d (a) and 2.0 c/d (b) stimuli of normal, ocular hypertensive, and glaucomatous observers obtained using a 0.70 td illuminance level.

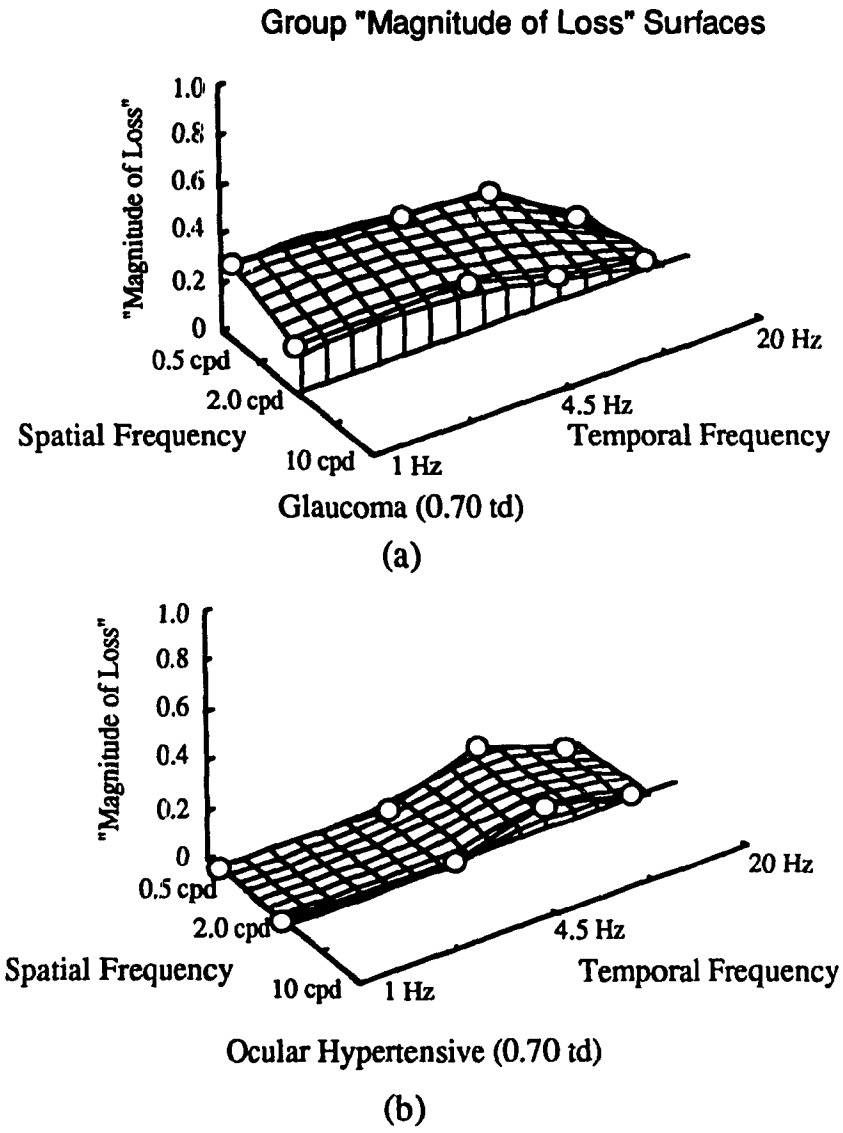


Figure 16. "Magnitude of Loss" spatio-temporal threshold surface for the glaucoma (a) and ocular hypertensive (b) observers obtained under a 0.70 td illuminance condition.

Figure 16 that the magnitude of loss increases in the range of low spatial frequencies and low temporal frequencies. There is a low-pass spatio-temporal sensitivity loss function. Graph (b) shows the magnitude of loss for the ocular hypertensive group. In this case, the loss is only evident at the highest visible temporal frequency. No loss can be observed at 15 Hz because the sensitivity is virtually zero for all observers, including the normal group. Like Figure 11 (b) in the previous experiment, Figure 16 (b) does not adequately represent the drop of sensitivity from 0 Hz, and 3.75 Hz to 7.5 Hz condition demonstrated by the ocular hypertensive group because all positive differences, as a result of subtracting the normal data from the ocular hypertensives, were equated to zero on the z-scale. Figure 17 shows the group means when collapsed across spatial frequency. A large drop of sensitivity from 0 Hz and 3.75 Hz to 7.5 Hz is experienced by the ocular hypertensive group. The graph also demonstrates that the two experimental groups show opposite trends regarding the sensitivity reduction relative to normals. The glaucoma group shows greater loss as the targets become more static and the ocular hypertensive group's sensitivity levels decrease with increasing temporal rates.

Figures 18 and 19 show the individual MLS plots for the early glaucoma and ocular hypertensive observers respectively. The same three glaucoma observers showing the mid- to low-spatial-high-temporal frequency losses in the previous experiment show dramatic sensitivity decrements under 0.7 td. Only subject 12 of the ocular hypertensive group shows a small loss.

A 3x2x3 ANOVA with one between factor (group) and two within factors (spatial x temporal) was performed on the data (Appendix C). The 15 Hz condition was excluded from the analysis because these targets were not visible under the illuminance condition used. No significant main effect of group was found. A significant main effect of spatial frequency, $F(1, 12) = 37.35$, $p <$

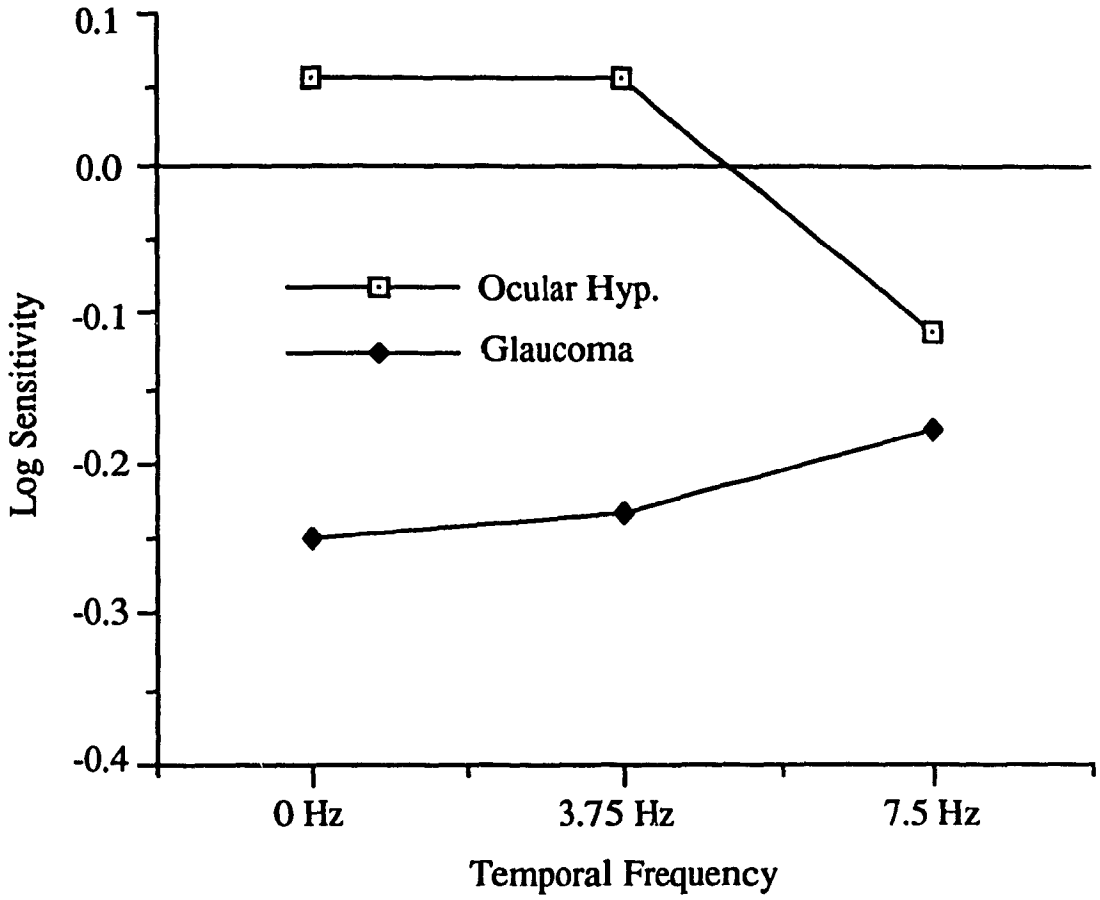


Figure 17. Visuogram of the data collapsed across spatial frequencies as a function of temporal frequency for the glaucoma and ocular hypertensive groups for a 0.7 td illuminance level.

"Magnitude of Loss" Surfaces: Early Glaucoma Observers

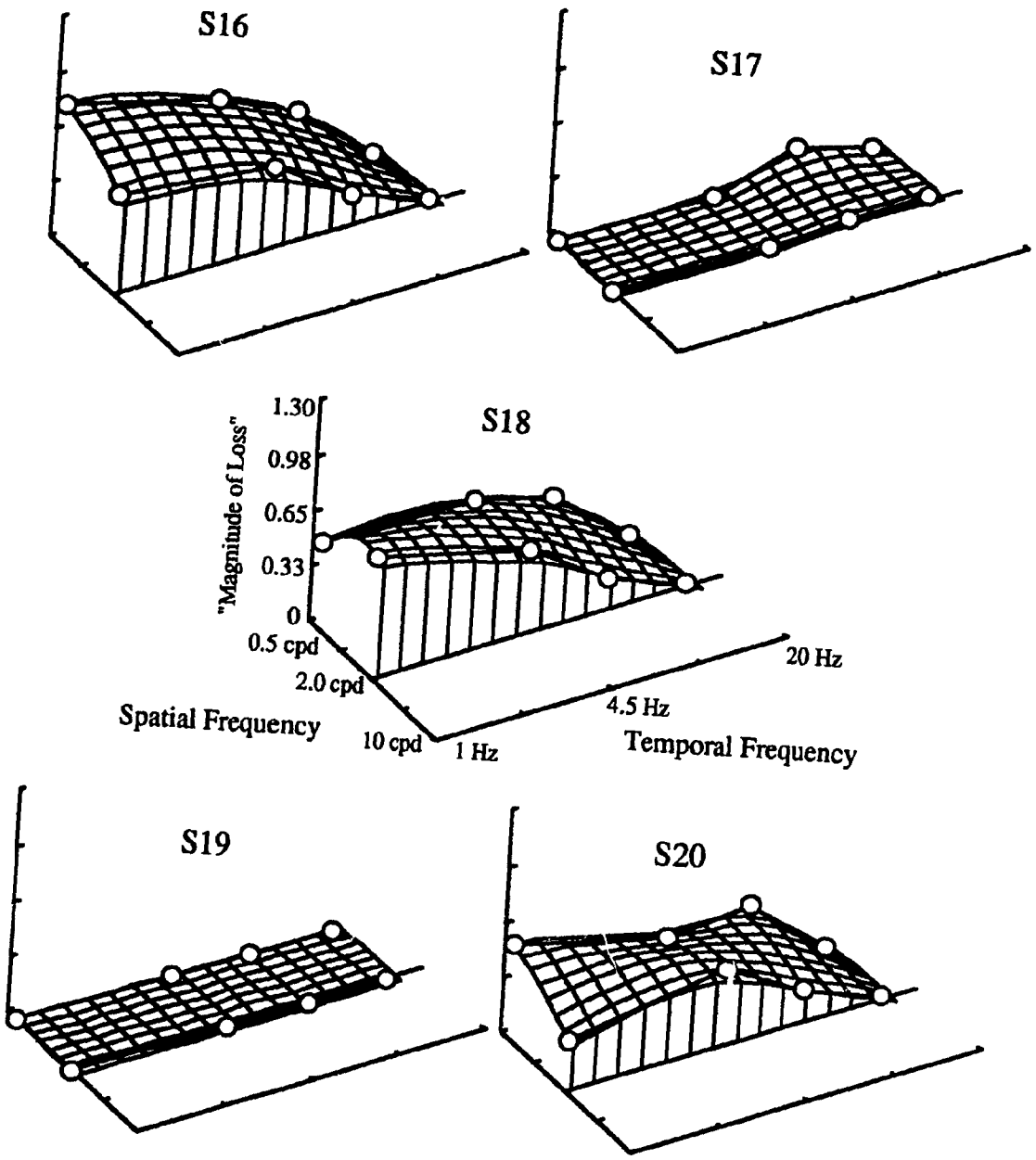


Figure 18. MLS for early glaucoma observers (subjects 16 to 20) obtained under a 0.7 td illuminance condition.

"Magnitude of Loss" Surfaces: Ocular Hypertensive Observers

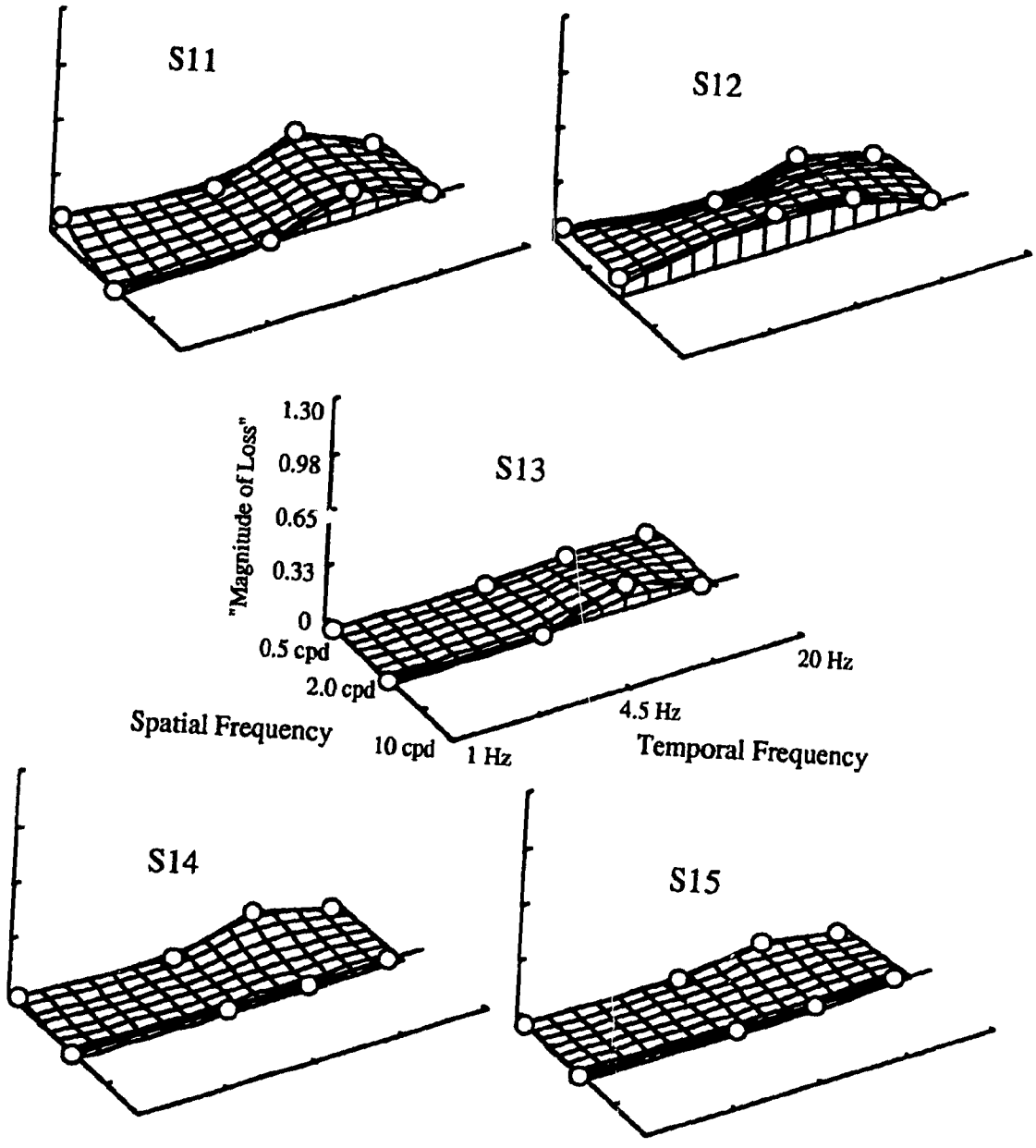


Figure 19. MLS for ocular hypertensive observers (subjects 11 to 15) obtained under a 0.7 td illuminance condition.

0.001, temporal frequency, F (2, 24) = 116.41, $p < 0.007$, and a significant spatial by temporal interaction, F (2, 24) = 6.14, $p = 0.007$, was found. No significance was found for the group by spatial, group by temporal, or the group by spatial by temporal interactions.

Discussion

The results are consistent with the notion of M cell loss in glaucoma for three of five glaucoma observers who show a profound loss of sensitivity. According to the electrophysiology data, reducing the illuminance to 1 td or less will isolate the M pathway. The present experiment used a retinal illuminance level of 0.70 td, well within this range. As evidenced by Figures 15 to 18, the glaucoma group demonstrates sensitivity losses under these luminances. An interesting result is the fact that the glaucomatous observers who show losses show a large loss under this illuminance condition.

The most intriguing result is that the ocular hypertensives show sensitivity decrements relative to normals only at the highest visible temporal rates while the glaucoma observers show the greatest loss at low temporal rates. It is possible that ocular hypertensives are showing a sensitivity loss due to a mechanism which is different than that of the glaucoma patients. Another possibility is that this high temporal frequency drop in ocular hypertensives represents very early damage caused by glaucoma where the temporal components are the first affected independent of the spatial characteristics.

General Discussion

The series of experiments in this study attempted to identify the different retino-geniculate pathways responsible for the production of the spatio-temporal threshold surface. Specifically, it attempted to isolate the different pathways *via* psychophysical and pathophysiological means. Another interest was to determine the effect of aging alone on the spatio-temporal threshold surface.

In Experiment 1, the sensitivities of a young group with normal vision and of an older group with normal vision were assessed with a series of 12 spatio-temporal combinations. The psychophysical technique controlled for criterion shifts, observer biases, and reaction time to avoid any sensitivity differences due to these factors. The spatio-temporal threshold surface obtained under these conditions was similar to those obtained in previous research. Generally, detection of small spatial targets is facilitated by low temporal rates and large spatial targets by rapid flicker. This relationship is best demonstrated in Figure 5 (a) showing the sensitivity levels obtained for the young observers in Experiment 1. The results from the older group demonstrated that the greater loss on the surface is found in three distinct areas: the smaller targets at lower temporal rates, the larger targets at the higher temporal rates, and the middle size targets at medium temporal rates. These data do not support the notion that aging selectively affects large fibers. However, they do support the notion that nerve fibers are affected indiscriminately by aging and that these losses are best detected at the preferred temporal rates of the spatial targets used.

The latter conclusion is further supported by the results of Experiment 2. In this experiment an attempt was made to isolate the M pathway by reducing the illuminance levels below 1 td which, according to Shapley (1988), inhibits

the P pathway from responding altogether while the M pathway is still relatively active. The difference between the young observers and the older group was less evident under these conditions. The small difference that was observed, however, resided in the low spatial frequency targets under the static condition. This is the optimal cell response condition under these illuminance levels.

Based on the results from Experiment 1 and Experiment 2, several conclusions may be drawn. First, that under 70 td illuminance conditions, the threshold surface shows the typical shape that has been shown by other researchers using different psychophysical procedures. Second, aging does not selectively affect certain physiological pathways and, in fact, there seems to be a general loss of sensitivity which is best detected for optimal stimulus combinations. Third, the threshold surface is very much affected by reducing the illuminance level to 0.70 td, a level which presumably isolates the M pathway. The surface essentially demonstrates a low spatio-temporal band-pass function, with aging preferentially affecting the low spatial and low temporal combinations.

The results of Experiment 3 lend support to the hypothesis that the spatio-temporal properties of the threshold surface for which the M pathway is responsible are the low-spatial and high-temporal ends of the surface. The results obtained from the glaucoma patients, which are thought to have selective M cell loss according to pathophysiological evidence, fit nicely with the results obtained from Merigan and his coworkers on acrylamide treated monkeys (Merigan & Eskin, 1986). Figure 11 (a) shows the MLS of the glaucoma observers relative to normals. This function which is essentially the part of the spatio-temporal threshold surface that is affected by glaucoma is complementary to the data obtained by Merigan and Eskin (1986). The sensitivity profile that they were left with, after destroying the P pathway in

monkeys (presumably leaving the M pathway to respond), demonstrated unaffected sensitivities for large targets flickered at higher rates. The glaucoma group also shows losses throughout the surface but these are small relative to the low-spatial-high-temporal combinations. A loss throughout the surface is expected because glaucoma, although assumed to affect primarily large fibers early, does produce some small cell loss. The individual data from the glaucoma observers shown in Figure 12 clearly demonstrates that, in individuals showing a loss, this loss is typically seen in the low- to mid-spatial-high-temporal regions of the surface consistent with the large cell loss hypothesis.

The results obtained from the glaucoma group in Experiment 3 are also consistent with the proposition that glaucoma destroys M cells and that these M cells can be isolated under low illuminance conditions. Figure 16 (a) demonstrates that the glaucoma group shows a sensitivity loss which is greatest at the low-spatio-temporal region of the surface. The most significant finding is shown in Figure 17 where the same three observers with a low-spatial-high-temporal loss for the 70 td condition have a large sensitivity decrease under 0.7 td while the other two observers show no loss.

The results obtained in Experiment 3 from the ocular hypertensive group are interesting in themselves as they pertain to the pathology. The results show that the ocular hypertensives are not significantly different from normals. This, in itself, is not a surprising discovery but there is a temporal by group interaction. Figure 14 demonstrates that, when the data were collapsed for spatial frequency, the ocular hypertensives, who in fact had suprasensitivity for the slower temporal frequencies, showed the greatest drop of sensitivity from the three lower temporal rates to the highest temporal rate used (15 Hz), while the glaucoma patients had a monotonic decrease in sensitivity as the temporal

frequency increased. This is interesting because it shows a different pattern of loss. A qualitative difference between the ocular hypertensives and the glaucoma patients, not just a quantitative one, is emerging. This may mean one of two things. Either the very early visual defects caused by glaucoma are in the high temporal frequency range, exclusively discarding spatial components, or there are two very different processes.

The latter hypothesis is further supported by the results of Experiment 4. Figure 20 shows visuograms for the glaucoma patients (a) and the ocular hypertensives (b). Graph (a) shows the means, collapsed across spatial frequency, obtained from the glaucoma group in Experiment 3 (70 td) and those obtained in Experiment 4 (0.70 td). Graph (b) shows the ocular hypertensive data obtained in Experiment 3 and Experiment 4. It can be seen from graph (b) that the pattern of sensitivity loss for the ocular hypertensives is similar whether one illuminance condition or another is used. These observers show suprasensitivity which reduces sharply at the highest temporal rates. The glaucoma data, however, demonstrate a very different pattern. Graph (a) shows that the sensitivity loss increases as the temporal rate increases under higher luminances. This is consistent with the notion that M cells are affected in glaucoma and that this cell loss would best be represented when the cell type is presented with its optimal stimulus combinations.

If these findings are reproducible, they could have very interesting clinical implications. One of the difficulties in the treatment of ocular hypertensives is that very few go on to develop glaucoma, as defined with traditional methods. Thus, it is difficult to determine in which cases treatment would be beneficial. An objective way may be to assess their differential sensitivity losses observed under medium to high luminance levels and under

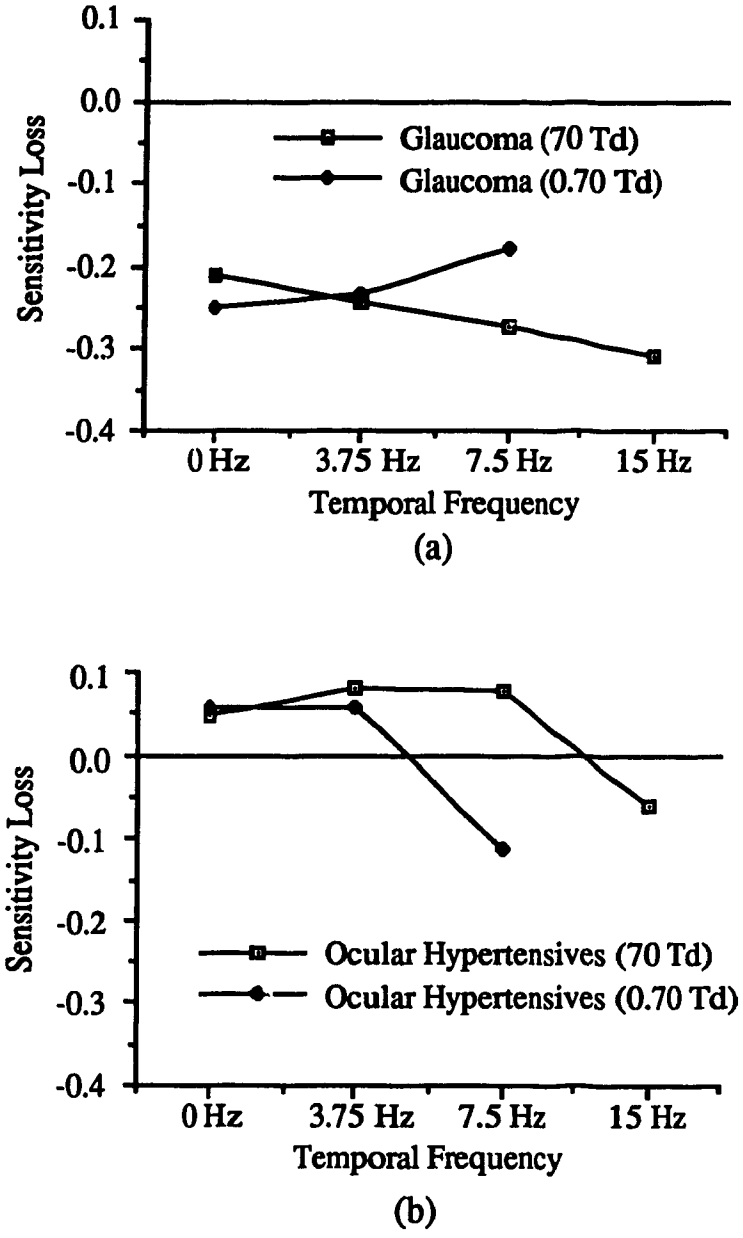


Figure 20. Visuograms of the data collapsed across spatial frequencies as a function of temporal frequency obtained under the 70 td and 0.70 td illuminance conditions for the glaucoma (a) and the ocular hypertensive (b) groups.

low luminance levels. If one observes a reverse in direction, as was observed here with the glaucoma group, this may imply glaucoma-related damage.

There are many interesting avenues to pursue following this research. As mentioned above, the group by temporal interactions obtained in Experiments 3 and 4 are interesting and may represent two distinct pathophysiologies. Given that the peripheral retina is generally the first region affected in glaucoma, it would be interesting to determine whether the effect observed in Figure 20 is also present in the periphery. This may be a very sensitive method of distinguishing ocular hypertensives from those who have had glaucoma-related, irreversible cell loss.

One of the interesting notions which stems from this research is the possibility of using glaucoma as an experimental model for the study of other visual functions which are presumably under the control of one cell type as opposed to another. For instance, if some aspect of depth perception or motion sensitivity is thought to be under the control of higher cortical levels which receive input from the M pathway (Livingstone & Hubel, 1988), it follows that glaucoma patients should have lower than normal performances on sensitive measures which assess these abilities and this may provide greater insight as to how these functions are controlled by the different cell types. However, it is also clear from these results that the clinical classification of early glaucoma may not in itself represent an instance in which there is a selective cell loss. A careful evaluation of the glaucoma patient with measures such as the ones that were used in this study appear necessary prior to making the assumption of a selective cell loss.

It is possible that other visual or cortical deficiencies may lead to a greater understanding of how the normal visual system works. Therefore, the study of impaired systems may be of great benefit to the understanding of

normal visual function notwithstanding the benefit to the comprehension and possible treatment of the disorders themselves.

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Appendix A

Demographic information for subjects in the different group categories that participated in the study.

Young Normal

Sub. #	Age	Acuity	IOP	Eye tested
1	31	6/6	<22	Right
2	23	6/6	<22	Right
3	31	6/6	<22	Left
4	28	6/6	<22	Right
5	33	6/6	<22	Right

Mean age = 29.2, sd = 3.9

Older Normal

Sub. #	Age	Acuity	IOP	Eye tested
6	58	6/6	<22	Left
7	60	6/6	<22	Right
8	63	6/6	<22	Right
9	65	6/6	<22	Left
10	65	6/6	<22	Left

Mean age = 62.2, sd = 3.11

Ocular Hypertensive

Sub. #	Age	Acuity	IOP	Eye tested
11	59	6/6	29	Right
12	59	6/6	26	Left
13	63	6/7.5	14/23	Left
14	65	6/6	29	Right
15	66	6/7.5	33	Left

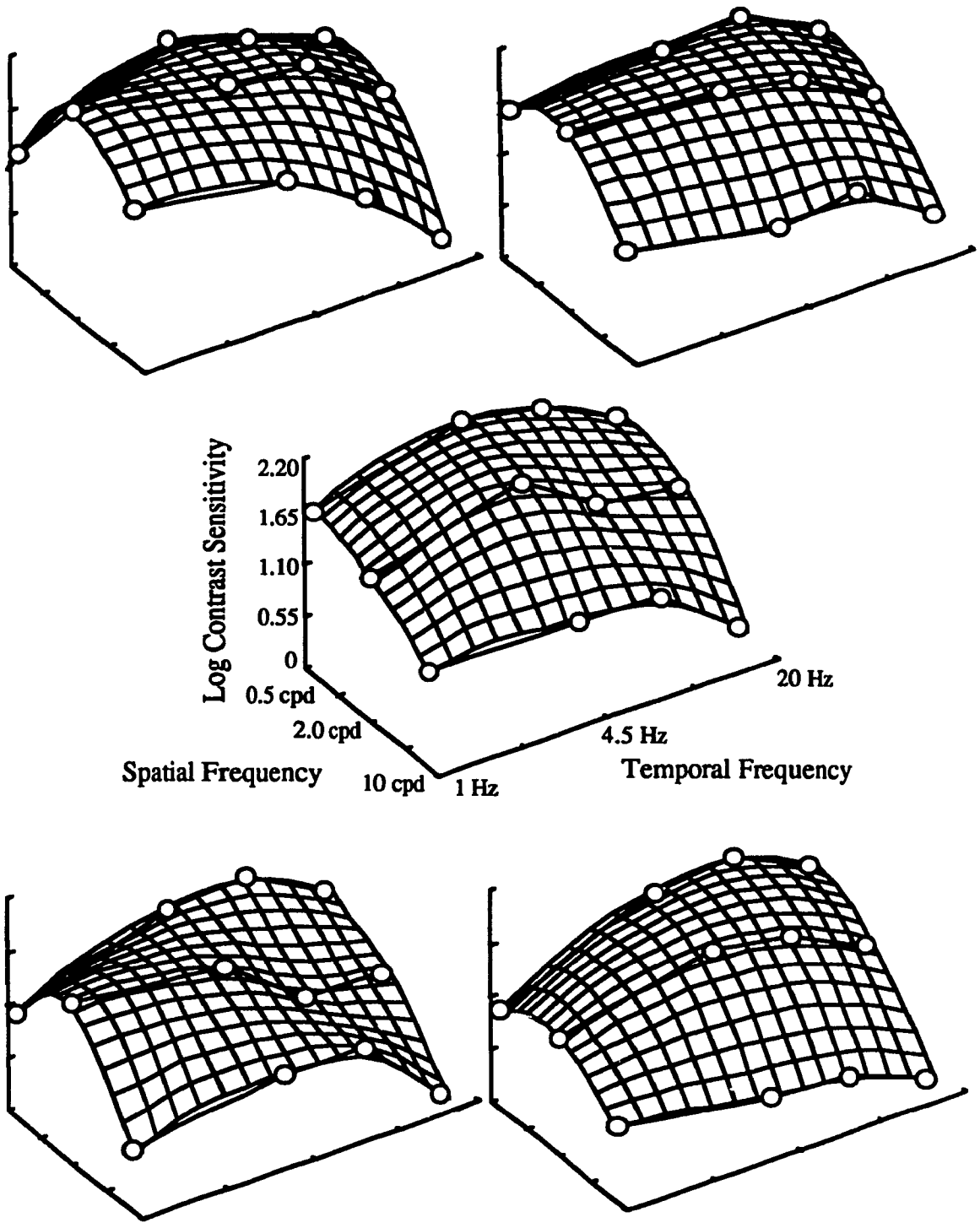
Mean age = 62.4, sd = 3.29

Glaucoma

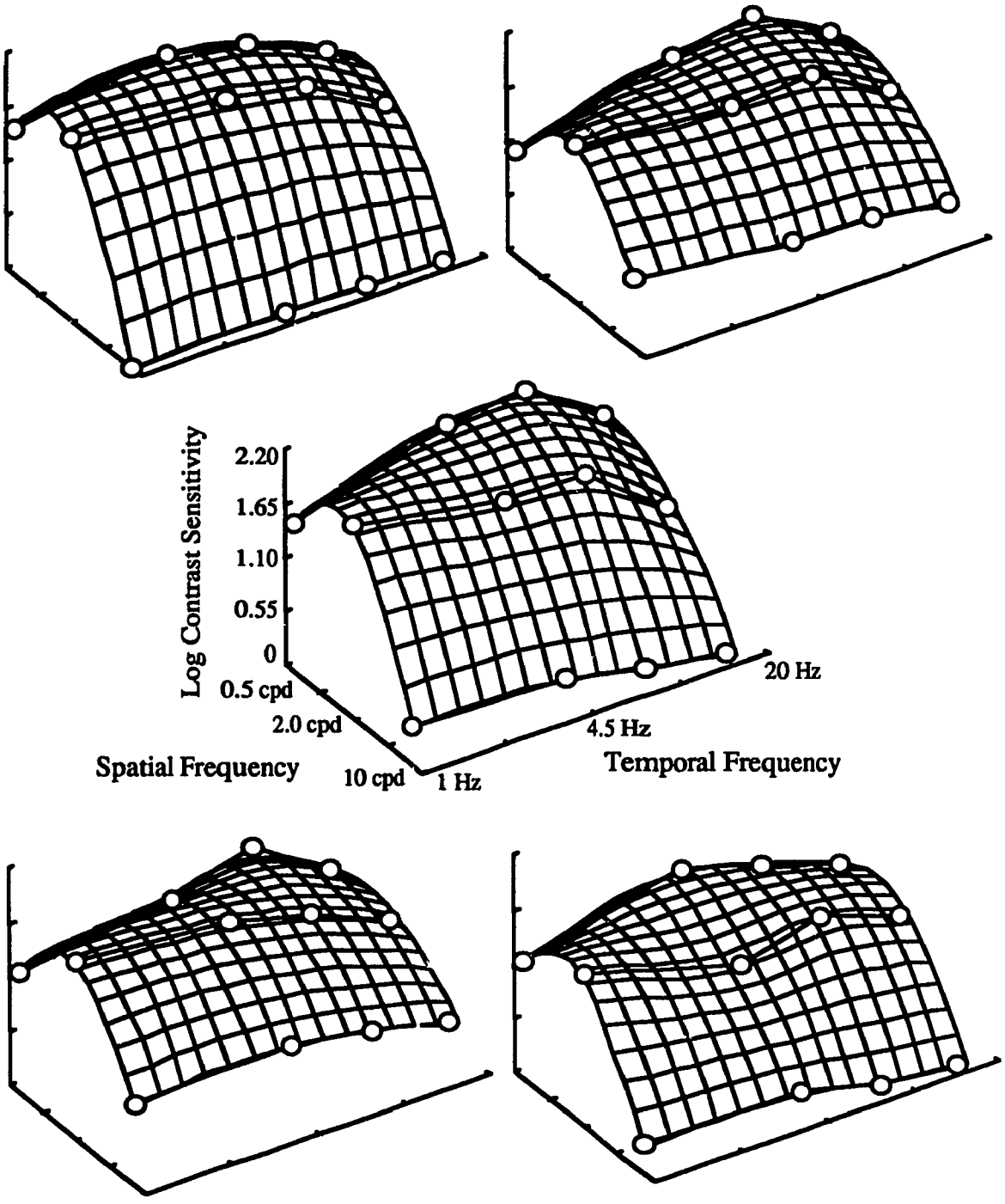
Sub. #	Age	Acuity	IOP	Eye tested
16	59	6/7.5	23	Right
17	59	6/7.5	27	Left
18	61	6/6	23	Left
19	63	6/6	24	Right
20	67	6/6	31	Left

Mean age = 61.8, sd = 3.35

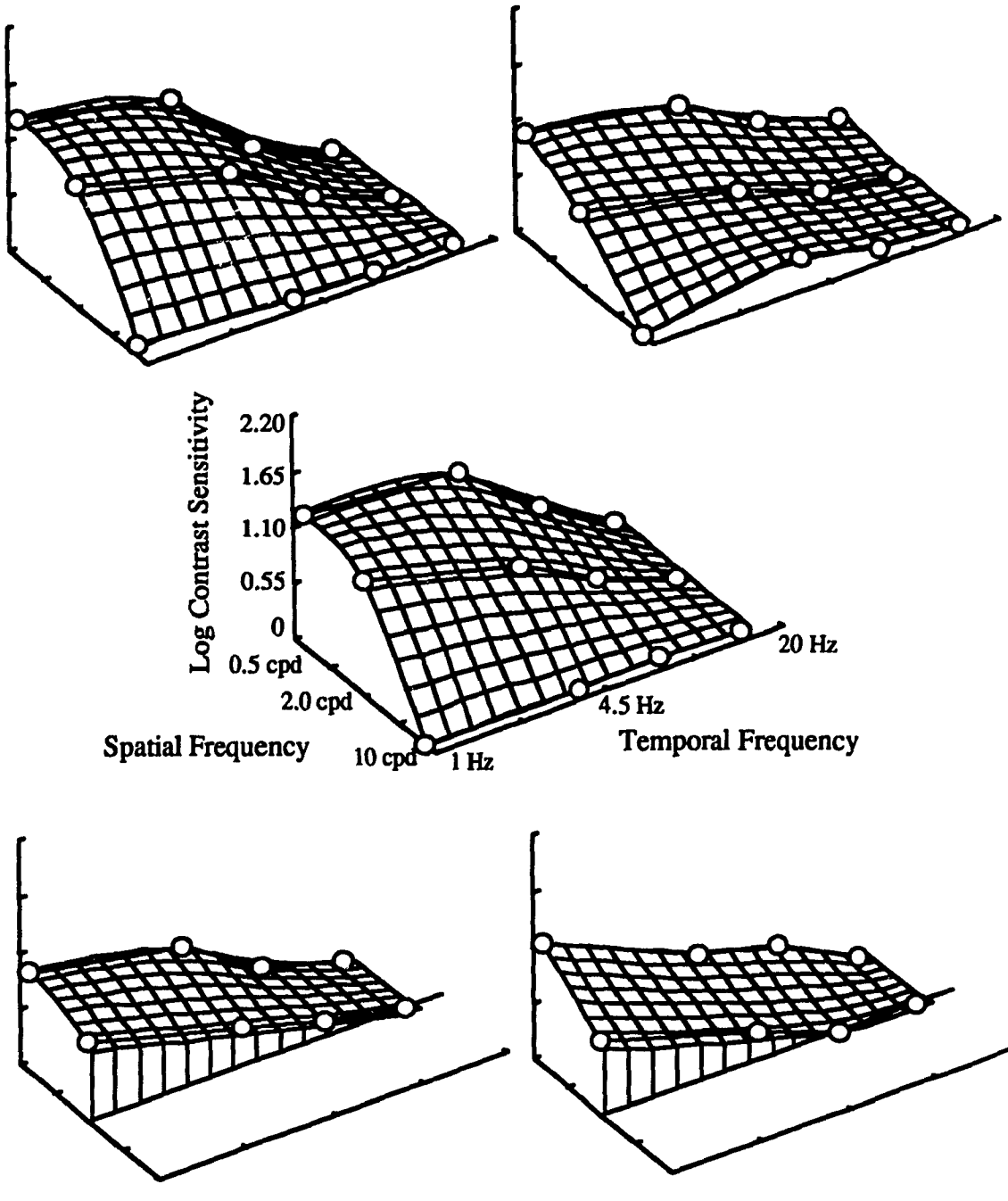
Appendix B



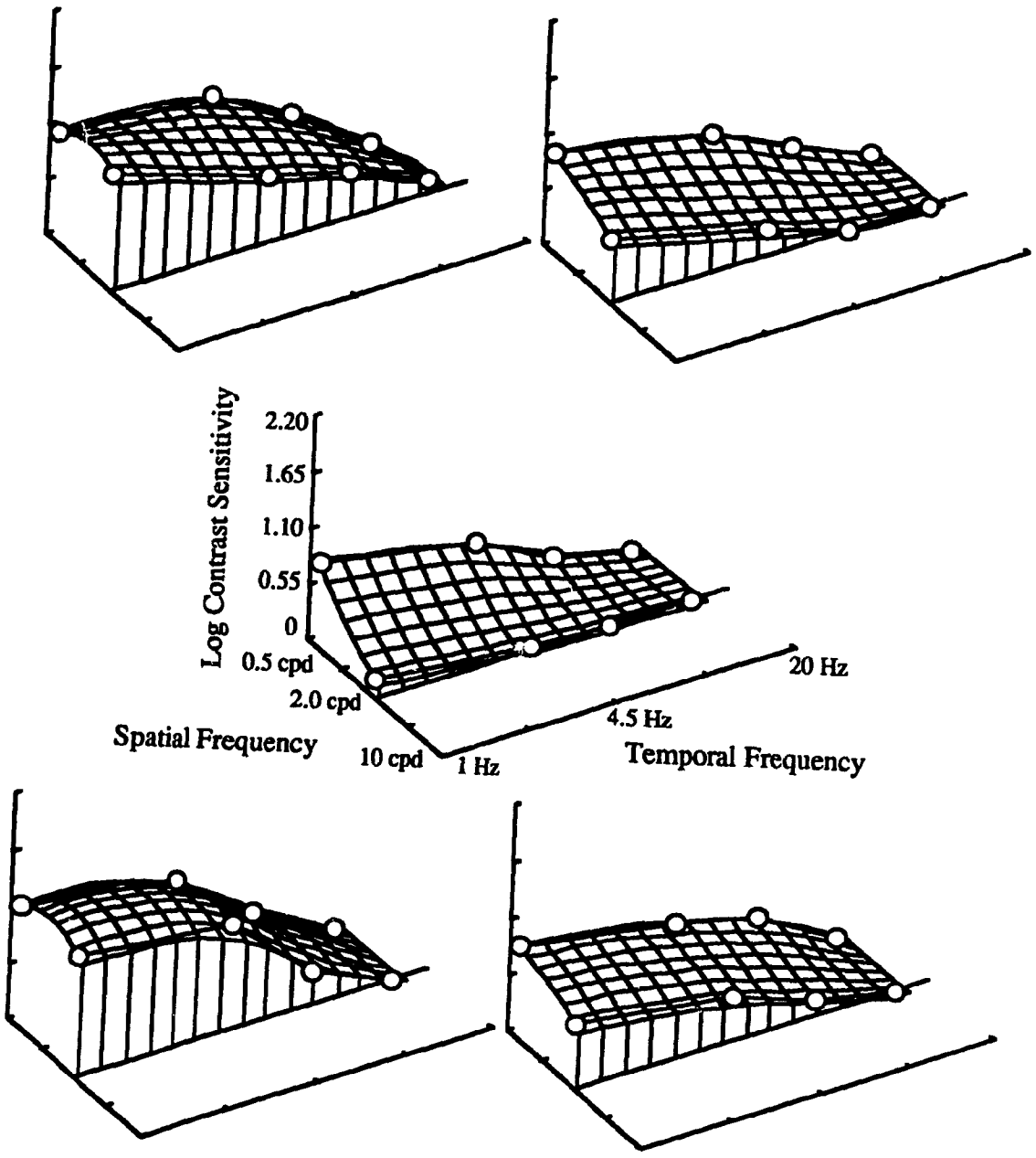
Spatio-Temporal Threshold surfaces
Young Normals (70 td)



Spatio-Temporal Threshold surfaces
Older Normals (70 td)



Spatio-Temporal Threshold surfaces
Young Normals (0.7 td)



Spatio-Temporal Threshold surfaces
Older Normals (0.7 td)

Appendix C

ANOVA Table from Experiment 1

Source	SS	df	MS	F	p
Age	1.243	1	1.243	4.27	0.073
Error	2.329	8	0.291		
Spatial Frequency	25.645	2	12.822	97.307	0.000
Age x Spatial	0.706	2	0.353	2.679	0.099
Error	2.108	16	0.132		
Temporal Frequency	3.325	3	1.108	51.049	0.000
Age x Temporal	0.134	3	0.045	2.052	0.133
Error	0.521	24	0.022		
Spatial x Temporal	1.711	6	0.285	13.134	0.000
Age x Spatial x Temporal	0.459	6	0.076	3.521	0.006
Error	1.042	48	0.022		

ANOVA Table from Experiment 2

Source	SS	DF	MS	F	P
Age	0.075	1	0.075	0.291	0.604
Error	2.073	8	0.259		
Spatial Frequency	1.022	1	1.022	29.827	0.001
Age x Spatial	0.002	1	0.002	0.055	0.821
Error	0.274	8	0.034		
Temporal Frequency	4.594	2	2.297	112.274	0.000
Age x Temporal	0.097	2	0.048	2.358	0.127
Error	0.327	16	0.020		
Spatial x Temporal	0.037	2	0.019	2.166	0.147
Age x Spatial x Temporal	0.004	2	0.002	0.256	0.777
Error	0.138	16	0.009		

ANOVA Table from Experiment 3

Source	SS	df	MS	F	p
Group	3.109	2	1.555	2.143	0.160
Error	8.705	12	0.725		
Spatial Frequency	45.177	2	22.588	138.937	0.000
Group x Spatial	0.187	4	0.047	0.288	0.883
Error	3.902	24	0.163		
Temporal Frequency	5.031	3	1.677	222.485	0.000
Group x Temporal	0.127	6	0.021	2.819	0.024
Error	0.271	36	0.008		
Spatial x Temporal	2.553	6	0.425	30.331	0.000
Group x Spatial x Temp	0.256	12	0.021	1.522	0.136
Error	1.010	72	0.014		

ANOVA Table from Experiment 4

Source	SS	df	MS	F	p
Group	0.975	2	0.487	1.354	0.295
Error	4.319	12	0.360		
Spatial Frequency	0.982	1	0.982	37.347	0.000
Group x Spatial	0.053	2	0.027	1.016	0.391
Error	0.315	12	0.026		
Temporal Frequency	5.714	2	2.857	116.410	0.000
Group x Temporal	0.192	4	0.048	1.960	0.133
Error	0.589	24	0.025		
Spatial x Temporal	0.110	2	0.055	6.142	0.007
Group x Spatial x Temp	0.035	4	0.009	0.982	0.436
Error	0.215	24	0.009		