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INDIVIDUAL DIFFERENCES IN SPATIAL FREQUENCY-DEPENDENT VISIBLE PERSISTENCE: THE ROLE OF TEMPORAL SUMMATION

by

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Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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January, 1995
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INDIVIDUAL DIFFERENCES IN SPATIAL FREQUENCY-DEPENDENT VISIBLE PERSISTENCE: THE ROLE OF TEMPORAL SUMMATION

Abstract
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The relationship between visible persistence and temporal summation was examined in young and elderly subjects. Four experiments were conducted. In Experiment 1, temporal sensitivity was determined for young and elderly subjects for low and high spatial frequencies over five levels of contrast ranging from 5 to 62 percent. Subjects identified the missing element in a 5x5 matrix. Elderly subjects had lower temporal sensitivity with larger high spatial frequency effects.

In the remaining experiments visible persistence was tested with the two-frame Di Lollo paradigm (1977). The matrices had the same characteristics (spatial frequency, visual angle, mean luminance) as those in Experiment 1 except that the elements were randomly separated into two frames.
In Experiment 2, visible persistence was measured with 34 percent contrast and duration set near threshold levels for each subject (as determined in Experiment 1). Young subjects had greater persistence for both low and high spatial frequency information. Similar results were found for Experiment 3 where duration was set to 29 msec, and contrast was set near threshold. In Experiment 4, both duration and contrast were set to a constant value as has been the case in previous studies investigating individual differences in visible persistence. Longer persistence was found for high spatial frequency information. Elderly subjects had longer persistence but more so for the high spatial frequency condition. Those results demonstrated that the stimuli and procedure used in the present study yield "typical" age and spatial frequency effects under "typical" test conditions.

Within a certain critical interval, contrast and duration combine to determine temporal summation (e.g., Legge, 1977). Under the typical test conditions that generate age effects in visible persistence, the greater temporal sensitivity of young subjects under a given level of contrast would lead to more complete temporal summation and hence shorter visible persistence. The failure to obtain longer visible
persistence for elderly adults in Experiments 2 and 3 when the salience of the image is equated across age and spatial frequency suggests that previously reported visible persistence age effects are the result of age differences in the rate of temporal summation.
Dedication

To Emma
Acknowledgement

Professor Douglas K. Detterman has my gratitude for providing me with the rich environment here at CWRU as well as the encouragement and the freedom to pursue my research interests. Few graduate students are better served than I have been by Doug.

to pursue graduate work would be a good environment to pursue my graduate work. He could not have been more right, and in no small measure because of his presence. Professor Detterman served me well as an advisor and mentor as I grappled with higher order cognitive processing. and later, as a member of my Dissertation Committee
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Introduction

The purpose of the present research was to examine age-related differences in the sustained and transient visual response. Four experiments were performed that examined differences between young and elderly adults in how rapidly a visual image can be captured, and in how long that visual image lingers once it is captured. The experiments were designed to take into account the role of temporal summation or how the combined factors of stimulus duration and contrast influence response sensitivity and response duration over low and high spatial frequency information.

Previous studies that have examined age-related differences in visible persistence did not manipulate contrast and stimulus duration. Both contrast and duration determine the course of visible persistence and there is considerable evidence that young and elderly subjects differ in both contrast and temporal sensitivity. The results of the two studies are expected to detail age-related differences in transient and sustained visual processing.

Visible Persistence

Visible persistence refers to the continuation of the phenomenal presence of a stimulus for a brief period after the offset of the stimulus. Coltheart
(1980) has defined visible persistence as that form of visual persistence where the duration is influenced by the physiological properties of the inducing stimulus. Visible persistence is related inversely to luminance (Bowen, Pola, & Matin, 1974), contrast (Bowling, Lovegrove & Mapperson, 1979), stimulus duration (Bowling & Lovegrove, 1980) and positively related to spatial frequency (Bowling, et al., 1979; Bowling and Lovegrove, 1980; 1981; Meyer and Maguire, 1977; 1979). The mediating effects that luminance, contrast, and stimulus duration have on visible persistence reflect processes carried out at different stages within the visual pathways from the level of the retina on through subcortical and cortical levels of visual processing.

**Individual Differences in Visible Persistence**

Visible persistence is interesting to those investigating individual differences in visual information processing because it provides a way to assess differences in visual temporal resolution. Those who have lingering images have visual systems that are less capable of dealing with rapidly changing visual information. There is a considerable body of evidence to suggest that elderly adults have more sluggish visual systems than young adults. For example, measures of critical flicker frequency (CFP),
which is the rate a pulsating light is seen as continuous rather than flickering, is longer in elderly than young adults (Coppinger, 1955; McFarland, Warren, & Karis, 1958; Misiak, 1947). Measures of backward masking which assess interference to a leading visual display resulting from a trailing display indicate that the elderly need longer to escape the effects of the mask (Di Lollo, Arnett, & Kruk, 1982; Hertzog, Williams, & Walsh, 1976; Kline & Szafran, 1975; Walsh, 1976).

In the last decade both visible persistence and individual differences in visible persistence have been examined more closely within a model of visual information processing called the multichannel model. This view of early visual processing now dominating both physiological and psychophysical investigations of early visual processing provides a coherent framework with which to explain persistence phenomena. Spatial-frequency related visible persistence, and more specifically, age-related differences in spatial frequency visible persistence will be examined in more detail after a review of the anatomical, physiological and psychophysical basis of the multichannel model.
The multichannel model is the result of a convergence of psychophysical information with information about the neurophysiology of subcortical and cortical processes in the visual system (Shapley & Lennie, 1985). The model originated from a proposal by Campbell and Robson (1968) that for a given retinal location there are several receptive fields of varying size. According to their hypothesis, an image falling on a given location would maximally stimulate the receptive field that most closely corresponded to the size of the image, whereas receptive fields that differed in size by a factor of two or more would respond less or not at all. An explosion of research followed this proposal which investigated in detail the mechanisms governing spatial-frequency selective channels (Marr, 1982).

The model of early visual processing that has emerged from research over the past two decades is one where different aspects of information received from the same retinal location are segregated into two separate pathways and projected in parallel, with some capacity for crosstalk (Van Essen & Maunsell, 1983), to different subcortical and cortical locations (Livingstone & Hubel, 1987). Neurophysiological studies have shown that there are two major channels,
called the magno- and parvocellular pathways, that have overlapping but independent capacities and limitations for processing important features of visual information that include spatial frequency, temporal modulation, luminance contrast, and wavelength. Physiological studies have found that of the two independent channels, the magnocellular pathway is superior to the parvocellular pathway in processing low spatial frequency information that is rapidly changing. The parvo channel, on the other hand, excels at processing high spatial frequency information that is static, or slowly changing. Psychophysical studies, including many that preceded the physiological evidence, also provided support for the existence of independent channels for processing spatial and temporal aspects of visual information. Evidence supporting the existence, as well as describing the properties of independent visual channels is described in the next three sections on the neuroanatomical, neurophysiological, and psychophysical bases for independent visual pathways.

Anatomical Evidence of Independent Pathways

The magnocellular and parvocellular pathways originate in two distinct classes of retinal ganglion cells that project their signals along separate
pathways to a laminated subcortical structure with six
distinct layers of cells called the lateral geniculate
nucleus (LGN). The cells from the LGN relay the
retinal signals to the primary visual cortex. These
two pathways can be distinguished by the morphological
characteristics of the cells and their processes that
make up these pathways. Retinal ganglion cells that
project to the two magnocellular layers of the LGN (m-
ganglion cells) are distinguished by the large size of
their cell bodies and their large radiating dendritic
trees and large axons (Silveira & Perry, 1991).
Retinal ganglion cells that project to the
parvocellular layers (p-ganglion cells) have small to
medium size cell bodies with small, bushy dendritic
trees and fine to medium size axons. Both types of
retinal cells have their greatest concentration near
the fovea, declining in number, but increasing in size,
as distance from the fovea is increased. At any given
eccentricity, m-ganglion receptive field size is always
larger than that of p-ganglion cells (Perry, Oehler, &
Cowey, 1984). By conservative estimates, the
proportion of m-cells appears to be about 6 to 10
percent of the total ganglion cells near the fovea and
about 8 to 10 percent over much of the rest of the
retina, although at very peripheral eccentricities m-
ganglion cells constitute as much as 20 percent of the population (Silveira & Perry, 1991).

Like their retinal counterparts with whom they form synapses, neurons within the magnocellular layers of the LGN are large, whereas parvocellular LGN neurons are small to medium size. The magnocellular neurons comprise about 8 to 10 percent of the volume of the LGN (Kaas, Huerta, Weber & Harting, 1978; Malpeli & Baker, 1975). Each of the six LGN layers contains a complete topological representation of the visual field. Neurons in the LGN share the same receptive field neighbors as at the retinal level (Kuffler, Nicholls, & Martin, 1984). The distinct topological arrangement found in the LGN is preserved at the level of the cortex.

From the LGN, neurons project via anatomically segregated pathways to layer IV of the primary visual cortex, but within that cortical layer, magnocellular and parvocellular neurons terminate in different levels (Kandel, 1985). The segregation of these pathways between the retina and the primary cortex subserved by the magno- and parvocellular layers of the LGN has given rise to the terms labeling these channels as the magnocellular and parvocellular pathways.
Neurophysiological Evidence

In both neurophysical and psychophysical studies, gratings have been used to examine the mechanisms subserving early visual processing. A single grating contains a set of several alternating black and white bars of equal width. In its most simple form the luminance of the bars is varied sinusoidally along one axis, typically the horizontal axis. By manipulating the width of the bars, their contrast, orientation, and temporal modulation, characteristics of the magnocellular and parvocellular channels have been identified that are consistent across both neurophysical and psychophysical domains.

Unless otherwise indicated, the studies described in this section have examined the response properties of individual retinal ganglion and geniculate cells in Macaque monkeys. Because of the striking similarities between the visual systems of humans and Macaques in anatomy and in performance on visual tasks (De Valois, Morgan, & Snodderly, 1974; Harwerth, Boltz & Smith, 1980; Merigan, 1989; Shapley & Perry, 1986), it is generally assumed that the physiological properties found for the neurons in the Macaque are substantially the same for humans (Derrington & Lennie, 1984).
Retinal Ganglion Cells

Retinal ganglion cells that project to the magnocellular layers are functionally different from those that project to the parvocellular layers. Difference in response patterns to light wavelength define the two major functional classifications of retinal ganglion cells as broad-band or color-opponent cells (Gouras, 1969; Schiller & Malpeli, 1977). Broad-band cells respond to a wide range of light wavelengths, although some cells respond more vigorously to some wavelengths than to others. Unlike broadband cells, color-opponent cells exhibit a selective response to wavelength (Schiller & Malpeli, 1977). Broadband cells also differ from color-opponent in the duration of their response to maintained stimuli. Color-opponent cells tend to maintain a sustained response to static or slowly-changing stimuli, whereas the response of broadband cells tends to be more transient. Broad-band retinal ganglion cells are the anatomically larger cells described earlier, that project to the magnocellular layers of the LGN, whereas the color-opponent cells project exclusively to the parvocellular layers (Kaplan & Shapley, 1986; Leventhal, Rodieck, & Dreher, 1981). Thus, the broad-band and color-opponent retinal ganglion cells, with their separate terminations in the
different layers of the LGN provide the initial
division of the retinogeniculocortical pathway.

Broad-band cells differ from color-opponent cells
in their sensitivity to luminance contrast. Kaplan &
Shapley (1986) compared the contrast sensitivity of
ganglion cells projecting to the magnocellular layers
of the LGN (broadband) to cells projecting to the
parvocellular layers (color-opponent). They
found striking differences in contrast sensitivity,
with broad-band cells displaying markedly higher levels
of sensitivity than the color-opponent cells. In
response to small increases of contrast, the broadband
cells showed steep increases in response rate, so
that with contrasts of as little as 8 to 10 percent,
the broad-band cells approach their maximum response
rate. Color-opponent, or parvocellular projecting
cells display a very gradual response to increases of
contrast and by 64 percent contrast had not approached
saturation levels. At any given contrast measured, the
magnitude of response of m-cells was much greater than
p-cells, and at the maximum contrast of 64 percent, the
magnitude of response of the m-ganglion cells was more
than twice that of the p-ganglion cells.
Lateral Geniculate Cells

Functional differences between geniculate neurons in the magno- and parvocellular layers of the LGN parallel those of the broadband and color-opponent retinal ganglion cells whose axons terminate in those two divisions. Much of the neurophysiological evidence for independent channels, however, comes from studies investigating the functional differences of cells that were so obviously segregated to separate layers of the LGN.

Spectral sensitivity differences are marked between the parvocellular and magnocellular neurons of the LGN. Both magno and parvo neurons have a center-surround organization. Magno neurons have centers that are stimulated by any wavelength and surrounds that are inhibited by any wavelength (and the opposite arrangement). The response of the cell is determined by the difference between the activity of the center and activity in the surround. The greater the difference between the center and the surround, the greater the response.

Ninety percent of parvo neurons on the other hand, respond selectively to either a long, medium, or short wavelength, with the center and surround each responding maximally and in opposite direction to two different wavelengths. For example, a cell that
is excited by red light on its center, will have a 
surround that is inhibited by green light, and thus 
activity in the cell will increase to red light, but 
decrease to green light. Light that has a wavelength 
midway between green and red will result little change 
in firing from that of resting state. Thus, the 
response of cells in the parvocellular layers is very 
specific, providing information about wavelength 
whereas the information provided by the magnocellular 
broad-band cells is about light differences between the 
center and the surround, with less regard to specific 
wavelength (DeValois & DeValois, 1988; Livingstone & 
Hubel, 1988b).

Another difference between magno- and 
parvocellular divisions is in the distributions of X 
and Y cells within the LGN magno- and parvo-layers. 
Parvocellular layers contain X- but not Y-cells, 
whereas magnocellular layers contain both X- and Y- 
cells (Shapley et al., 1981), with Y-cells constituting 
approximately one-fourth of the magnocellular units 
(Kaplan & Shapley, 1982). A cell is classified as an 
X- or Y- cell based on the spatial summation properties 
of the cell. In a nutshell, X-cells yield information 
about both changes in luminance and of phase, whereas 
Y-cells provide only information about changes in
luminance. Spatial summation properties are characterized as linear or nonlinear and are determined by the response rate of a cell to the spatial phase of a sine grating as it is drifted across the receptive field (Kaplan & Shapley, 1982). The degree of response exhibited by a cell with linear spatial summation characteristics corresponds directly to the sinusoidal variation of the contrast of the sine wave as it is drifted across the receptive field. The strongest response, for example, of an on-center cell is generated at the lightest portion of the sine wave, with an equally strong response in the reverse direction at the darkest portion, and a null response (resting state) midway between the lightest and darkest position. This pattern in response to the contrast of the sinewave occurs for the fundamental frequency as well as for higher spatial frequencies that the cell is capable of resolving. A Y-cell approximates the linear behavior of X-cells for low spatial frequencies, but when exposed to a grating containing the second harmonic (a doubling of the fundamental frequency), the Y-cell exhibits a doubling in the frequency of its response rate to both the light and the dark portions of the sinewave (Hochstein & Shapley, 1976; Shapley & Hochstein, 1975; So & Shapley, 1979). Such a response
indicates that the response of a Y-cell to the higher frequency grating is independent of phase. Thus, neurons in the parvocellular layers, that are all X-cells provide information about phase whereas in the magnocellular layers, about three-fourths of the neurons provide phase information with the remainder providing only information about changes in luminance.

Several studies that have examined the contrast sensitivity of individual LGN cells have shown that magnocellular neurons are much more sensitive than parvocellular neurons. Contrast sensitivity is defined as the reciprocal of the contrast required to generate a criterion response. Luminance contrast refers to the difference in luminance between the lightest and darkest portions of a sinewave relative to the sum of the highest and lowest level of luminance of the entire stimulus \((L_{\text{max}} - L_{\text{min}})/(L_{\text{max}} + L_{\text{min}})\) and is expressed as a percentage. For magnocellular neurons, contrast as low as 1 to 1.25 percent generates a criterion response, yielding a sensitivity of 80 to 100 (Hicks, Lee, & Vidyasagar, 1983; Derrington & Lennie, 1984; Kaplan & Shapley, 1982; Shapley, Kaplan, & Soodak, 1981). Parvocellular neurons, on the other hand, required contrast levels of 10 to 12.5 percent which yield sensitivities of 10 and 8 respectively.
Neurons in the magnocellular and parvocellular channels differ in their characteristic response latency as well as in the transience of their response. Typical response latency is shorter in magnocellular neurons and decays more rapidly than is true for parvocellular neurons (Derrington & Lennie, 1984; Hicks, Lee, & Vidyasagar, 1983; Schiller & Malpeli, 1978). Moreover, unlike parvocellular units, magnocellular units became unresponsive at very low temporal modulation rates (Derrington & Lennie, 1984). The short response latency and duration of response of neurons in the magnocellular channel results in greater temporal resolution. The slower and more sustained response of parvocellular neurons, on the other hand, provide spatial resolution for slowly changing, or static stimuli. The temporal resolution properties in these two channels are reflected in contrast sensitivity measures. Temporal modulation rates differentially influence contrast sensitivity in magno- and parvo neurons with peak contrast sensitivity found for magnocellular units at higher temporal modulation rates than for parvocellular units (Derrington & Lennie, 1984).

Selective lesioning of the magnocellular or parvocellular layers of the LGN of Rhesus monkeys has
demonstrated differences between the two systems. The results of such studies indicate that the parvocellular system is important to color vision, and to sensitivity to achromatic stimuli of high spatial and low temporal frequencies (Schiller, Logothetis, & Charles, 1990; Merigan, 1989; Merigan, Katz, & Maunsell, 1991). Magnocellular lesions greatly reduced contrast sensitivity to high temporal, low spatial frequencies. In a study by Merigan and Maunsell (1990), magnocellular lesions eliminated the detection of low spatial frequency Gaussian blobs. In addition, contrast sensitivity was greatly reduced to gratings of 1 cpd drifted at 10 Hz while sensitivity to 2 cpd gratings was unaffected. Schiller et al, (1990) found that flicker sensitivity was severely impaired by magnocellular lesions. Merigan and Maunsell (1990) also found flicker resolution impaired at low contrast (22 percent) but found that increasing contrast to 100 percent eliminated the deficit. The results of their work and that of others suggested to Merigan and Maunsell (1990) that there is little contribution by the magnocellular system to visual sensitivity when the stimuli are modulated at low to moderate temporal frequencies.
During the past two decades a body of psychophysical studies has evolved with results that parallel those from the neurophysiological work suggesting two major pathways for visual information processing. The psychophysical studies, like the physiological studies, provide evidence for the existence of two distinct classes of channels in the human visual system which operate selectively according to the spatiotemporal properties of the stimulus. Differences in the mechanisms underlying those channels have been elaborated in the psychophysical literature under transient/sustained theory of visual perception (e.g., Breitmeyer, 1975; Harwerth & Levi, 1978; Kulikowski & Tolhurst, 1973; Lennie, 1980; Tolhurst, 1973). The term transient/sustained was borrowed from the physiological literature because the psychophysical results appeared to correspond to the spatiotemporal resolution properties then attributed to X and Y retinal ganglion and geniculate cells that had been labeled within the neurophysiological literature as transient/ sustained by Cleland, Dubin, and Levick (1971). However, the short-latency and transient temporal response which initially appeared to differentiate Y-cells from X-cells has since been found to belong not only to Y-cells, which are
segregated to the magnocellular pathways, but to belong also to most of the remaining cells within that pathway which also share the spatial resolution characteristics of X-cells found in the parvocellular layers. Despite the revision and elaboration of the early neurophysiological basis for independent channels in visual processing, the revisions to the neurophysiological basis for independent visual channels remain in agreement with the psychophysical results found early on that suggest separate mechanisms for two distinct classes of channels which operate selectively according to the spatiotemporal frequency of the stimulus. Indeed, the neurophysiological account of separate visual pathways currently available "...invites comparisons with the longstanding distinction, based largely on psychophysical measurements in humans and monkeys, between the 'transient' and 'sustained' visual mechanisms..." (Merigan, Byrne, & Maunsell, 1991, p. 3426).

**Psychophysical Basis for Independent Channels**

Psychophysical support for Campbell and Robson’s (1968) notion of multiple, spatial-frequency tuned channels in the visual system came from psychophysical studies involving adaptation. For example, for spatial
frequencies greater than 3 cpd, adaptation to a stationary sinewave grating of a single spatial frequency was found to decrease sensitivity to a limited band of frequencies centered on the adapting spatial frequency with the maximum loss of sensitivity occurring at the adapting frequency (Blakemore & Campbell, 1969). For spatial frequencies that differed in size from the adapting frequency by a factor of 2 or more there was little or no loss in sensitivity. The effect of an adapted grating upon the sensitivity of a limited band of spatial frequencies is consistent with the notion of multiple, spatial-frequency tuned channels in the visual system.

Tolhurst (1973) also examined the effects of adaptation to sinewave gratings, but in addition to adaptation to stationary gratings he tested the influence of temporal modulation on adaptation effects. For stationary gratings his results were similar to those of the Blakemore and Campbell (1969) study. Adaptation to stationary gratings reduced sensitivity to the adapting frequency for gratings 3 cpd and greater. For spatial frequencies lower than 3 cpd, the greatest reduction in sensitivity occurred, not at the adapting frequency, but at one centered at 3 cpd. The effects of adaptation to drifting gratings were
different from that of stationary gratings in two important ways. First, adaptation to drifting gratings reduced sensitivity not only to drifting gratings but to stationary gratings as well, whereas stationary gratings did not diminish sensitivity to drifting gratings. Secondly, for drifting gratings, reduced sensitivity specific to the adapting grating was found for spatial frequencies lower than 3 cpd. The failure of the low spatial frequency channels to adapt to stationary gratings indicated their dependence on movement. These results led Tolhurst to conclude that there are two classes of channels that are independent and operate over different spatial frequency ranges. The low-spatial frequency channels were movement dependent, whereas the higher spatial frequencies were not.

Differences in the nature of the spatiotemporal characteristics of the two channels were further examined by Kulikowski and Tolhurst (1973). Over a range of temporal frequencies contrast was sinusoidally modulated for stationary gratings to determine thresholds for detecting flicker and also for resolving gratings of low (0.8 cpd) and high (12 cpd) spatial frequencies. Recognition (i.e., resolution) of both gratings was maximally sensitive to static gratings
whereas flicker detection increased in sensitivity with increases in temporal modulation to about 5 Hz. However, for the low spatial frequency grating, considerably more contrast was required to resolve the grating than was required for the detection of flicker whereas for the high spatial frequency grating, just the opposite was true, that is, more contrast was required for flicker detection than for resolution. Thus, for a given spatial frequency the temporal character of a grating and the spatial character are apparent at different thresholds. Moreover, those thresholds vary independently with temporal and spatial frequency. This finding is consistent with Tolhurst’s (1973) notion that there are two independent channels with different temporal and spatial properties.

Evidence indicating faster response latencies for the lower spatial frequencies was provided by Breitmeyer (1975) who measured reaction time to the onset of sinusoidal gratings varying from .5 to 11 cpd. Reaction time increased from 200 msec for spatial frequency of .5 cpd to 350 msec for gratings of 11.0 cpd. Because subjective contrast decreases with increasing spatial frequency, Breitmeyer tested reaction time with the gratings equated for subjective contrast. Despite equivalent contrast across spatial
frequency, response latency was shorter for lower spatial frequencies.

Breitmeyer and Julesz (1975) compared contrast sensitivity to abrupt-onset gratings to those with a gradual onset. Consistent with Tolhurst's (1973) notion that low spatial frequency channels are specialized for rapid temporal change, higher sensitivity was found for low spatial frequencies when the onset of the grating was abrupt whereas for high spatial frequencies sensitivity was unaffected by the abruptness of the onset.

Differences in response latency and duration between the transient and sustained channels was also shown by Lupp, Hauske, and Wolf (1978). They hypothesized that reaction time to the detection of a grating would be facilitated if the grating was preceded by a brief presentation of a subthreshold grating of the same spatial frequency. Difference in reaction time was measured as a function of the onset asynchrony (SOA) between subthreshold and suprathreshold presentations of a grating for a range of intervals. The contrast of the subthreshold grating was .6 threshold contrast, whereas the suprathreshold grating was presented at a contrast 1.6 times threshold. Their results supported their hypothesis but the intervals
over which facilitation took place varied as a function of the spatial frequency of the grating. Facilitation occurred for high spatial frequencies (16.0 cpd) for SOAs as long as 500 msec. That is, when the subthreshold grating preceded the suprathreshold grating by as much as 500 msec there was a pronounced reduction in the reaction time to the suprathreshold grating. Facilitation began to decline systematically for SOAs less than 100 msec. Although facilitation began to decline for 16 cpd at SOAs of 100 msec, for gratings of 1 cpd there was little of no facilitation for SOAs greater than 200 msec, with peak facilitation at SOA’s of 30 to 40 msec. The long intervals (or SOAs) over which facilitation took place for the 16.0 cpd grating indicated the sustained nature of the response for the high frequency grating compared to the more transient one found for the 1 cpd grating. In addition, the shorter response latencies of low spatial frequencies is demonstrated by the finding that maximal facilitation for the 1 cpd grating was obtained at SOAs of 30 to 40 msec in comparison to that found for the 16 cpd grating, where a systematic decrease in facilitation was found below SOAs of 100 msec.

Contrast threshold across the spatial frequency range as a function of stimulus duration was examined
explicitly by Legge (1978). In a forced-choice procedure, Legge (1978) varied the duration of gratings to determine contrast sensitivity. For low spatial frequency gratings of .375 and .75 cpd, increasing the duration of the gratings produced greater sensitivity up to a duration of 100 msec. Further increases in duration did not reduce the response threshold. However, for higher spatial frequencies of 1.5 to 12.0 cpd, sensitivity continued to increase as the duration of the grating was increased to a maximum duration of 1000 msec beyond which no increases in sensitivity were obtained. The relationship between duration and contrast described by Legge's data was also found in an earlier study by Breitmeyer and Ganz (1977). They described reciprocal relationship between duration and contrast as a form of Bloch's law. Bloch's law stated that within some limit, an increase in stimulus duration can be compensated for by decreasing the intensity of the stimulus such that either event is equally detectible. Beyond some critical interval, however, it is not possible to offset the effects of one by adjustments in the other. Breitmeyer and Ganz observed that the critical duration differed as a function of spatial frequency, but also that the transient channels had a substantially shorter
integration time than the sustained channels. The study by Legge (1978) extended the Breitmeyer and Ganz finding to show that the critical duration over which the reciprocity between stimulus duration and contrast held was substantially longer for sustained channels than for the transient channels. These results were consistent with Tolhurst’s notion that there are two sets of channels that are independently mediated by different temporal and spatial properties.

Thus, psychophysical evidence indicates that there are multiple spatial-frequency tuned channels as suggested by Campbell and Robson (1968). In addition, these channels have been subdivided into two sets or independent classes of channels termed transient and sustained based on their spatial and temporal characteristics. The spatial frequency domain of the transient channels overlaps that of the sustained channels. The transient system is more sensitive over the low end of the spatial frequency range while the sustained channels are more sensitive for high spatial frequencies. As the names given these two classes of channels suggests, it is primarily the differences in the temporal response properties of the transient and sustained systems that most clearly differentiates one from the other. Response latency of the transient
system is short as is the duration of that response despite the continued presence of the stimulus. Sustained channels, on the other hand, not only respond with a long latency but activity in these channels tends to be prolonged. Thus, transient channels excell at processing large, rapidly changing, low contrast stimuli whereas sustained channels excell at processing static, or slowly changing, detailed, high contrast stimuli.

Correspondence between the psychophysical and the physiological evidence for independent visual channels: the effects of duration and contrast

The strong correspondence between the spatiotemporal response characteristics of the psychophysical transient and sustained channels to those of the physiological magnocellular and parvocellular neural pathways has been recognized by investigators in both psychophysics and in neurophysiology (e.g., Breitmeyer & Williams, 1990; Drasdo, Thompson, & Deeley, 1991; Lee, 1991; Livingstone and Hubel, 1987; Merigan, 1991; Merigan, Byrne, & Maunsell, 1991). While the correspondence is striking, the actual contribution of the magnocellular pathway that is captured in psychophysical measures is probably a matter of degree, determined not only by the spatial and temporal characteristics of the stimuli but
also by contrast. In psychophysical studies, the
duration of the stimulus at contrast threshold is an
important factor that mediates sensitivity and defines
the transient and sustained systems (e.g., Legge,
1978). The correspondence between the magno- and
parvocellular channels to the transient and sustained
channels is most apparent for measures obtained at or
near threshold contrast. That is, it is at contrast
threshold that neurons in the magnocellular pathway
respond with greater sensitivity to rapidly changing
low spatial frequency stimuli relative to the more
slowly generated but sustained response of
parvocellular neurons. However, when luminance
contrast exceeds threshold levels, the correspondence
of the magnocellular pathway to the transient channel,
and the parvocellular pathway to the sustained channel
is less clear cut. Both psychophysical and
physiological studies have found overlapping spatial
and temporal capacities between the transient and
sustained channels. Physiological studies indicate
that the temporal overlap between the two channels is
mediated by contrast. The overlap in the temporal
response capability of the parvocellular and
magnocellular pathways is illustrated in the Merigan
and Maunsell (1990) study. They found that monkeys
with magnocellular lesions had impaired flicker sensitivity at 22 percent contrast. However, sensitivity was less impaired when contrast was increased to 44 percent, and at 100 percent contrast flicker sensitivity was not impaired. This finding indicates that the temporal capacity of the parvocellular system can be equivalent to that of the magnocellular system if contrast is sufficiently high.

The stronger response of the magnocellular pathway relative to the parvocellular pathway at low contrast was also demonstrated in LGN cell studies cited earlier. In those studies it was found that at contrast levels below 10 percent, the response from parvocellular neurons is very weak compared with that of the magnocellular neurons (Derrington & Lennie, 1984; Hicks, Lee, & Vidyasagar, 1983; Kaplan & Shapley, 1982; Shapley, Kaplan, & Soodak, 1981). According to Shapley (1990), the ratio of contrast gain in LGN magnocellular neurons to that of parvocellular neurons is 8 to 1. Contrast gain describes how quickly sensitivity increases with each unit increase in contrast. An 8 to 1 ratio has also been reported by Kaplan and Shapley (1986) for retinal ganglion cells that map to the magnocellular and parvocellular LGN layers.
The finding that neurons in the magnocellular pathway, but not those in the parvocellular pathway, respond at contrast below 10 percent was utilized to examine contrast sensitivity of specific subdivisions of the primary visual cortex by Tootell, Hamilton, & Switkes (1988) during C-2-deoxy-d-glucose infusion. They found that the cortical area that receives direct projections from the magnocellular layers of the LGN showed substantial uptake when macaques were stimulated by gratings of 8 percent contrast. The cortical areas which received projections from the parvocellular layers, on the other hand, showed no evidence of activity from 8 percent contrast gratings. Such studies suggest that there is greater magnocellular input into a behavioral response for very low contrast. However, that is true only for stimuli that have very short durations because even at low contrast, the parvocellular input gains strength over time whereas the magnocellular input rapidly peaks and then decays rapidly. Thus, for any given stimulus, regardless of spatial frequency, reductions in the proportion of the magnocellular contribution relative to that of the parvocellular input to a behavioral response will occur with increases in time or increases in contrast even for very low spatial frequency stimuli.
The greater magnocellular input for contrast levels below ten percent corresponds to the high sensitivity observed for the transient channel for contrast levels below ten percent. A very straightforward demonstration of transient system low contrast sensitivity was provided by Arend (1976) who had subjects adjust the contrast of a grating until it was just detectible. For briefly flashed gratings, low spatial frequencies were detectible with much lower contrast than high spatial frequencies. For example, with a duration of 40 msec, a .30 cpd grating was detectible with contrast near 6.5 percent whereas a 10 cpd grating needed nearly 9 times that contrast (56 percent) to be detectible. The 8.6 to 1 ratio of sustained to transient thresholds (e.g., 56/6.5) is strikingly close to the 8 to 1 contrast gain described by Shapley for the magnocellular as opposed to the parvocellular neurons. Arend also showed that when compared with the 40 msec flashed gratings, sensitivity to steady state presentations was reduced for the transient channels while it was enhanced for sustained channel. Under steady state presentations, the contrast needed to detect the .3 cpd grating increased to 31 percent contrast (from 6.5 percent for 40 msec flashed gratings) whereas for the 10 cpd grating the
required contrast decreased to 22 percent (from 56 percent). Arend's work demonstrates the high sensitivity of the transient channel to rapidly changing low contrast information in contrast to the low sensitivity of the sustained channel. The sensitivity of the transient channel is greatly reduced for static information. The sustained channels, on the other hand, which demonstrated low sensitivity to the brief grating, showed much higher sensitivity when the presentation was nonchanging.

In addition to studies of contrast sensitivity that reflect sensitivity differences between the transient and sustained channels under low contrast conditions, there is suggestive evidence from other psychophysical studies that indicates a transition from the transient to the sustained channels at contrast levels of 10 percent. For example, Harwerth and Levi (1978) examined reaction time to sinusoidal gratings over a wide range of stimulus durations and contrast. They found that the reaction time data deviated significantly from a linear function at 10 percent contrast, whereas for higher contrast levels, a linear relationship was found between contrast level and reaction time. Harwerth and Levi (1978) observed that a similar deviation at low contrast appeared in the
data of another study (Hamerly, Quick, & Reichert, 1977). Campbell and Maffei (1981) reported that the perceived motion obtained from rotating gratings saturated at contrasts greater than 5 percent. In a more recent study that measured temporal integration of large, low-spatial frequency information, the ISIs over which the matrices could be integrated at above chance levels was similar across a range of contrast levels, but persistence duration markedly increased for matrices with contrast set to near threshold levels (Shiori & Cavanagh, 1992). Those psychophysical findings suggest a disproportionate involvement by the transient system in visual information processing for rapidly changing, very low contrast stimuli. The characteristics that differentiate the transient system processing are the same as those that differentiate the magnocellular system, high sensitivity to low contrast stimuli, under conditions of rapid temporal modulation.

The Multichannel Model and Visible Persistence

The multichannel model of visual information processing describes two systems that are independent but operate in parallel to process different aspects of visual information. Both the physiological and the psychological evidence depict the transient channel as most responsive under conditions of rapid temporal
change. It responds rapidly and also fades rapidly. It operates most independently on spatial information that is of large extent and low contrast. The sustained system, on the other hand, appears specialized to process finely detailed spatial information and is most sensitive under high contrast, temporally unvarying conditions. In contrast to the transient system, the sustained system is relatively slow to respond, and its response fades slowly as well. The differences between the sustained and transient systems have been used to frame studies of visible persistence over the last couple of decades.

**Visible persistence as a function of spatial frequency**

Visible persistence increases with increasing spatial frequency (Bowling & Lovegrove, 1980; 1981; Bowling et al., 1979; Meyer & Maguire, 1977) but decreases with increases in luminance (Bowen et al., 1974), contrast (Bowling & Lovegrove, 1981; Bowling et al., 1979) and stimulus duration (Bowling & Lovegrove, 1980). Bowling and Lovegrove (1981) observed that the function that described the relationship between visible persistence and temporal integration was the same as the one that related detection sensitivity and temporal summation. Temporal summation relates the detectibility of a stimulus to the product of contrast
and duration. Increases in stimulus duration can be compensated for by decreases in contrast. Breitmeyer and Ganz (1977), and Legge (1978) demonstrated that there was a range of durations over which a sinusoidal grating could be made equally detectible by adjusting the contrast. Beyond some critical duration, however, further increases in stimulus duration cannot be offset by further decreases in contrast.

While the function describing the reciprocity between contrast and duration has the same shape across spatial frequency, differences in the intercepts of those functions indicate that the amount of energy needed by each spatial frequency is different. Energy requirements (contrast x duration) for detection are increased as spatial frequency increases. The functions described by the Legge data show that low spatial frequencies have much smaller energy requirements, in that they are completely integrated within 100 msec at threshold levels of contrast. Spatial frequencies 1.5 cpd and above, e.g., the sustained channels, require more contrast to be detected and do not completely integrate until duration has reached 1000 msec.

Bowling and Lovegrove (1980), and Bowling, Lovegrove, and Mapperson (1979) observed a similar
relationship between visible persistence and energy. They found that over some critical interval, visible persistence decreased with increasing energy until some point where further increases in energy did not affect the duration of visible persistence. While the functions had the same shape across spatial frequency the amount of energy (contrast x duration) that defined the relationship for each spatial frequency was different, as indicated by differing intercepts. Energy levels for low spatial frequencies reached asymptotic levels of visible persistence sooner than high spatial frequencies. Thus, Bowling et al. (1979) and Bowling and Lovegrove (1980) attributed at least part of the relationship between persistence and spatial frequency to the underlying temporal integration mechanisms that govern spatial frequency-selective channels.

The relationship indicating that visible persistence is governed by temporal integration mechanisms was supported by the finding that showed that flickering sinewave gratings increase persistence for low but not for high spatial frequencies (Breitmeyer, Levi, & Harwerth, 1981). Detection of oblique sinewave gratings require longer durations and have longer visible persistence than is true for
horizontal or vertical gratings of the same contrast (Bowling and Lovegrove, 1981; L’Hommedieu & Meyer, 1982).

Marx and May (1983) examined the relationship between temporal integration mechanisms, spatial frequency and visible persistence by manipulating separately and together the effects of stimulus duration and contrast across spatial frequency. For near-threshold sinewave gratings and a constant duration of 50 msec, the spatial frequency effect was obtained. That is, visible persistence increased with increasing spatial frequency. However, when visible persistence was again measured with near threshold contrast but with stimulus duration set to some fraction of the temporal integration values for each spatial frequency, no effects of spatial frequency were obtained. The results by Marx and May indicate that visible persistence is a product of the temporal integration mechanisms that govern the response to information varying in spatial frequency. By setting temporal integration factors (contrast and stimulus duration) to an equal fraction of the temporal integration rates for each spatial frequency, Marx and May found that the duration of visible persistence is equivalent across spatial frequency.
Individual differences in visible persistence related to spatial frequency

The finding that temporal integration mechanisms influence visible persistence across spatial frequency has implications for the study of individual differences in persistence. Individual differences in visible persistence as a function of spatial frequency have always been evaluated under a given contrast and stimulus duration. The use of given contrast and stimulus duration would have the effect of compressing persistence for spatial frequencies with integration constants that were lower than the product of contrast and duration that was chosen for a given test situation. Under such test conditions, persistence variability would have been most suppressed for spatial frequencies dominated by the transient system, with its high sensitivity to low contrast and tendency toward attenuated responses as duration and/or contrast increases. Evaluating transient channel persistence differences under such conditions would in effect be attempting to map individual variations with a single measure. Thus, the effect of failing to control for spatial frequency related temporal integration while assessing individual differences would be to reduce or lose the ability to detect individual differences in
persistence particularly for transient-dominated spatial frequencies.

**Age related differences in visible persistence**

As indicated earlier, there is evidence to suggest that elderly adults have more sluggish visual systems than young adults. Elderly need longer intervals separating the pulses of a flickering light stimulus to detect the flicker (CFF) compared with young adults (Coppinger, 1955; McFarland et al., 1958; Misiak, 1947) and they need longer to escape the interference from backward masking (Di Lollo et al., 1982; Hertzog et al., 1976; Kline & Szafran, 1975; Walsh, 1976). Although contrast sensitivity is often more reduced in the elderly for high spatial frequencies (Klein, Schieber, Abusamra, & Coyne, 1983; Owsley, Sekuler, & Siemsen, 1983), low spatial frequency deficits become apparent when gratings are temporally modulated (Owsley et al., 1983; Royer & Gilmore, 1985b). Because optical factors can be used to account for the reduction in high spatial frequency sensitivity they are less interesting than low-spatial frequency deficits which are not as easily affected by optical factors. Deficits in low spatial frequency processing can be attributed to changing neural events and as a
consequence generate considerable interest from investigators who track age-related neural functioning.

Because the elderly exhibit evidence of reduced temporal resolution, it might be expected that they would generate longer visible persistence. Indeed, there is evidence of longer visible persistence for the elderly (Di Lollo et al., 1982; Royer & Gilmore, 1985a). However, few studies involving the elderly have manipulated spatial frequency on visible persistence tasks. Thus, little is known about age-related changes in transient-system generated visible persistence. One study that did examine spatial frequency dependent visible persistence, however, found differentially longer low spatial frequency persistence for elderly as compared with younger subjects. Kline, Scialfa, Lyman, & Schieber (1990) examined visible persistence in young and elderly subjects by determining the longest interval that a grating was seen as continuous when it was flashed twice in succession separated by a variable ISI. It might be expected that the true magnitude of the deficit was underestimated in this study, however because of the high contrast (66 percent) and long stimulus durations (100 msec) used to generate visible persistence. If there is a transient system deficit, it should be most
apparent when tested with low spatial frequency information of very low contrast that is presented for very limited duration or where it undergoes rapid temporal modulation. Not only should putative transient channel deficits be more detectible but it seems reasonable to draw inferences about the physiological substrates of the transient channels. Under such conditions (low contrast, short duration) it might be reasonable to extrapolate any differences between the young and the elderly to the large cells of the magnocellular system because we know that the parvocellular system is fairly unresponsive under those conditions. In the Kline et al. study it is not possible to even speculate about the specific underlying magno/parvo neural contributions because the high contrast and long durations would be expected to draw heavily from not only the magnocellular system but the parvocellular system as well. Finally, if the stimuli had been presented at low contrast with stimulus durations adjusted to account for varying temporal integration rates across spatial frequency of ideal (young) observers, then it would be possible to see not only the magnitude of age related changes from the young baseline for transient/sustained visible persistence, but it would also be possible to directly
compare the relative functioning of the transient versus the sustained channels within the elderly group.

Summary

Both physiological and psychophysical studies describe independent visual channels that respond differentially depending on the spatial and temporal characteristics of the stimulus. Psychophysical studies have shown that the transient system responds more sensitively to rapidly changing, large, low contrast stimuli while the sustained system is more sensitive to static, finely detailed high contrast stimuli. Between those two extremes it is more difficult to evaluate which system supplies greater input to a behavioral response because they both have the capacity to respond. Physiological evidence also describes two independent visual systems. The characteristics that differentiate the parvocellular system from the magnocellular system are the same that differentiate the sustained from the transient. The parvocellular system responds more sensitively to finely detailed, slowly changing, high contrast visual information. Like the transient system, the magnocellular system is more sensitive to rapidly changing, large, low contrast stimuli. The defining features of the magnocellular and parvocellular system
suggest that they subserve the psychophysical transient and sustained visual channels. For any given behavioral response, however, it is not possible to attribute a response strictly to one or the other system because of their overlapping capacities. Nonetheless, when stimulus conditions are dichotomized along spatial and temporal domains to correspond to those that define both the magnocellular/transient and the parvocellular/sustained systems near threshold contrast, it should be possible to draw inferences from the psychophysical information regarding the relative input from neural systems that subserve those responses. The present research was designed to examine transient and sustained channel individual differences related to age under conditions that make it reasonable to extrapolate the results to differences in the independent neural systems that are believed to subserve the psychophysical channels.

Studies investigating the relationship between age and visible persistence have always been conducted using stimuli with contrast and duration fixed (Di Lollo et al., 1982; Kline et al., 1990). The only study of age-related differences in the duration of the visual response over a range of spatially varying stimuli (Kline et al., 1990) was conducted using
contrast and duration set to a fixed value well above threshold. But visible persistence, or the duration of the early visual response, is inversely related both to contrast and to stimulus duration (i.e., temporal summation), and sensitivity to contrast varies with age and spatial frequency. Thus, differences between young and elderly subjects attributed to visible persistence may be the result of age differences in the sensitivity of the visual response to low and high spatial frequency information. The lower sensitivity of the visual response of elderly subjects would generate a weaker response which in turn would generate longer visible persistence.

In the present study, the paradigm used to infer visible persistence was adapted from one developed by Di Lollo (1977). In this task, two 5x5 matrices are presented in succession separated by a variable interval (ISI). Twelve of the 25 possible elements of the matrix are present in the first frame, while the second frame contains 12 of the remaining 13 elements. When the two frames are separated by a sufficiently short interval, the image from the first frame will merge with that from the second frame to yield a matrix with 24 of the possible 25 elements. The subject’s task was to identify the location of the missing
element which, in this study, was restricted to one of the nine elements of the 3x3 matrix embedded within the 5x5 matrix. While only one of the central 9 elements is missing, the presentation of the entire 5x5 array preserves the complexity inherent in the 5x5, which reduces the salience of any particular spatial configuration that might be present in the 3x3 array alone. At very short ISIs the visual information from frame 1 merges with that from frame 2 so that the missing element is easily identifiable. As ISI increases, visual information from the first frame is decreasingly salient and accuracy in detecting the missing element decreases. The decline in accuracy with longer ISIs could be expected to be less pronounced in individuals who have reduced temporal resolution. Reduced temporal resolution would allow the visual response to the image from the first frame to persist longer and bridge the temporal gap between the presentation of first and second frame. Thus, the magnitude of visible persistence is inferred from the length of the interval over which the two matrices can be reliably integrated.

Present Research

Studies that show that visible persistence is longer with shorter stimulus durations and/or lower
contrast suggest that the less salient an image, the more it lingers within the visual system. Conversely, a very salient image will be processed rapidly through the visual system. In the present research it was hypothesized that there are differences between young and elderly subjects in temporal summation processes, and that these differences are greater for low spatial frequency information. If temporal summation is slower for elderly subjects, they would be expected to have a weaker response to an image at any point in time. The weaker visual response of the elderly to the image would result in less complete temporal integration and allow the image to linger longer at low levels of visual processing. Thus, when young and elderly subjects are tested for visible persistence with a stimulus of the same contrast and stimulus duration, young subjects should have less visible persistence than elderly subjects. Whether visible persistence differs when stimuli are equivalently visible for young and elderly subjects and whether there are differential effects related to age of spatial frequency information in response to such stimuli are questions that have not been previously addressed.

In the first experiment, temporal sensitivity, i.e., the time required to make a stimulus completely
visible, was tested. Contrast and spatial frequency information were manipulated. Subjects were presented with a single frame containing an image of a 5x5 matrix with one element missing from the 3x3 matrix embedded within the 5x5 matrix. The minimum duration of the single frame that allowed the missing element to be identified with 100 percent accuracy over a set of 20 trials was determined for each subject. Thus, those who have higher temporal sensitivity should be able to accurately detect the missing element with shorter stimulus durations.

In the second, third, and fourth experiments, the Di Lollo matrix integration paradigm was used to estimate visible persistence in young and elderly subjects. Spatial frequency information was manipulated. The span over which the matrices were integrated was measured in three ways using the information obtained from Experiment 1 to set values of contrast and stimulus duration. In Experiment 2, the interval over which two matrices could be reliably integrated was tested in young and elderly subjects with contrast set to a constant value. Duration was adjusted for each subject to a value that allowed the matrices to be just visible for the level of contrast used. Both low and high spatial frequency information
were tested. Contrast was set to the lowest level, based on the results of Experiment 1, that assured that the matrices were minimally visible to every subject for the stimulus duration that was tested. In Experiment 3, stimulus duration was set to a constant value for all subjects, but contrast was adjusted for each subject so that the matrices are just visible. Finally, in Experiment 4, both contrast and duration were set to a constant value while spatial frequency was manipulated.

Thus, estimates of visible persistence were obtained from young and elderly subjects for both low and high spatial frequency matrices in three ways. The method used in Experiment 4 is similar to the way individual differences have typically been estimated for visible persistence (i.e., constant contrast, constant duration) by others (Kline et al., 1990). Unlike the Kline et al. (1990) study, however, the response was objectively measured. In Experiment 2, and in Experiment 3, either duration or contrast was fixed while the other was set to a value that allowed the matrices to be just visible for each subject. In Experiments 2 and 3 the purpose of the manipulations was to allow the salience of the visual image to be equated across subjects. The methods used in those
experiments allow age effects of visible persistence to be evaluated separately from the effects of contrast and temporal sensitivity differences that exist between the two age groups. The method used in Experiment 4 determines whether typical age related persistence effects obtain for the stimuli and paradigm used to generate persistence.

Thus, in Experiment 1, the minimum time that a stimulus needed to be presented to allow the subject to form a complete visual image was determined for both low and high spatial frequency information over a range of contrast levels. In Experiment 2, the interval of time over which the image lingers within the visual system was assessed across spatial frequency information. In Experiment 2, contrast was set and duration was allowed to vary across individuals so that the matrices were equivalently visible for all subjects and within spatial frequency information. In Experiment 3 duration was set and contrast allowed to vary so that visibility of the matrices was relatively constant across subjects and spatial frequency information. In Experiment 4 contrast and duration was set to the same value for all subjects for both low and high spatial frequency information.
The experiments were unique in several ways. One unique aspect is the evaluation of age-related differences in temporal sensitivity of very short duration, large extent spatial-frequency varying stimuli using stimulus energy levels (contrast \( \times \) duration) that approach threshold levels. The low level of stimulus energy was expected to maximize visible persistence for all subjects. In addition, the measure used to test those differences provided an objective evaluation of performance. The spatial frequency characteristics of the stimuli were designed specifically to extract measures of transient system processing that exclude as much as possible input from the sustained system and vice versa. Finally, by using stimuli that are equated for visibility across subjects, to measure the span of time over which two images can be visually integrated allowed the response obtained to be independent of, in one case contrast sensitivity, and in the other case, temporal sensitivity.

The pattern of results was expected to show that in order to detect individual differences in either sustained or transient channel processing it is important to adjust the measures so that each channel is isolated from the other as much as possible.
Maximum differentiation of sustained from transient channel processing requires careful consideration not just of spatial frequency information, but also of the combined effect of stimulus duration and contrast. Finally, the results found for young and elderly subjects in these studies describe developmental changes in transient and sustained system processing. While sustained channel differences need to be regarded cautiously, as possibly reflecting age-related optical changes, transient channel differences are less affected by optical factors and can thus be viewed as reflecting neural events associated with development.
Experiment 1

The purpose of Experiment 1 was to examine the relationship between contrast and stimulus duration for low and high spatial frequency information in young and elderly subjects. The minimum duration required to accurately report the single missing element within a 3X3 matrix embedded within a 5X5 matrix was tested across five levels of contrast. Low spatial frequency temporal sensitivity was tested with 5X5 matrices where the most dominant energy centered around .25 cpd. High spatial frequency temporal sensitivity was tested with 5X5 matrices where the most dominant energy was centered on 3.2 cpd. These stimuli will be referred to as the low and high spatial frequency matrices, respectively. Figure 1 depicts the relative distribution of energy across spatial frequency information contained in the images of the low and high spatial frequency matrices.

The distribution of energy across spatial frequency information contained within the low and high spatial frequency matrices provides as great a separation between low and high spatial frequency information as was possible given limitations involved in creating the stimuli. The energy distribution depicted in Figure 1 for the low spatial frequency
matrices indicates that those matrices should tap strongly into the transient channel. Although the dominant energy within the high spatial frequency matrices is centered on the lower end of the high spatial frequency spectrum, high spatial frequency information is well represented with very little contamination from low spatial frequency information. From psychophysical studies (e.g. Harwerth & Levi, 1978; Legge, 1978; Tolhurst, 1974) it is clear that the temporal and spatial domains of the transient and sustained channels overlap particularly for the midrange channels from 1.5 to 4 cpd. The overlap of the sustained and transient channels, however, decreases as spatial frequency values decrease below 1.5 cpd or increase above 4 cpd. Thus, the overlap of the temporal and spatial domains of the transient and sustained channels should be minimal for the low and high spatial frequency matrices used in this experiment for short duration stimuli, and the results should reflect relatively independent responses from each of those channels.
Method

Subjects

Subjects were 10 students from CWRU and 10 elderly individuals who live independently within the community. Mean age of the young subjects was 21 years, while the older subjects had a mean age of 71 years. Young subjects were in the last semester of their third year of college except for one who was a senior. The number of years of education completed for the elderly subjects was 17 years (S.D.=2.6). Snellen visual acuity at 10 feet was 20/21 for the young subjects and 20/24 for the elderly subjects. Visual acuity was also measured at the test distance of 69 cm. Mean visual acuity for measures obtained at 69 cm was 20/24 for the young subjects and 20/27 for the elderly subjects.

Apparatus

Stimuli were generated with a Matrox PIP 1024 imaging board under the control of an IBM compatible 486 computer. The Matrox board was used to set the level of contrast and spatial frequency content of the stimuli. Contrast of the stimuli was measured with a Spectra Pritchard Photometer. Stimulus presentation was under the control of a fast video tachistoscope.
that can display images with a temporal resolution of 417 Hz.

Stimuli

The 5x5 matrix was 24.4 x 24.4 cm. Center to center of each element is 5.08 cm both horizontally and vertically. From the center of each element to outer edge was 2.03 cm. The separation between two elements was 1.02 cm. The area of each element subtended a visual angle of 3.37 degrees at a viewing distance of 69 cm with a separation between the elements of 0.84 degrees of visual angle. The entire 5x5 array subtended a visual angle of 19.46 x 19.46 degrees, with the center 3x3 matrix subtending a visual angle of 11.65 x 11.65 degrees. The luminance of each circular element in the matrix was distributed along the radius in a cosinusoidal fashion (see Figure 2). Thus, contrast could vary without changing mean luminance.

Mean luminance was set to 10 cd/m2. Temporal sensitivity decreased with decreasing mean luminance (De Valois et al., 1974; Sloane, Owsley, & Jackson, 1988). By setting mean luminance to low photopic levels, the time course of temporal integration is maximized. In addition, Sloane et al. (1988) reported age related differences in temporal sensitivity to low-
spatial frequency information under mean luminance levels of 10.7 cd/m².

Design

A 2 x 2 x 5 mixed factorial design was used. The between-subject variable was Age (Young or Old). The within-subject variable was Spatial Frequency (Low and High) and Percent Contrast (5, 12, 21, 34 and 61). Contrast is expressed in percent form, (Imax - Imin)/(Imax + Imin) where Imax and Imin are the maximum and minimum luminance respectively within one period along the radius of each grating element. Trials were blocked by spatial frequency and contrast.

Task

The psychophysical task involved locating the single missing element from the 3x3 array embedded within a 5x5 array. The duration of the matrix was adjusted until the minimum duration was found where the subject could correctly report the missing element with 100 percent accuracy for 20 trials. A card containing a stylized version of the 5x5 matrix was placed just below the viewing screen. The card depicted the 5x5 matrix and the numbering system used for the central 9 elements. Feedback was provided after each trial by the experimenter who indicated whether the response was correct.
Figure 2. The distribution of energy as a function of spatial frequency information for matrices that subtend a visual angle of 20 degrees.

a) Low Spatial Frequency Matrix

b) High Spatial Frequency Matrix

c) Low and High Spatial Frequency Matrices Combined
Figure 2. The distribution of luminance along the diameter of a 2D low-pass filter matrix.

Low Spatial Frequency Matrix

High Spatial Frequency Matrix

Diameter of Matrix Element
Degrees of Visual Angle
Procedure

Subjects were tested in three to four sessions that lasted approximately 45 to 60 minutes each. They were seated at a distance of 69 cm from the fast video tachistoscope with their head position maintained with a chin rest. After the demands of the task were described they were given sample presentations while they learned to identify the missing elements by number. Learning trials consisted of a set of 20 trials. A trial consisted of the presentation of a single frame containing a 5X5 matrix with one missing element out of the central 3x3 matrix. Contrast was set to 34 percent and stimulus duration to 50 msec for the low spatial frequency matrices. Learning trials for the high spatial frequency matrices had a stimulus duration of 100 msec. The purpose of the learning trials was to allow the subjects to be sufficiently practiced in locating the missing element in the matrix and identifying it by number. After the initial 20 practice trials given to all subjects, practice continued until accuracy of 100 percent was achieved over a set of 20 trials.

After the subject became proficient in identifying the missing element the minimum stimulus duration was determined. The minimum stimulus duration was
determined for each of five levels of contrast for both low and high spatial frequency matrices. Five subjects in each age group were tested first with the low spatial frequency matrices and five were tested first with the high spatial frequency matrices. Within each spatial frequency group each subject began the experimental procedure with a different level of contrast. Both levels of spatial frequency matrices were tested before testing with the next level of contrast.

Testing began with a set of 20 trials. If all 20 trials were accurately reported stimulus duration was decreased by .1 log unit. Each set of 20 trials completed with 100 percent accuracy resulted in a decrease in the stimulus duration by .1 log unit. If a mistake was made, a second set of 20 trials was tested at the same duration. Testing at that duration was terminated if a second error was made. Duration was then increased by .05 log units or one frame, (2.4 msec) whichever was larger to a maximum duration of 200 msec. Testing at a given level of contrast and spatial frequency was terminated if the subject was not able to identify the missing element within 200 msec. With each reversal in direction, the change in the stimulus duration was half of the change (in log units) that
occurred in the previous reversal. Because the minimum
duration possible for an image was 2.4 msec, each
duration was the closest multiple of 2.4 msec. Thus,
if stimulus duration of 100 msec was tested, 42 frames
(42 x 2.4=100.7 msec) would be required. Where all 20
trials were completed with 100 percent accuracy,
stimulus duration was decreased .1 log unit. (A
reduction of .1 log unit of 100.7 msec yields 80 msec;
80 msec/2.4 msec yields 33 frames (times 2.4 msec)
which in turn yields a duration of 79 msec.) In the
event of an error, the duration was increased .05 log
units to 37 frames or 89 msec. If all 20 trials were
correctly reported, the duration was then reduced by
nearest multiple of 2.4 msec that yielded a decrease of
.025 log units. The shortest duration for each level
of contrast that allowed the missing element to be
detected with 100 percent accuracy over 20 trials was
called the critical duration.
Temporal Sensitivity

Elderly subjects were not able to identify the missing element in the high spatial frequency matrices under the 5 and 12 percent contrast conditions when matrix duration was 200 msec or less. In addition, under the 62 percent contrast condition all young subjects were able to correctly identify the missing element under the most rapid presentation rate possible for the low spatial frequency matrices, resulting in a ceiling effect for the 62 percent contrast condition. Thus, statistical analyses were conducted over the remaining two levels of contrast, 22 and 35 percent where there were no ceiling or floor effects and responses were obtained for all subjects.

Sensitivity was derived in the same way as Nagano (1980), Log (1/critical matrix duration). This method is similar to the way contrast sensitivity measures are derived. As can be seen in Figure 3, the graph of the mean temporal sensitivity (Log (1/critical matrix duration)) within each condition describes a strong and consistent pattern within and between all factors manipulated. It should be noted that there was no overlap between the young and the elderly subjects’ low or high spatial frequency scores within any level of
contrast. That is, within any level of contrast and spatial frequency, the temporal sensitivity for the most sensitive elderly subject was always lower than the least sensitive young subject. In addition, the same pattern of results appeared for every subject. Within each level of spatial frequency, temporal sensitivity always increased as contrast increased, and low spatial frequency sensitivity was always higher than high spatial frequency sensitivity.

An Age (Young or Elderly) X Spatial Frequency (Low or High) X Contrast (22 or 35 percent) ANOVA was conducted on Temporal Sensitivity (1/log (critical duration)). Several expected results emerged. First high spatial frequency temporal sensitivity was lower than low spatial frequency sensitivity, $F(1,18) = 621.28$, $MS_e = 13.5$, $p < .0001$. The temporal sensitivity of elderly subjects was lower than that for young subjects, $F(1,18) = 126.58$, $MS_e = 4.9$, $p < .0001$. Temporal sensitivity increased as contrast increased $F(1,18) = 159.92$, $MS_e = 1.2$, $p < .0001$. These results are consistent with what was expected based on the literature review. The results suggest that the characteristics that typically describe the low and high spatial frequency domains were present in the stimuli used in the present experiment while also
confirming an expected deficit associated with age in visual temporal processing.

There were two interactions. High spatial frequency temporal sensitivity increased more as contrast increased, $F(1,18) = 5.54, MS_e = .02, p < .01$. This result is consistent with that reported by Nagano (1980) who found that, in general, the lower the temporal sensitivity, the greater the gain with increases in contrast. Thus, while low spatial frequency temporal sensitivity is greater than that for high spatial frequency sensitivity, these results indicate that the sustained channel is more affected than the transient channel by increases in contrast.

The second interaction indicated that age interacted with spatial frequency such that elderly subjects had differentially lower high spatial frequency temporal sensitivity, $F(1,18) = 9.65, MS_e = .05, p < .01$. The interaction between age and spatial frequency remained significant when separate ANOVAs were conducted on the 22 percent contrast condition, $F(1,18) = 6.76, MS_e = .11, p < .02$, and the 35 percent contrast condition, $F(1,18) = 7.3, MS_e = .09, p = .01$. While high spatial frequency sensitivity was differentially higher in young subjects than elderly subjects, separate analyses of the low spatial
frequency condition indicated that young subjects exhibited greater low spatial frequency sensitivity than elderly subjects for the 22 percent condition, \( F(1,18) = 56.15, \, MS_e = .90, \, p < .0001 \) as well as the 34 percent contrast level, \( F(1,18) = 39.56, \, MS_e = .66, \, p < .0001 \).

What stands out in the graph of the results is a bend in the functions at the 12 percent contrast level. That turn upward in response sensitivity may represent the increased participation of the parvocellular pathway as contrast increases above 10 percent described by Shapley and Kaplan (1986) and Tootell et al. (1988). If that were the case, then the increased sensitivity for low spatial frequency information could be attributed to not only a more sensitive magnocellular system but a more sensitive parvocellular system as well. That is likely to be the case given that approximately 80 percent of the neurons in the visual system are connected to the parvocellular pathways.

The pattern of results of Experiment 1 show that young subjects are differentially more temporally sensitive to high spatial frequency information at least under contrast conditions of 22 percent and 34 percent. The greater high spatial frequency
sensitivity along with the failure of elderly subjects to see the high spatial frequency matrices with durations of 200 msec or less under lower contrast conditions may be, at least partially, attributed to optical changes associated with age.

However, young subjects also exhibit greater low spatial frequency temporal sensitivity than elderly subjects for both levels of contrast. Optical factors do not explain the reduction in temporal sensitivity in response to low spatial frequency information that was apparent in the statistical analyses conducted on the 22 and 35 percent contrast conditions. Moreover, the graph of the data in Figure 3 indicate that for levels of contrast below 22 percent the difference in the young and the elderly subjects low spatial frequency temporal sensitivity is greater than under the higher levels of contrast. The reduced sensitivity exhibited by the elderly subjects in response to low spatial frequency information is most likely neural in origin for the 22 and 34 percent contrast conditions but the specific pathways that contribute to the neural deficit are not differentiated by these results. However, given the absent or sluggish response of the parvocellular system for contrast levels for 10 percent or less described by physiological studies (Kaplan &
Shapley, 1986; Tootell, 1988), it does not seem likely that the parvocellular system contributes to the separation in response sensitivity between the young and the elderly low spatial frequency response apparent in the graph of the results for the 5 and 12 percent conditions.
Figure 1. The effect of contrast, spatial frequency, and age on temporal sensitivity.

Empty Symbols: Low Spatial Frequency
Filled Symbols: High Spatial Frequency
Squares: Elderly
Circles: Young
Experiment 2

Several studies have shown that visible persistence is inversely related to both contrast and stimulus duration (Bowen et al., 1974; Bowling & Lovegrove, 1980; Bowling et al., 1979). The detectability of visual information has just the opposite relationship to contrast and stimulus duration. Detectability is increased as contrast or stimulus duration, or both are increased. Moreover, within some range of values for contrast and stimulus duration, increases in contrast can be offset by decreases in stimulus duration to maintain the same level of visibility (Breitmeyer & Ganz, 1977; Legge, 1978). Thus, the same factors of contrast and duration that relate positively to the detection of an image are negatively related to visible persistence. The inverse relationship between stimulus energy (contrast x duration) and visible persistence suggests that those with reduced contrast and/or temporal sensitivity could be expected to have longer visible persistence when persistence is measured with a stimulus of a given contrast and duration. Thus, differences in visible persistence that have been found between young and elderly subjects may be attributed, at least in part, to differences in contrast and/or temporal sensitivity.
The purpose of Experiment 2 was to examine the relationship between age and the duration of the visual response to low and high spatial frequency matrices in each of three conditions while controlling the effects of temporal and contrast sensitivity within each spatial frequency condition. In Experiment 2, stimulus visibility was equated across subjects and spatial frequency information by setting contrast to the same level for all subjects while stimulus duration was adjusted. In Experiment 3, stimulus visibility was again equated across subjects and spatial frequency. But in this case stimulus duration was held constant and contrast was individually adjusted so that the matrices were just visible for each level of spatial frequency tested. Thus, the matrices were equated for visibility within spatial frequency information across all subjects. In Experiment 4 all subjects were tested with the same contrast and stimulus duration. This method allowed the visibility of the matrices to be influenced both by the spatial frequency content of the matrices as well as by the sensitivity of the subject within low and high spatial frequency information.

Visible persistence was estimated in young and elderly subjects with the Di Lollo matrix integration paradigm for both low and high spatial frequency
matrices. The purpose of Experiment 4 was to replicate the finding that, at least under conditions of a given contrast and stimulus duration, elderly subjects have longer visible persistence than young subjects, and that high spatial frequency information produces longer visible persistence than low spatial frequency information. In addition, if temporal summation is inversely related to visible persistence, then the dependent variable from Experiment 1 (critical stimulus duration) should be inversely related to the dependent variable from Experiment 2 of this study, the critical interstimulus interval (CISI), the longest interval over which the matrices can be integrated.

The results of a study by Sloane et al. (1988) indicated that there are differences in the temporal sensitivity of young and elderly subjects independent of contrast threshold differences between the two groups. They found that under low mean luminance (10.7 cd/m2) the threshold contrast sensitivity was suppressed equivalently for elderly and young subjects with increased temporal modulation for high spatial frequency gratings (8 cpd). For low spatial frequency gratings (.5 cpd) however, the increase in temporal modulation increased threshold sensitivity for young but not for elderly subjects. Thus, independent of
age-related-differences in threshold contrast sensitivity, young subjects exhibited greater temporal sensitivity than elderly subjects but only for low spatial frequency information.

Equating the visibility of the stimuli across subjects and spatial frequency was expected to reduce the effects of age and spatial frequency that could contribute to differences in visible persistence. Differences in visible persistence that remain after removing sensitivity differences related to age and spatial frequency content would thus provide an estimate of visible persistence within and between age groups and spatial frequency information that is independent of differences in sensitivity.
Method

Subjects

The subjects were the same as in Experiment 1.

Stimuli

Stimuli were generated in the same manner as in Experiment 1. Mean luminance was 10 cd/m². Contrast was set to 34 percent which was determined in Experiment 1 to be the lowest level that all subjects were able to see the matrices. Stimulus duration was set individually for each subject as follows. The leading frame was given a duration of .3 log units longer than the critical duration obtained for the subject in Experiment 1 for the 34 percent contrast. The trailing frame was set to .15 log units above the critical duration. Pilot testing indicated that the amount of time needed to identify a single frame of the 5x5 matrix was not a sufficient amount of time to identify the missing element when the visual information was divided into two frames and separated by a brief interval. Visibility was sufficiently high however, if the duration of the leading frame was increased by as little as .1 log units above that needed to make a single frame just visible. Thus, if threshold was determined to be 24 msec, the leading frame would be set to 48 msec and the trailing frame to
34 msec. The duration set in such a way allowed the 
matrices to be easily visible and more equivalently 
visible than in previous experiments assessing the 
relationship between age and visible persistence. The 
shorter trailing frame minimizes the disruptive effects 
of the trailing frame upon the visibility of the 
leading frame. Dixon and Di Lollo (1994) have shown 
that the duration of the trailing frame produces 
effects similar to that of the duration of the leading 
frame in that shorter durations increase the interval 
over which two frames can be integrated. Such effects 
have also been suggested by the psychophysical (Royer 
and Gilmore, 1985) and physiological studies of others 
(Phillips & Singer, 1974; Singer & Phillips, 1974). 
Pilot work with the stimuli used in this study showed 
that by keeping the duration of the trailing frame 
shorter than that of the leading frame increased the 
interval over which two frames could be reliably 
integrated.

Design

The design was a 2 x 2 mixed factorial design. 
The between-subject variable was Age (Young or Old). 
The within-subject variable was Spatial Frequency (Low 
and High). The Trials were blocked by spatial
frequency. For each subject order of spatial frequency was the same order as in Experiment 1.

Task

The psychophysical task involved the temporal integration of elements in two sequentially-presented 5x5 matrices which were separated by a brief interval (ISI). Elements in the first of the two frames occupied twelve randomly determined locations out of the 25 possible in the matrix. The second frame contained elements in 12 of 13 remaining locations. When the interval between presentations of the two matrices is sufficiently short, the two matrices appear as a single 5x5 matrix with 24 of the 25 elements filled leaving one location empty. At longer intervals the matrices appear as two temporally discrete arrays of randomly distributed elements from which it is difficult to determine the missing element. The task of the subject was to indicate which element of the central 3x3 elements was missing. A card containing a stylized version of the 5x5 matrix was placed just below the viewing screen. The card depicts the 5x5 matrix and the numbering system used for the central 9 elements. For the blocks of trials where ISI was 50 msec or less feedback was provided after each trial by
the experimenter who indicated whether the response was correct.

**Procedure**

Subjects were tested in one to two sessions each lasting approximately 45 to 60 minutes. No more than one session was conducted on any given day. They were seated at a distance of 69 cm from the fast video tachistoscope with their head position maintained with a chin rest. Mean luminance was the same as in Experiment 1, 10 cd/m2.

After a series of 20 practice trials set at 0, 10, or 20 msec ISI, the Critical ISI (CISI) was determined for each level of contrast tested. The Critical ISI is the longest interval over which the matrices can be integrated accurately and was determined in the following way: Testing began with a series of 30 trials over three ISIs (0, 10, 20 msec). Order of presentation for each ISI was random across those 30 trials (10 trials at each ISI). If accuracy was at least 70 percent for all three ISIs tested then testing continued. The next series tested contained a series of 30 trials with 10 trials for each of 3 ISIs, each incremented 10 msec above the other. If accuracy was less than 70 percent for any of the ISIs in the sequence, additional testing was conducted over the
same three ISIs. If the entire set of 20 trials had 70 percent or more correct a new series of three ISIs was tested. If accuracy was found to be below 70 percent for the set of 20 trials, testing was repeated on the set of ISIs that preceded the below chance performance. The critical ISI (CISI) became the next highest ISI where performance was accurate to at least 70 percent over 20 trials. The CISI is thus the longest ISI at which the matrices were integrated over a series of 20 trials with accuracy of at least 70 percent. A minimum of 20 trials was conducted before determining that any given ISI was the CISI.

The 70 percent accuracy cutoff was based on the binomial distribution for 20 trials when the probability of success of is .5. The binomial distribution describes the probability that a given number of successes occurs within a given number of trials. Based on the binomial distribution, a series of 20 trials with 14 correct trials will occur less than 5 percent of the time where the probability of success on any given trial is .5. The .5 probability of success was derived from testing subjects over ISIs ranging from 0 to 1000 msec. Accuracy was found to drop as ISI increased until a plateau was reached usually between 100-300 msec ISI. Asymptotic accuracy
ranged from 41 to 53 percent correct. Beyond 100 to 300 msec ISI, accuracy typically oscillated about the 50 percent correct point out to the maximum ISI tested of 1000 msec. The asymptotic accuracy observed is well above the 20 percent accuracy that would be expected for a random correct guess over the 5 empty cells in the center 3x3 matrix presented in the second frame. Shioiri and Cavanagh (1992) observed a similar plateau in performance in temporal integration and considered the plateau to be the end of visible persistence. They attributed the higher than chance asymptotic accuracy to other factors such as short term visual memory. The 70 percent accuracy cutoff point based on the binomial distribution for 20 trials used in the present study allows the C ISI to remain significantly above asymptotic accuracy.
Results

An Age (Young vs. Old) x Spatial Frequency (High vs. Low) analysis of variance (ANOVA) was carried out on the dependent measure, CISI. Mean CISIs for each condition are presented in Table 1.

Table 1. Experiment 2.

Mean CISI (msec) - Age by Spatial Frequency

<table>
<thead>
<tr>
<th>Group</th>
<th>Young</th>
<th>Elderly</th>
<th>Marginal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial Frequency</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>96.0 ± 4.8</td>
<td>72.0 ± 7.0</td>
<td>84.0 ± 5.9</td>
</tr>
<tr>
<td>High</td>
<td>93.0 ± 12.4</td>
<td>34.0 ± 14.3</td>
<td>63.5 ± 13.3</td>
</tr>
<tr>
<td>Marginal</td>
<td>94.5 ± 8.6</td>
<td>53.0 ± 10.6</td>
<td>73.7 ± 9.6</td>
</tr>
</tbody>
</table>

A main effect of age was found, $F(1,18)$, $MS_e = 1498$, $p < .01$. As can be seen from the mean CISIs in Table 1, young subjects integrated the matrices over longer intervals than elderly subjects. This result indicates that when visibility of stimuli are adjusted so that they are equivalently visible for young and elderly subjects, that the duration of the visual response is not longer in elderly subjects. Indeed, the result suggests that under the conditions tested,
young subjects appeared to have longer visible persistence.

There was a main effect of spatial frequency, $F(1,18) = 6.47$, $MS_e = 1498.06$, $p < .02$. However, that effect was moderated by an interaction with age $F(1,18) = 4.72$, $MS_e = 649.17$, $p < .05$. The mean CISI (Table 1) for high spatial frequency information for elderly subjects of 34 msec is much lower than for young subjects. Post hoc analyses conducted on the mean CISIs with the Tukey HSD (Honestly Significant Difference) test indicated that the difference in the mean CISI for low and high spatial frequency matrices was not significantly different for young subjects, Tukey HSD $(2,9) = 21.81$, $MS_e = 464.5$, $p > .05$ whereas it was for elderly subjects, Tukey HSD $(2,9) = 28.30$, $MS_e = 782$, $p < .05$. The CISI was not significantly shorter for elderly subjects as compared with young subjects in the low spatial frequency condition, Tukey HSD $(2,16) = 17.09$, $MS_e = 649.17$, $p > .05$. Young and elderly subjects were significantly different in the high spatial frequency condition, Tukey HSD $(2,16) = 39.08$, $MS_e = 782.0$, $p < .05$.

The significant difference between the young and elderly high spatial frequency visible persistence may be attributed at least in part to the differentially
greater reduction in sensitivity to high spatial frequency information exhibited by elderly subjects described in Experiment 1. The relatively lower sensitivity to high spatial frequency information for elderly subjects would mean that they would need differentially longer stimulus durations in order to make the high spatial frequency matrices just visible. The mean stimulus duration required by elderly subjects to see the high spatial frequency matrices was 146 msec (S.D. = 27 msec) as compared to 43 msec (S.D. = 18) required by young subjects to see the matrices with the 34 percent contrast used in this condition. While elderly subjects may require much longer durations to see the matrices, those longer durations may have the effect of differentially reducing high spatial frequency visible persistence for those subjects. There was not a significant difference between visible persistence between young and elderly subjects in the low spatial frequency condition and the difference between the duration for the young and elderly mean duration in the low spatial frequency condition are not so great. The mean matrix duration required for young subjects to see the images in the low spatial frequency condition was 9.6 msec (SD=0) as compared to 21 msec (SD=8) for elderly subjects. It seems reasonable to
consider that optical differences between young and elderly subjects may be at least in part accountable for the longer durations required by elderly subjects.

Thus, in this experiment the well established effect of spatial frequency was lost for the young subjects or reversed in direction in the elderly subjects. In addition, relationship between age and visible persistence was also reversed in direction. The difference between these results and those of others may be explained at least in part by the experimental manipulation which equated stimulus visibility. The relatively shorter visible persistence observed for elderly subjects in the high spatial frequency condition may be the result, at least in part, of optical factors. The results suggest that much or all the longer persistence attributed to age may be attributable to differences in temporal sensitivity between the two groups.
Experiment 3

Method

Subjects

The subjects were the same as in Experiment 1.

Stimuli

Stimuli were generated as in Experiment 1. Mean luminance was the same as in Experiment 1, 10 cd/m².

Stimulus duration was set to 29 msec for the leading frame, and 24 msec for the trailing frame. Stimulus duration was kept short to maximize persistence.

The results of Experiment 1 were used to establish the minimum level of contrast for each subject that allowed the matrices to be just visible. Because no young subject required more than 24 msec to see the matrices for the low spatial frequency condition under the lowest level of contrast available, that stimulus duration became a limiting factor. Stimulus duration of 29 msec was chosen because it allowed the matrices to be just visible for young subjects in the low spatial frequency condition after .1 log unit was added to the 24 msec required by the least sensitive young subject in Experiment 1. Because contrast could not be adjusted to less than five percent to compensate for the high temporal sensitivity of young subjects in the
low spatial frequency condition, persistence for young subjects could be expected to be markedly reduced if the stimulus duration used in this experiment was much longer than 24 msec.

The graph of individual data for one elderly and one young subject (Figure 4) are used in this description of how contrast level will be determined. In Figure 4, a line has been drawn horizontally across the page so that it corresponds to a stimulus duration of 24 msec. The contrast level that corresponds to the point where that line intersects the function for each subject is the lowest level of contrast that allows the subject to see the matrix correctly 100 percent of the time for a duration of 24 msec. Thus, for the low spatial frequency matrices, the minimum contrast level needed to allow the matrix to be visible for the young subject is 5 percent. For the elderly subject, the matrices are not visible until about 8 percent. For the high spatial frequency matrices the young subject needs about 25 percent contrast while the elderly requires about 40 percent. Only a limited range of contrast levels are available for the matrices. At the lower end of the range they consist of 5, 8, 12, 15, 19, 22, 26, 29, 32 and 35. The contrast level chosen for each subject would be the lowest level contrast
that allowed the matrices to be just visible for 24 msec. Thus, temporal sensitivity would be extrapolated from the graph of each subjects data, and then confirmed using the method from Experiment 1 to determine the lowest level of contrast that allows the high spatial frequency matrices to be visible for each subject for a stimulus duration of 24 msec.
Figure 4. The flow of orientation for two different age groups. Points below the line are not used.

- Circles: Young subject
- Squares: Elderly subject
- Empty Symbols: Low Spatial Frequency
- Filled Symbols: High Spatial Frequency
Design

The design was a 2 x 2 mixed factorial design. The between-subject variable was Age (Young or Old). The within-subject variable was Spatial Frequency (Low and High). The Trials were blocked by spatial frequency.

Task

The psychophysical task was the same as in Experiment 2.

Procedure

Subjects were tested in one to two sessions each lasting approximately 45 to 60 minutes. They were seated at a distance of 69 cm from the fast video tachistoscope with their head position maintained with a chin rest. After a series of 30 practice trials set at 0, 10, or 20 msec ISI, the Critical ISI (CISI) was determined in the same way as in Experiment 2.
Results

An Age (Young vs. Old) x Spatial Frequency (High vs. Low) analysis of variance (ANOVA) was carried out on the dependent measure, CISI. The mean CISIs are reported in Table 2.

Table 2. Experiment 3.
Mean CISI (msec) - Age by Spatial Frequency

<table>
<thead>
<tr>
<th>Group</th>
<th>Young</th>
<th>Elderly</th>
<th>Marginal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial Frequency</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>93.0 ± 5.4</td>
<td>58.0 ± 11.6</td>
<td>75.5 ± 8.5</td>
</tr>
<tr>
<td>High</td>
<td>113.0 ± 9.6</td>
<td>78.0 ± 13.4</td>
<td>95.5 ± 11.5</td>
</tr>
<tr>
<td>Marginal</td>
<td>103.0 ± 7.5</td>
<td>68.0 ± 12.5</td>
<td>85.5 ± 10.0</td>
</tr>
</tbody>
</table>

The analyses showed a main effect of age, $F(1,18) = 8.53, \text{MS}_e = 1435, p < .01$. But, as can be seen from the mean CISIs in Table 2, young subjects integrated over longer intervals than elderly subjects. This result is opposite in direction to that reported in previous experiments which measured visible persistence in young and elderly subjects. But the effect observed here, is consistent with the effect observed in
Experiment 2. In both cases, when visibility of the stimuli were equated across subjects, elderly subjects demonstrated less visible persistence than young subjects. A main effect was also found for spatial frequency, $F(1,18) = 6.37$, $MSE = 627.78$, $p < .01$. High spatial frequency CISIs were longer (95.5 msec) than were the low spatial frequency CISIs (75.5 msec). This result is consistent with previous studies which found longer visible persistence for high spatial frequency information.

A possible explanation for the relatively lower CISIs for the low spatial frequency matrices is the relatively limited levels of contrast available, particularly for the low spatial frequency matrices, reduced ability to equate contrast sensitivity for the two spatial frequency conditions tested. In particular, as can be seen in the graph of the data (Figure 4), all young subjects were easily able to see the low spatial frequency matrices for the lowest level of contrast available (5.2 percent) for a duration of 24 msec. The failure to be able to adjust contrast closer to the sensitivity of most of the young subjects would have the effect of reducing the CISI for these subjects in the low spatial frequency condition. While all young subjects were tested with a mean contrast of
5.2 percent (SD=0), the mean contrast of 31 percent (SD=8) used to test the high spatial frequency matrices was more variable in line with the variability in the young subjects high spatial frequency sensitivity.

Elderly subjects were tested with a mean contrast level of 31 percent (SD=8) for the low spatial frequency matrices and for the high spatial frequency matrices mean contrast was 68 percent (SD=7).

Despite the failure to equate low and high spatial frequency visible persistence, the magnitude of the effect of spatial frequency in this experiment is reduced relative to that observed in other studies where high spatial frequency persistence is often more than 100 msec longer than that observed for low spatial frequency persistence.

In any case, the relationship between age and visible persistence found in this experiment is the reverse of that reported by others where contrast sensitivity was not equated between young and elderly subjects.
Experiment 4

Estimating the duration of the visual response, i.e., visible persistence, with contrast and duration set to a constant value has been found to produce longer visible persistence for high than for low spatial frequency information (Bowling et al., 1980; Kline et al., 1990; Meyer and Maguire, 1977). In addition, the results of the study by Kline et al., 1990 suggested that elderly subjects have longer visible persistence than young subjects but only for low spatial frequency information. Those results were expected to be replicated in Experiment 4 of the present research.

In Experiment 4, visible persistence was estimated with contrast and duration of the stimulus set to the mean duration required by elderly subjects for the high spatial frequency matrices in the 34 percent contrast condition, 97 msec. It was expected that the interval over which the matrices can be integrated would be influenced by the visibility of the stimuli related to spatial frequency information and age. Thus, elderly subjects, who demonstrated reduced temporal sensitivity in Experiment 1 as compared to young subjects are expected to have longer CISIs than young subjects. In addition, high spatial frequency information should be
associated with longer CISIs for both young and elderly subjects. The differentially lower temporal sensitivity exhibited by elderly subjects in response to the low spatial frequency matrices could be expected to result in relatively longer visible persistence for elderly subjects for the low spatial frequency matrices as compared to young subjects.
Method

Subjects

The subjects were the same as in Experiment 1.

Stimuli

Stimuli were generated as in Experiment 1. Mean luminance was the same as in Experiment 1, 10 cd/m². The contrast level was set to 34 percent, the same as in Experiment 2. Stimulus duration of the leading frame was set to 100 msec, while the trailing frame was set to 72 msec. These values represent approximately the mean stimulus duration of the elderly subjects in the high spatial frequency condition plus .15 log units.

Design

The design was a 2 x 2 mixed factorial design. The between-subject variable was Age (Young or Old). The within-subject variable is Spatial Frequency (Low and High). The Trials were blocked by spatial frequency.

Task

The psychophysical task was the same as in Experiment 2.
Procedure

Subjects were tested in one to two sessions each lasting approximately 45 to 60 minutes. The procedure was the same as that in Experiment 2.
Results

An Age (Young vs. Old) x Spatial Frequency (High vs. Low) analysis of variance (ANOVA) was carried out on the dependent measure, C ISI. There was a main effect of age, $F(1,18) = 10.93$, $MSe = 667.22$, $p < .01$.

Table 3 contains the mean CISIs for the separate conditions of this experiment. The mean C ISI of 38.5 for elderly subjects was significantly greater than the mean C ISI of 11.5 that found for young subjects.

There was also a main effect for spatial frequency condition, $F(1,18) = 21.81$, $MSe = 469.44$, $p < .001$. This effect was expected based on the results of others.

The direction of this effect was the same as has been reported in other studies where stimulus visibility was not equated across subjects. That is, young subjects have less visible persistence than elderly subjects and low spatial frequency visible persistence is lower than high spatial frequency visible persistence.
Table 3. Experiment 4.

Mean CISI (msec) - Age by Spatial Frequency

<table>
<thead>
<tr>
<th>Group</th>
<th>Young</th>
<th>Elderly</th>
<th>Marginal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial Frequency</td>
<td>6.0 ± 3.1</td>
<td>12.0 ± 2.9</td>
<td>9.0 ± 2.9</td>
</tr>
<tr>
<td>Low</td>
<td>17.0 ± 4.2</td>
<td>65.0 ± 13.4</td>
<td>41.0 ± 8.8</td>
</tr>
<tr>
<td>High</td>
<td>11.5 ± 3.6</td>
<td>38.5 ± 8.1</td>
<td>25.0 ± 5.8</td>
</tr>
</tbody>
</table>

There was also an age by spatial frequency interaction, $F(1,18) = 9.39$, $\text{MSE} = 469.44$, $p < .01$. Post hoc analyses of mean scores indicated that elderly subjects had longer CISIs in the high spatial frequency condition, Tukey HSD(2,16) = 14.53, $\text{MSE} = 469.44$, $p < .01$ but not in the low spatial frequency condition. Young subjects had longer CISIs in the high spatial frequency condition as compared to their low spatial frequency CISI, Tukey HSD(2,9) = 8.42, $\text{MSE} = 69.33$, $p < .05$. Elderly adults also demonstrated a longer CISI in the high as compared to low spatial condition, Tukey HSD(2,9) = 42.6, $\text{MSE} = 856.1$, $p < .01$. 
All of the significant effects obtained in Experiment 4 have consistently been reported by others. The results of this experiment indicate that the method and stimuli produced results expected based on the work of others regarding the effects of age and spatial frequency on visible persistence when stimulus visibility is not adjusted to account for sensitivity differences.

These results strengthen the conclusion that the loss or reversal of the direction of the effect of age and/or spatial frequency observed in Experiments 2 and 3 of this study can be attributed to the experimental manipulations.

Equating the visibility of the stimuli across subjects and spatial frequency to estimate visible persistence as in experiments 2 and 3 of this study appeared to have the effect of reversing or eliminating the effect of age and age effects related to spatial frequency that have been previously reported by others.

The possibility that an age by spatial frequency effect would be found in this study was suggested by the results of Kline et al., 1990, with greater differences expected between the young and elderly subjects for the low as compared to the high spatial frequency condition. Although the results from
Experiment 1 indicate reduced low spatial frequency temporal sensitivity for elderly subjects, those differences did not translate to differential low spatial frequency response persistence for elderly subjects in Experiment 4. No other studies have examined visible persistence differences across the spatial frequency domain as a function of age. However, the type of stimuli used to examine age-related differences in visible persistence in other studies such as that by Di Lollo et al. (1982) would best be described as containing a substantial high spatial frequency component. Those results would generally be in agreement with the results of Experiment 4 of this study and inconsistent with those reported by Kline et al. who found that elderly subjects exhibited increased persistence only in response to low but not high spatial frequencies when compared with young subjects.
Summary of Results

This study examined age effects in visible persistence. Low and high spatial frequency information was used to test transient and sustained channel functioning, respectively. The results of Experiment 1 showed that elderly subjects exhibit reduced temporal sensitivity to both low and high spatial frequency information, with greater age differences observed for the high spatial frequency condition. While the high spatial frequency deficit in sensitivity can be attributed in part to optical effects, optical degradation has less impact on low spatial frequency information. Thus, optical factors do not explain the temporal sensitivity deficit of elderly subjects to low spatial frequency information. Because low spatial frequency processing is less impacted by optical factors, it provides a more direct measure of neural processing that begins with retinal ganglion cells and continues on through the LGN to the visual cortex. The results found in Experiment 1 would be consistent, perhaps, with the idea that the rate of change with age of the neural processes that subserve the sustained and transient channels is equivalent, but the greater deficit found for sustained channel processing in this and other psychophysical studies
reflect the additional effects on the sustained channel from optical degradation.

Experiments 2, 3 and 4 explored the possibility that longer visible persistence frequently exhibited by elderly adults could be accounted for by the reduction in temporal and/or contrast sensitivity experienced by elderly subjects. The results of the three experiments indicate that when contrast or temporal sensitivity differences between young and elderly subjects were reduced or eliminated, typical age effects were either absent or reversed in direction with young subjects even exhibiting longer visible persistence.

The failure to obtain longer persistence for elderly adults in Experiments 2 and 3 suggests that previously reported differences in persistence and those suggesting specifically a differential transient channel deficit (e.g., Kline et al., 1990) related to age, as well as those found in Experiment 4 of this study, were the result of age differences in temporal sensitivity or contrast sensitivity or both. Lower contrast and/or temporal sensitivity associated with increased age would result in less complete temporal summation and hence slower temporal processing. Thus, the results of these experiments suggest that longer visible persistence that has been reported for elderly
adults can be attributed in large degree to age related differences in contrast and/or temporal sensitivity.

The loss or reduction of the effect of spatial frequency on visible persistence for young adults in Experiment 2 provides some evidence in support of Marx and May (1983), that the longer persistence associated with high spatial frequency information is not the result of differences between high and low spatial frequency integration mechanisms. Such a notion would have been strengthened by a similar result in Experiment 3, but the failure to eliminate the spatial frequency effect in Experiment 3 may be attributed to a reduction in the ability to test with contrast levels more precisely set to the individual threshold levels.

Conclusion

Individual differences in visible persistence are frequently reported as being related to age (as well as other variables such as dyslexia, and intelligence). This study examined the independence of age-related visible persistence effects from those age effects related to contrast and temporal sensitivity. Because there is strong evidence that independent systems subserve the visual processing of low and high spatial frequency information, both low and high spatial frequency information was considered. The results
showed that when temporal sensitivity differences were reduced or eliminated, elderly adults failed to exhibit longer visible persistence than young adults. This result also obtained when contrast sensitivity differences were minimized. Because the same procedure, with the same stimuli, produced longer persistence for elderly adults in Experiment 3 when sensitivity was not equalized, the magnitude of persistence appears to reflect the degree of temporal summation in the same way that contrast or temporal sensitivity represents the degree of temporal summation. That is, if one has a measure of sensitivity, no new information appears to be gained in determining visible persistence. Thus, the results of these experiments are in agreement with the notion that visible persistence represents the degree of temporal summation.

The results of Experiment 1 indicate that elderly subjects experience a reduction in temporal sensitivity for both transient and sustained processing with a larger reduction for sustained channel processing. It is possible that the greater sustained channel deficit reflects the differential impact that optical degradation has on high spatial frequency information as compared to low.
Future Research

The present study was conducted under low photopic mean luminance. Further research is needed to examine the impact of higher luminance levels. Luminance level influences the rate of temporal integration. It is possible that increases in mean luminance would have a differential effect on the gain in sensitivity for the sustained as compared to the transient channel particularly for elderly subjects. It is possible, however, that young subjects would benefit more than elderly, and moreso for low spatial frequency information, by increases in luminance. That possibility is based on the finding by Sloane et al. (1988) that on measures of contrast sensitivity, young subjects exhibited a differentially greater increase in sensitivity as mean luminance increased, but only for flickered and not static gratings.

The results of the present research showed that presenting stimuli near threshold levels allowed strong individual differences to emerge. While there are strong differences even for low spatial frequency stimuli, near threshold temporal differences between young and elderly subjects, for the low spatial frequency stimuli were, in absolute terms, very small. For the 22 percent contrast condition in Experiment 1, the mean difference between young and elderly subjects
in the time needed to accurately identify the missing element in the 5x5 matrix Experiment 1, was only 11 msec. Under 62 percent contrast, all young subjects were 100 percent accurate with a stimulus duration of 2.4 msec, while elderly took on the average, only 4.5 msec longer. The average age difference for the high spatial frequency matrices under 22 percent contrast was 100 msec while under 62 percent contrast the difference was only 17 msec. What that suggests is that in order for investigators to be able to capture spatial frequency related individual differences, very high temporal resolution is needed. Even then, it is important to use low levels of contrast.
References


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