Orientation Discrimination Across the Visual Field: Size-Scaling Estimates are Contrast-Dependent

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ABSTRACT

Orientation discrimination across the visual field: Size-scaling estimates are contrast-dependent

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Performance in many visual tasks depends on visual field location and generally declines with increasing retinal eccentricity. The expression [$F=1+E/E_2$] represents a theory of how one may compensate for eccentricity-dependent variations in sensitivity by appropriate scaling (F) of the stimuli at each eccentricity. E_2 indicates the eccentricity (E) at which the size of the stimulus must be doubled, relative to the foveal standard, to achieve equivalent performance. The parameter E_2 is considered to reflect changes in the spatial scale of mechanisms that subserve task performance. Unfortunately, E_2s tend to vary widely, even for the same task. The present experiments have addressed this issue using orientation discrimination. These findings suggest that considerably heterogeneity of size-scaling E_2s results from uncontrolled variations in perceptual contrast. Initial experiments indicated that the commonly used spatial-scaling technique of presenting stimuli at a fixed high level of contrast can result in inflated E_2s. A method of controlling for perceptual contrast at high levels of stimulus contrast was therefore introduced. E_2s recovered under these conditions were in the range of 1.29° to 1.83° (Sally & Gurnsey, 2003a). These estimates are in line with those of the classic spatial-scaling study on orientation discrimination of Mäkelä, Whitaker and Rovamo (1993) conducted at high contrasts. The E_2 for orientation discrimination was then determined using

two methods (Melmoth, Kukkonen, Mäkelä & Rovamo , 2000a,b and Poirier & Gurnsey, 2002) that provide estimates of size- and contrast-scaling at near-threshold levels of stimulus contrast. Size-scaling E_2s were reasonably consistent across methods and were substantially larger than those obtained at high stimulus contrasts, ranging from 3.71° to 6.86°. The high-contrast experiment (Sally & Gurnsey, 2003a) was then replicated at low levels of stimulus contrast; perceptual contrasts were equated through a matching procedure. Size-scaling E_2s were again large: 3.42° and 3.50°. In concludion, E_2s for orientation discrimination depend critically on stimulus contrast and are small at high contrasts and large at low contrasts. This may be due to dynamic changes in the spatial structure of orientation selective mechanisms at low stimulus contrasts.

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I designed all of the experiments in collaboration with my supervisor Dr. Rick Gurnsey. The internal thesis committee composed of Dr. Michael von Grünau, Dr. Olga Overbury and Dr. Rick Gurnsey provided guidance concerning the direction and focus of the project. I co-developed the software for testing along with Dr. Gurnsey. I performed all psychophysical tests and data analyses. Fred Poirier helped with technical direction for the manuscript for which he is coauthor and provided comments on an earlier draft of the paper. I wrote all manuscripts and Dr. Gurnsey provided comments and editing.

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CHAPTER 1

THESIS INTRODUCTION

Eccentricity-dependent limitations on visual perception

Performance on many spatial vision tasks declines as a stimulus of a fixed size is moved into the visual periphery (e.g., Rovamo & Virsu, 1979; Weymouth, 1958). Over the last 30 years or so there has been a tremendous amount of interest in relating the rate of decline in visual performance on various tasks to anatomical and physiological limitations. The main goals of this introduction are to bring together anatomical, physiological and psychophysical findings in the area of peripheral pattern perception and to explore the factors that limit performance on various spatial vision tasks. To achieve this end, it is of course necessary to discuss the factors that constrain pattern perception throughout the visual field.

Information contained in a real-world scene is processed by means that allow some attributes to be easily detectable (e.g., lines, contours) but it also sets certain limits on what can be perceived. For example, under certain conditions it may be difficult to discern the orientation of a sinusoidal grating stimulus though one can easily detect its presence (Thibos, Cheney & Walsh, 1987a). The characteristics of visual processing, specifically, spatial filtering and spatial sampling set limits on what is perceived. These concepts are borrowed from systems theory and have proven very useful in understanding the way in which the visual system represents spatial information.

The receptive fields of neurons can be described as *spatial filters* "whose momentary output is the weighted sum of the light intensities falling at different points in the field"(Fiorentini, Baumgartner, Magnussen, Shiller & Thomas, 1990,

p. 152). Equivalently, receptive fields can be considered in the Fourier or frequency domain as sensitivity to sine or cosine gratings as a function of spatial frequency, orientation, phase and amplitude or contrast.

Sampling is described in systems theory as the number of samples per spatial unit. Collections of cells at various levels of the visual system form neural arrays and the number, size and spacing of individual elements determine their ability to accurately represent spatial information. Sampling or Nyquist theory states that a two-dimensional array of uniformly spaced elements can exactly represent any sinusoidal grating for which there are at least two spatial samples per cycle. More formally,

$$\omega_N = 1/2\Delta x \qquad [1.1]$$

where ω_N is the Nyquist frequency, and Δx is the spacing between samples. Thus, all spatial frequencies up to this limit can be accurately encoded by the visual system.

This introduction is concerned with the way in which information contained in a visual scene is sampled and filtered. These processes allow the visual system to break down a visual scene into basic elements and set limits on how this information can be represented. Certain image attributes appear to be fundamental to visual processing. Fourier analysis tells us that any real visual image is equivalent to a sum of sinusoidal grating patterns of various spatial frequencies, orientations, contrasts and spatial phases (Bracewell, 1965). Although the visual system does not appear to perform exactly such an analysis, the data are in agreement with Robson's (1975) suggestion that Fourier amplitude spectra are calculated on a patch-by-patch basis (i.e., over small patches of the visual field). Particular attention will be paid to the way in which information regarding orientation is handled by the visual system because the

research of this thesis relies heavily on an understanding of this process. Other aspects of visual processing such as binocularity, motion and depth have been purposely avoided.

The present discussion focuses on the potential anatomical and physiological limitations on visual performance of spatial discrimination tasks imposed by the visual system. Consideration will also be given to various psychophysical procedures that have been used to infer something of the neural mechanisms that govern performance on particular tasks.

In a discussion of peripheral visual mechanisms it is often important to express changes in processing resources as a function of retinal eccentricity. This may refer to such measures as cell numbers, surface area or linear extent or nuclear volume. Very often these anatomical changes can be, to a first approximation, captured with a simple hyperbolic function of the form

$$y = k(a + E)^{-x} \qquad [1.2]$$

where k expresses the number of cells, for example, when eccentricity (E) =0, x gives the rate at which the function declines and a is a constant. A function specified in this way has an inverse linear form when $x = 1$. Thus, the slope and intercept ($1/k$) will completely describe this inverse function. This information is commonly presented by normalizing all data to a foveal value of unity. The rate of change of this function can then be described with a single parameter, referred to as E_2 - the eccentricity at which the foveal value changes by a factor of two (Levi, Aitesboamo & Klein, 1984). In the nonnormalized case, E_2 is simply the intercept divided by the slope.

Optics of the eye

In forming the representation of a real-world scene an image is projected onto the retina at the back of the eye. The first stage of processing is limited by

optical blur as well as the density and regularity of the photoreceptor mosaic. The sampling aperture of individual cones can set limits on performance as well.

The optical quality of the eye has been measured for a range of pupil sizes using physical and physiological methods. Physical studies of the eyes' optics involve examining the nature of the fundus reflection from the bright image of a thin line or point source. These source images are Fourier analyzed to provide modulation transfer functions (MTF). Campbell and Gubish (1966) calculated that, under ideal conditions, the contrast transmission of a sine wave image of about 50 to 60 cycles per degree (cpd) for three subjects would be close to zero. This sets the limit of detection at about this value at the fovea. This finding has been verified in a more recent study using similar methods by Navarro, Artal and Williams (1993).

Campbell and Green (1965) used psychophysical techniques to examine the role of optical and neural factors in contrast sensitivity for grating targets. They determined the contrast sensitivity for 1) a sine wave pattern displayed on an oscilloscope and 2) interference fringes formed directly on the retina by imaging two coherent points of light derived from the beam of a single laser. The spatial frequency of the interference gratings was varied by changing the separation of the points of light and contrast was varied by superimposing a uniform wash of light. By finding the ratio between the contrast sensitivity measured by the two techniques, the contrast reduction due to the optics of the eye was calculated. Although the resulting transfer function did not reflect scattering of light by the media of the eye, it corresponded well with the transfer function that Campbell and Gubish (1966) obtained by ophthalmoscopic measures. The results indicated that the ocular media can transmit spatial frequencies up to 60 cpd. Thus, 50 to 60 cpd can be considered the limit imposed

by the optics of the eye.

Off-axis optical quality was examined by Jennings and Charman (1981) using physical measures. The authors reported that image quality (amount of spread) changes very little within the central 20 degrees. In a more recent study, Navarro et al. (1993) confirmed this observation and reported that the decline in optical quality is even slower than that reported previously. They reported that image quality decays only very slowly to ± 20°, becomes progressively worse from 20° to 50° and in the far periphery (60°) optical quality can be considered poor. The MTF at 0°, 5° and 20° showed a reasonably similar rate of monotonic decline with increasing spatial frequency (see Navarro et al., 1993, Figure 9). By 50° to 60° the data show a dramatic decline in transferred contrast with increasing frequency such that at 60° transmission of contrast for spatial frequencies of 20 cpd or higher is close to zero. Taken together, these studies indicate that the optics of the eye will not limit peripheral pattern discrimination to an appreciable extent within the central 20° of the visual field and that it is the higher spatial frequencies that will be most attenuated with increasing retinal eccentricity.

Cones and retinal ganglion cells

Cone density as well as the size of the individual cones also play a role in limiting pattern discrimination. The foveal cones comprise a regular matrix which is an almost perfect hexagonal mosaic (Hirsch & Hylton, 1984). Cone spacing has been calculated for various eccentricities for a human retina (Hirsch & Curcio, 1989) and that of a primate (Hirsch & Miller, 1987). Human foveal cone spacing is sufficiently dense to transmit spatial frequencies up to the Nyquist limit for the optics of the eye. Thus, the optical and cone limits coincide. In the periphery, however, the cone Nyquist frequency decreases rapidly because of a

very rapid decline in cone spacing (Curcio, Sloan, Packer, Hendrickson & Kalina, 1987), while the optical transfer function remains relatively unchanged throughout a wide visual field (20 to 30°, Navarro et al., 1993). As a result of this mismatch between cone and optical limits in the periphery, grating frequencies higher than the Nyquist limit are imaged on the peripheral retina yet cannot be transmitted by the cones without distortion. This distortion is referred to as spatial aliasing. Frequencies above the Nyquist limit appear as distorted gratings of a lower frequency. Several researchers have confirmed that spatial aliasing occurs in peripheral vision (Coletta & Williams, 1987; Smith & Cass, 1987; Thibos et al. 1987a). Spatial aliasing is, however, attenuated by the increased irregularity in the peripheral cone matrix (Yellot, 1982, 1984).

Spatial aliasing does not normally occur in the fovea because of the match between optical and cone limitations, but this phenomenon can occur in the fovea if blurring by the optics is eliminated through the use of laser interference fringes (Williams, 1985a, 1985b, 1986). In fact, spatial aliasing has been used to provide a psychophysical estimate of foveal cone spacing. Cone spacing is the determinant of the foveal Nyquist frequency, and this is calculated by determining the lowest spatial frequency at which aliasing is first perceived (Williams, 1985a). Foveal cone spacing determined in this manner is about 35 sec arc - a figure that agrees well with anatomical data (Hirsch & Curcio, 1989, mean = 31.6 sec arc).

Research conducted by Thibos et al. (1987a) suggests that pattern resolution is related to cone and retinal ganglion cell sampling, whereas pattern detection is limited by the size of individual cone cells. Their stimuli consisted of high-contrast sinusoidal gratings that were produced directly on the retina as interference fringes. Visual stimuli were placed at eccentricities of 0° to 35° along

the nasal horizontal meridian for three subjects. Gratings had a circular aperture of constant size (3.5°) for all eccentricities and were presented at various randomly selected orientations (horizontal or vertical, left or right oblique). For the resolution task, the subject had to reduce the grating's spatial frequency until the stimulus orientation could be just identified. To determine detection thresholds, subjects had to reduce the spatial frequency of the stimulus until spatial contrast was just evident.

The results of this study indicated a different rate of decline in performance with eccentricity for the two types of task. The threshold value for detection declined at a much slower rate than that associated with resolution. Best-fitting linear regression lines through their data (Thibos et al., 1987a; Figures 2 and 3) showed a fairly linear increase in the minimum angle of detection and resolution (half-period of the mean maximum detectable and resolvable spatial frequency, respectively) with increasing eccentricity. The foveal value doubled at about 2 to 3° for the grating resolution task and at more than 10° for the grating detection task. Thibos et al. compared these data with anatomy and physiology for the retina and showed that the minimal angle of resolution changes at a rate proportional to that associated with the sampling density of a type of retinal ganglion cell referred to as P_β (data from Perry, Oehler & Cowey, 1984), whereas the minimal angle of detection changes at a rate corresponding to the size of individual cones (data from Polyak, 1941 - cited in Thibos et al.). To conclude, peripheral pattern detection and resolution of grating stimuli appear to have different rates of performance decline and these changes can be related to the underlying neural physiology.

Classes of ganglion cells

There are two primary classes of retinal ganglion cell based on anatomical

(morphological) and electrophysiological criteria. Morphological criteria divide cells into P_α and P_β classes. P_β cells project to the parvocellular layers of the lateral geniculate nucleus (LGN), the P_α cells project to the magnocellular division of this nucleus (Perry et al, 1984). The two types of cells have a circular, centre-surround configuration (centre-surround antagonism) and, as such, are not sensitive to stimulus orientation. Both classes of cells have a wide range of centre diameters. The size of the centre diameter will, for the most part, determine the spatial frequency to which a neuron is most responsive. In any region that represents one particular area of visual space, there are receptive fields of different sizes. However, in general, the P_α cells are larger (and therefore more sensitive to lower spatial frequencies) and also have bigger axons. Early on, Fischer (1973) pointed out that the overall density of ganglion cells in each region of the cat's retina is inversely related to the average area of the receptive field centres in that region. This means that as ganglion density decreases there is a corresponding increase in the size of receptive fields.

Although cells in the retina can be distinguished in terms of morphological criteria, in early investigations, retinal cells were classified on the basis of their physiological response to visual stimulation. Kuffler (1953) first classified the cells in the cat retina into on- and off-centre types, referring to whether cells are excited or inhibited in response to visual stimulation. A further distinction was made by Enroth-Cugall and Robson (1966) who noted that the concentrically organized cells in the retina of the cat could be divided into two groups on the basis of the extent to which they displayed linear spatial summation over their receptive fields. They examined the responses of cells to stationary, drifting sinusoidal gratings and contrast edge stimuli and noted that X cells displayed the more linear behavior. This type of cell responded with a

periodic modulated discharge in tandem with the sinusoidal drift frequency. X cells also showed more sustained and less transient responses to step changes in the luminance of a spot stimulus in the centre of their receptive field. The Y cell type tended to respond to drifting sine wave gratings with an overall increase in response which was independent of the relative phase of the grating. These cells also typically displayed more transient responses. X- and Y-type cells have been identified with P_β and P_α morphological types, respectively (Boycott & Wässle, 1974; Cleland, Levick & Wässle, 1975).

Lateral geniculate nucleus

The LGN is organized into various layers. The LGN consists of six layers and each receives input from one eye. Layers 1 and 2 receive input from the P_α ganglion cells and are referred to as magnocellular layers, whereas layers 3, 4, 5 and 6 receive input from the P_β cells and are called the parvocellular layers. The LGN is retinotopic - cells in proximity at the retina are similarly positioned at the LGN. Cells representing different parts of visual space are represented in register in the layers of the LGN, yet there is no communication between cells in different layers. The receptive fields of LGN neurons have the same centre-surround configuration as those of retinal ganglion cells. They also respond to stimuli in a similar manner, and can be classified into the same X and Y (sustained and transient) types (Hubel & Wiesel, 1966). The vast majority of the parvocellular (P) cells are X-like, but magnocellular (M) cells may be X- or Y-like when tests of linearity of spatial summation are applied (Shapley, Kaplan & Soodak, 1981; Shapley & Kaplan, 1982). Shapley and Kaplan (1982) have shown that there are actually two distinct populations of X cells in the LGN. The X cells of the magnocellular divisions can be distinguished from those of the parvocellular layers by their much higher peak contrast sensitivity.

Cells of the magnocellular and parvocellular layers appear to mediate very different visual functions. P neurons have relatively small receptive fields, slow axonal conduction velocities and color-opponent responses (e.g., Hicks, Lee & Vidyasager, 1983; Kaplan & Shapley, 1982; Schiller & Malpeli, 1978). These characteristics suggest that cells of the P pathway may be specialized for color vision and visual acuity. Cells of the M layers have larger receptive fields, faster conduction velocities, show broadband luminance responses and higher contrast sensitivity (e.g., Hicks et al., 1983; Kaplan & Shapley, 1982; Schiller & Malpeli, 1978). These cells respond best to stimuli of higher temporal frequencies than those of the P pathway. They respond rapidly to stimuli and the response decays quickly even when the stimulus is maintained (Derrington & Lennie, 1984). These characteristics suggest cells of the M-pathway may be specialized for temporal resolution (i.e., the detection of fast moving objects) and the detection of low-luminance and low-contrast stimuli.

Direct evidence for the functional specialization of the M and P pathways has been provided by Merigan and Eskin (1986) and Merigan (1989). Through systemic administration of a neurotoxin acrylamide, they induced the selective loss of P_β retinal ganglion cells. They found that treated monkeys had normal sensitivity for stimuli of high temporal, low spatial frequency. Color vision was, however, severely disrupted and achromatic contrast sensitivity was greatly reduced, particularly at high spatial and low temporal frequencies. One rather unexpected finding was that contrast thresholds were elevated substantially at all spatial frequencies when measurements were made with both stationary and counterphase modulated gratings at the lowest rate of temporal modulation (0.5 Hz). This is surprising because the contrast sensitivity of cells of the M pathway is 7- to 20-fold lower than those of the P-pathway (Hawkin & Parker, 1984).

Merigan and Eskin suggested that probability summation (Watson, 1979) accounts for the greater sensitivity of the P pathway than that expected on the basis of single neuron responses. (Recall that P_β cells make up 90% of retinal ganglion cells.) Their results support the view that the two pathways are specialized for processing different types of visual input. This does not of course imply that the M-pathway has no involvement in the discrimination of form, and that the P-pathway plays no role in the detection of motion.

Mapping of the LGN

The first complete map of the visual representation in the LGN of the macaque was constructed by Malpeli and Baker (1975) using microelectrode recording techniques. They located the centre of receptive fields with small spots of light, a technique generally used for this purpose, and marked neural positions along electrode tracks using electrolytic lesions. Malpeli and Baker specified visual direction in terms of elevation and azimuth on illustrations of histological sections through the LGN. They did not, however, analyze their data in relation to the organization of individual layers. They calculated magnification factors which they defined as LGN volume per degree of visual angle and listed these values in tabular form (see Table 1, Malpeli & Baker, 1975). (An E_2 value cannot be easily calculated from these data because they are highly nonlinear.) Their data were subsequently used by Connolly and Van Essen (1984) who constructed two-dimensional maps of individual layers of the LGN in the monkey and compared the cell densities as a function of eccentricity for the parvocellular and magnocellular layers of the LGN.

Connolly and Van Essen (1984) reported that the parvocellular division of the nucleus has a more greatly expanded representation of the central visual field and a steeper decline in cell density (cells per deg^2) with increasing eccentricity.

The variation in cell density with eccentricity is referred to as cellular magnification (M_C). The best-fitting equations to represent the relationship between M_C and eccentricity for eccentricities near the fovea ($E < 2.5°$) were given as

$$M_CP = 8.37(1.28 + E)^{-1.96} \times 10^4 \quad [1.3]$$

$$M_CM = 3.52(3.1 + E)^{-1.56} \times 10^3 \quad [1.4]$$

Because these are areal measures, E_2 is derived from the inverse square root of the functions. The equations yield E_2s for linear cellular magnification of 1.13° and 4.44° for the parvocellular and magnocellular divisions, respectively. For eccentricities greater than 2.5°, data were fit with power functions (see Equation 1.5). The equations were identical to those Equations 1.3 and 1.4 except that they did not contain the additive constants; these serve to slow the rate of decline near the fovea.

$$M_CP = 8.37(E)^{-1.96} \times 10^4 \quad [1.5]$$

These equations become undefined at $E = 0°$, so an E_2 cannot be calculated. The two sets of functions do, however, yield comparable estimates of cellular magnification at greater eccentricities than about 5°.

Striate cortex

Striate cortex contains a single, retinotopic representation of the visual field (Van Essen, Connolly & Maunsell, 1984). The cells of this region are like those of the LGN in that they have excitatory and inhibitory subregions. However, instead of being arranged concentrically, the antagonistic regions form parallel strips that may be several times as long as they are wide. The cells are, therefore, selective for orientation.

Hubel and Wiesel (1962, 1968) classified the cells in the striate cortex of the cat and monkey using electrophysiological recording techniques and described cells as falling into three categories: simple, complex and hypercomplex. Simple cells respond strongly when a stationary stimulus such as a bar is presented within the excitatory region of the cell. Complex cells respond weakly or not at all to stationary stimuli. These cells do, however, respond well to moving bars and edges that are correctly oriented. Many of these cells are direction-specific - their response may be much greater to a stimulus moving in one direction than the same stimulus moving in the opposite direction. The response of most cortical cells to a moving bar or edge stimulus increases as stimulus length is increased up to some limit. Beyond this value, increases in stimulus length result in no further changes to the neuron's response. There are, however, some neurons that show response reduction or suppression when the stimulus exceeds a certain length. Because cells that exhibited this type of response otherwise behaved like the complex cells in their studies, Hubel and Wiesel classified these cells as hypercomplex. Later studies have, however, found that cells that show this defining characteristic respond in other respects like simple cells (Dreher, 1972). For this reason, this class of cells is currently referred to as end-stopped.

The next few sections are concerned with the way in which striate neurons encode spatial frequency, orientation, contrast and phase information. For comparative purposes, responses of neurons at lower visual levels to these stimulus attributes are considered as well.

Spatial frequency selectivity

Spatial frequency selectivity becomes progressively more narrow from the retina to striate cortex. This arises because the low-frequency decline in sensitivity of individual neurons tends become to steeper (Cooper & Robson,

1968; Maffei & Fiorentini, 1973; DeValois, Albrecht & Thorell 1982a). DeValois and colleagues (1982a) have reported that the spatial frequency bandwidth (full width at one-half of peak sensitivity) of striate neurons in the macaque averages about 1.4 octaves and that bandwidth tends to become narrower with increasing spatial frequency. Wilson, McFarlane and Phillips (1983) have observed a very similar result in humans using a psychophysical masking technique. They tested spatial frequency selectivity using stimuli that were localized in space with a one octave frequency bandwidth. Test stimuli ranging from 0.25 to 22.0 cpd were added to cosine masks of a slightly different orientation. For each test frequency, contrast thresholds were measured as a function of the spatial frequency of the masks. The resulting threshold elevation curves fell into six distinct groups. These data suggested that the fovea contains a small number of spatial frequency mechanisms with peak frequencies from 0.8 cpd to 16 cpd and bandwidths ranging from 2.5 octaves at low frequencies to 1.25 octaves at the highest frequency.

Orientation selectivity

Selectivity to orientation is first apparent at the level of the striate cortex. The average orientation bandwidth of cortical cells varies from about ± 15 to 30° at half amplitude in the macaque (DeValois, Yund & Hepler, 1982b). Higher frequency cells tend to have a smaller bandwidth and are, therefore, more sensitive to stimulus orientation. Phillips and Wilson (1984) have examined orientation selectivity of human visual mechanisms and have obtained comparable results. They measured orientation tuning curves at 10 spatial frequencies ranging from 0.5 to 11.3 cpd. The stimuli were spatially localized patterns added to cosine grating masks. Orientation-masking data for a test stimulus of a given peak frequency were obtained by measuring contrast

thresholds of the test as a function of the orientation of a grating mask of the same spatial frequency. They reported that bandwidths decreased somewhat with increasing spatial frequency from about 30° at 0.5 cpd to 15° at 11.3 cpd .

The orientation-selective cells at cortex are organized into columns or sheets that are oriented perpendicular to the surface. The cells in each column have the same preferred orientation. This columnar arrangement of orientation-selective cells is superimposed on a more coarse local grouping according to ocular dominance - which of the eyes provides the greatest excitatory input. Ocular dominance slabs are organized in long strips running parallel to the cortical surface. Hubel and Wiesel (1968) found that preferred orientations of neurons progress through about 180° across the width of a single ocular dominance slab (0.25 - .50 mm). The representation of both eyes therefore forms what they called a "processing module" or hypercolumn of about 1 mm in extent. They observed that hypercolumns were about the same size regardless of their location in striate cortex (Hubel & Wiesel, 1968, 1974).

Signaling contrast

The magnitude of the response of visual neurons to a grating pattern is a function of the contrast of the stimulus. The response of cells in the retina and LGN is directly proportional to the contrast at low-contrast levels, but becomes more nearly proportional to the logarithm of the contrast at higher levels (Maffei & Fiorentini; 1973; Robson, 1975; Shapley & Perry, 1986). Striate simple and complex cells respond to contrast in a similar way but show an additional threshold nonlinearity because of their low spontaneous rate of discharge (Maffei & Fiorentini, 1973, Movshon, Thompson & Tolhurst, 1978). Cells in LGN and retina and cortex can be distinguished on the basis of their sensitivity to contrast. P_α cells of the retina and M cells of the LGN have a much higher contrast and

luminance sensitivity than P_β and P cells of the LGN (Shapley & Perry, 1986). These cells respond much more vigorously to small changes in luminance contrast (Kaplan & Shapley, 1986) and are, therefore, said to have a higher contrast gain. Cells with very high sensitivity to luminance contrast have also been detected in striate cortical layer $4c_\alpha$, the layer which receives the afferents from the magnocellular layers of the LGN (Hawkin & Parker, 1984).

Representation of phase information

Spatial phase is encoded in the firing patterns of X cells of the retina (Enroth-Cugall & Robson, 1966) and LGN (Maffei & Fiorentini, 1973) and simple striate cortical cells (Movshon, Thompson & Tolhurst, 1987; DeValois et al., 1982a). When a sine wave grating drifts slowly over the receptive field of an X or striate simple cell, the cell's firing rate modulates in tandem with the advancing phase of the sinusoid. These cells are said to display linear spatial summation - their response is proportional to the sum of luminance signals coming from all parts of their receptive fields. Y cells, as well as complex cells, do not encode phase information. They tend to show an overall increase in response to a drifting grating that is not dependent on the phase of the stimulus (DeValois et al., 1982a).

Phase information is particularly important for pattern recognition. The appearance of images is specified to a much greater extent by their phase than their amplitude spectra. Oppenheim and Lim (1981) and Piotrowski and Campbell (1982) showed that when an image is produced with amplitude spectrum of an image A and the phase spectrum of an image B, it will resemble image B rather than A. It is the phase structure that determines the spatial structure of a pattern. If the phase information in an image of a face, for example, is scrambled it can no longer be identified (Shapley, Caelli, Grossberg, Morgan &

Rentschler, 1990). On this basis, Rovamo, Mäkelä, Näsänen and Whitaker (1997) have argued that phase information must be encoded by peripheral visual mechanisms because they found that the shapes of faces were visible at eccentric visual field locations given sufficient stimulus magnification.

Mapping of information onto the cortical surface

Cortical magnification factor in primates

Talbot and Marshall (1941) presented some very limited data on the mapping of the central visual field onto the posterolateral surface of the cortex in the monkey using microeletrode recordings. They devised an index of cortical representation that they expressed as increment of the visual angle (from fixation) that is represented on each millimeter of cortex. Their procedure involved stimulating cells with the smallest possible spot of light and determining the total area of visual space represented by cells within a mm area of cortex. Talbot and Marshall simply reported that an average of 18 min of visual angle were represented per mm in the 5° periphery but that this value decreased to 2 min per mm centrally. This implies that the amount of visual space processed per unit of cortex changes rapidly from the peripheral to central visual field.

Daniel and Whitteridge (1961) published the first complete map of macaque striate cortex based on microelectrode recordings. To determine cortical magnification they measured the angular distance separating the centres of two receptive fields in the visual field and the linear distance between the corresponding points on the cortical surface - a technique still in practice for this purpose.[1] To aid in establishing spatial relationships, they created a 3-dimensional model of the highly convoluted cortical surface. Daniel and

[1] Note that an estimate of cortical magnification at the exact foveal centre must be made by extrapolation.

Whitteridge used the term linear magnification factor to refer to the millimeters of cortex representing one degree of the visual field at any given eccentricity. They reported that 1 degree at the fovea occupies about 6 mm linearly on striate cortex and that the linear cortical magnification factor declined in a systematic way with increasing retinal eccentricity. They noted that the inverse magnification increased in a reasonably linear fashion with eccentricity from 1 to 60°. Further, they made the important observation that the magnification factors were independent of polar angle (direction from the centre-of-gaze). The findings of Daniel and Whitteridge concerning the mapping from retinal to striate coordinates have been extremely important and form the basis of an analytic representation of this mapping. This is an issue that will be examined shortly.

Hubel and Wiesel (1974) examined the cortical representation of the visual field in two rhesus monkeys. Cellular responses were studied at discrete locations in the visual field between 1° and 20°. They reported that over this eccentricity range, receptive field size, scatter and cortical magnification all vary in a similar way with increasing distance in the visual field. Linear receptive field size (square root of receptive field area) was inversely proportional to the linear magnification. Thus, the product of magnification and receptive field size was found to be approximately constant irrespective of visual field location, with a value of about 1 mm - the size of a cortical hypercolumn. This rather startling observation implied that the cortex is a remarkably uniform structure. They plotted average field size (r) and inverse magnification (M^{-1}) as a function of eccentricity for five cortical locations with an average of 18 cells per penetration and showed that both rise linearly with a similar slope. Although they did not attempt to fit the data with linear regression equations, these are easily calculated and are as follows:

$$M^{-1} = 0.0946°/mm + 0.06406E/mm \quad [1.6]$$

$$r = 0.2713° + 0.04766E \quad [1.7]$$

Equation 1.6 yields a foveal value of magnification (M_0) of 10.00° and E_2 = 1.48° (r^2 = .98) for cortical magnification. Equation 1.7 yields an E_2 = 5.7° (r^2 = .92) for the eccentricity-dependent variation in receptive field size. This rather large difference in E_2s is due to the fact that the intercept values are quite different; E_2 expresses the rate of change from the foveal (intercept) value. The E_2 of 5.7° for receptive field size is likely an overestimate of the true value, given the small sample size and lower amount of variance accounted for by the fit. Nevertheless, it seems that magnification factors and receptive field sizes change at somewhat different rates with eccentricity. This study had significant impact and motivated further research on the structural arrangement of striate cortex.

Dow, Snyder, Vautin and Bauer (1981) presented the only study that examined the decline in the cortical magnification factor in awake behaving monkeys. Macaques were trained to hold fixation (binocular) while cells at eccentricities very close to the foveal centre (0.083 to 2.67°) were mapped using slits of light. They carefully determined centre of a cell or cell(s)'s receptive field for each penetration which was then plotted as a single point in a scatter plot of visual space using mm graph paper. The relationship between cortical and visual field locations could be then calculated after correcting for occipital regions of high curvature. They plotted M^{-1} as a function of eccentricity for data obtained in two hemispheres of two monkeys along with the best-fitting regression line through the pooled data as follows:

$$M^{-1} = 0.040°/mm + 0.116E/mm \quad [1.8]$$

This equation gives M_0 = 24.78 mm/deg. and E_2 = 0.35°. Dow's method of fitting

of these data has been criticized by Levi et al. (1985) as well as Van Essen et al. (1984). The problem with pooling data of the two cases is that no data were collected for one monkey within 0.58° of the centralmost visual field. Pooling assumes a common foveal value. Levi et al. fit regression lines to the two data sets separately and derived similar E_2s for both. The regression line (Equation 1.9) which passes through the most complete data set yields $M_0 = 17.24$ mm/deg. and $E_2 = 0.77°$.

$$M^{-1} = 0.058°/mm + 0.076E/mm \quad [1.9]$$

Dow further noted that, in contrast to the report of Hubel and Wiesel (1974), receptive field size (r = square root of each cell's area) and the degree of receptive field scatter (s) change much more slowly than amount of cortex devoted to processing a particular area of space. Their best-fitting equations to these data were given as

$$r = 0.222° + 0.037E \quad [1.10]$$

$$s = 0.0553° + 0.0116E \quad [1.11]$$

These equations give E_2 values of 6.0° and 4.77° for receptive field size and scatter, respectively. Although Dow et al. did not calculate r^2 values for these equations, they note that the field size data (Equation 1.10) show considerable vertical scatter at each eccentricity in comparision to the data on inverse magnification and receptive field scatter. This reduces the certainty of the estimate associated with this parameter.

Van Essen, Newsome and Maunsell (1984) presented a very careful, detailed study of the representation of visual space on striate cortex using mainly multi-unit electrophysiological recordings. To aid in the determination visual field topography, they carefully constructed two-dimensional maps of striate cortex using histological sections. These maps were crucial to minimize errors in

discerning surface area and linear distances. They determined that, although there were some small deviations, magnification factors were independent of polar angle as originally reported by Daniel and Whitteridge (1961).

Although none of Van Essen et al.'s recordings were directly in the foveal representation, they estimated the foveal magnification by using information on the size and shape of the cortical map in this region. The equations to describe the decline in cortical areal magnification were as follows:

$$Ma = 103(0.82 + E)^{-2.28}\ mm^2/deg^2 \text{ (for } E < 2.5°) \quad [1.12]$$

$$Ma = 103E^{-2.28}\ mm^2/deg^2 \text{ (for } E > 2.5°) \quad [1.13]$$

Taking the inverse square root of Equation 1.12 we find that M_0=12.73 and E_2 = 0.69°. There is a slightly steeper function for eccentricities of 2.5° and above. Equation 1.13 is a power function for which E_2 cannot be derived because it becomes undefined at zero degrees. The inverse square root of the function is a linear function whose slope denotes the exponent of the power function. The two functions yield comparable estimates of the magnification factor at greater eccentricities (i.e., 5°) but diverge substantially as the foveal region is approached.

Van Essen et al. also examined changes in receptive field area as a function of eccentricity and noted that for eccentricities greater than about 5° the data points could be fit by a power function of slope 2.48. They noted that this is similar to but slightly greater than the slope for areal magnification (-2.28, Equations 1.12, 1.13) (i.e., the rate of decline in receptive field size is similar to the rate of increase in cortical magnification). Further, Van Essen et al. found that, below 5°, receptive field area changes slowly with eccentricity with the best-fitting power function having a slope of only 0.15. They stated that these results are in close agreement with those reported by Dow et al. (1981). The 5° cut-off

point may be somewhat artifactual because there are relatively few data points with a large amount of scatter for eccentricities less than this value.

One problem with physiological methods is that estimation of the magnification at the centralmost fovea must be made by extrapolation of the available data. A method that is inherently more precise for this purpose involves using deoxyglucose labeling. Tootell, Silverman, Switkes and DeValois (1982) used the 2-deoxyglucose (2DG) technique to map metabolic activity in the cortex of the macaque. They stimulated a monkey monocularly with a ring-and-ray pattern of concentric circles that were equally spaced on a logarithmic scale. The pattern was composed of small checks that were flickered between black and white at 3 Hz. The resulting 2DG map of cortex contained blackened segments in the same ring-and ray design. The segments corresponded to ocular dominance strips, as only one eye was stimulated. This transformed ring-and-ray pattern had a relatively even linear spacing.

From the 2DG autoradiographs, Tootell et al. calculated the reciprocal of the cortical magnification factor as a function of eccentricity, assuming that magnification factors are independent of polar angle. In two monkeys, they averaged over all ring and ray segments, from 0 to 10 degrees, and found that M^{-1} could be described by the function

$$M^{-1} = 0.077°/\text{mm} + 0.082E/\text{mm}. \qquad [1.14]$$

This equation yields M_0 = 12.99 mm/deg and E_2 = 0.94°. This study was important for two reasons. Firstly, the foveal representation was mapped with great precision allowing an accurate determination of the cortical magnification factor. Secondly, this study clearly showed that visual field is transformed from a linear to logarithmic representation at striate cortex. This is discussed further in the section "logarithmic transform".

The studies that have been discussed above describe the structural and functional organization of macaque striate cortex. The striate cortex contains a very orderly and systematic representation of visual space. Hubel and Wiesel (1977), Dow et al. (1981), Van Essen et al., (1984) and Tootell et al. (1982) provided estimates for the foveal magnification factor (M_0) ranging from 10 to 17.24 mm with average value of 13.24 mm. Estimates of the E_2 associated with the cortical magnification factor ranged from 0.69 to 1.48° with an average value of 0.97°. There is more uncertainty associated with the E_2 for changes in average receptive field size. There is evidence that this parameter changes more slowly at eccentricities less than about 5° (Dow et al., 1981, E_2 = 6.0° for E = 0.083 to 2.67°) and then rises at more rapid rate, more or less in line with the change in cortical magnification (Van Essen et al., 1984), thereafter. This suggests that a single linear regression (i.e., E_2) to describe changes in receptive field size may be inappropriate. At any rate, these data along with those of Hubel and Wiesel (1977, E_2 = 5.7°) suggest that the E_2 for changes in average receptive field size is somewhat greater than that for cortical magnification.

Logarithmic transform

The visual field is mapped onto striate cortex in a systematic fashion. Recall that Daniel and Whitteridge (1961) observed that the cortical magnification factors were inversely proportional to eccentricity and independent of polar angle (direction from the centre-of-gaze) A mapping function which satisfies these conditions, was noted by Fischer (1973) and later exploited by Schwartz (1980). The analytic representation starts with the simplifying assumption that the spherical retinal surface and convoluted cortical surface can be approximated by planar surfaces. The cortical magnification factor (M) expresses the rate of change, or derivative, of radial cortical distance with

respect to visual angle. The systematic decline in M with increasing eccentricity, originally observed by Daniel and Whitteridge is accurately expressed by Equation 1.2 with x≈1 (Schwartz, 1977; Van Essen et al, 1984). Integration of this function results in a particularly simple mapping function which gives the distance (D) of the mapping from foveal centre to eccentricity (E)

$$D(E) = \int_0^E k(a+E)^{-x} dE \qquad [1.15]$$

$$D(E) = k \log(a+E) \qquad [1.16]$$

This means that equal distances in the visual field are expanded logarithmically in the striate cortex as the foveal representation is approached. To a first approximation, Equation 1.16 provides an accurate description of the transformation of the visual field representation onto striate cortex. This was most clearly demonstrated in work of Tootell et al. (1982).

Cortical magnification factor in humans

An early, important study of the way that visual field information is mapped onto the human cortex was conducted by Brindley and Lewin (1968). They implanted an array of radio receivers connected to electrodes onto the right occipital cortex in a blind patient. The patient experienced sensations of spots of light (phosphenes) when appropriate radio signals were delivered. The authors then mapped where the sensations of light evoked by electrical stimulations of the visual cortex appeared in the lower left visual field using two techniques. In the first, the patient had to grasp a knob located inside a hemispheric bowl, look at the grasping fingers and then point to the phosphene with her other hand. The second technique involved presenting pairs of stimuli sequentially, the patient then described the spatial relations between the phosphenes. The second method was optimal for determining the fine details of the relations between

phosphenes, but the first was needed to discover the scale of the map. This study was important because it provided the most direct data on the human M at this particular time.

Cowey and Rolls (1974) calculated the cortical magnification factor for the first lower 30° of the visual field based on the data of Brindley and Lewin (1968). The distance between electrodes on the cortex was specified by Brindley and Lewin, so Cowey and Rolls could calculate M for the many pairs of electrodes by measuring the angular separation and mean eccentricity of the corresponding pairs of phosphenes. They compared the decline in cortical magnification factor with increasing eccentricity with the corresponding decrease in visual acuity using Wertheim's (1894, cited in Cowey & Rolls, 1974) data[2] because both were made in the lower part of the visual field. Cowey and Rolls showed that the reciprocal of M and the minimum angle of resolution (reciprocal of visual acuity) increased in similar linear fashion as a function of eccentricity. Cowey and Rolls then used Wertheim's acuity data to extrapolate the foveal value of M which could not be calculated directly because the nearest phosphene to fovea was 1.6° eccentricity in Brindley and Lewin's study. They thereby obtained a value for M_0 of 15.1 mm/deg. and provided magnification factors in tabular form. The best-fitting linear regression line through the Cowey and Rolls' data for eccentricities of 0 to 30° can be calculated and is described by the function

$$M^{-1} = .066°/\text{mm} + .05307E/\text{mm}. \qquad [1.17]$$

This expression yields an E_2 of 1.11° ($r^2 = .987$) with $M_0 = 15.1$ mm. The work of Cowey and Rolls is still considered to provide a reasonable estimate of the cortical magnification factor.

[2] In Wertheim's study subjects viewed a small patch (5 cycles) of a square wave grating. The distance of the patch was increased until subjects could no longer identify its orientation (horizontal or vertical).

Drasdo (1977) calculated M for each of the principal meridians using a less direct method. The starting point of his analysis was Rolls and Cowey's (1970) observation that, in the macaque, for eccentricities greater 10°, M is proportional to the square root of the projected ganglion cell density (cells/deg^2) [linear density is $D^{0.5}$, or frequency of ganglion cells (cells/deg)]. More centrally, this relationship breaks down because cells are displaced from their receptive fields by an amount that is difficult to determine. Drasdo suggested that, if data on receptive field density were available, they might relate to M at every point in the visual field. He pooled the empirical estimates of the human ganglion cell density from several sources and extrapolated to the foveal area primarily by means of the density of the fovealmost cones. Based on his calculations, he determined that M_0 = 11.5 mm/deg. Drasdo fitted four empirical equations to the data to describe receptive field density distributions for the principal meridians. He presented a simplified linear equation of the form

$$V = k(1 + SE) \qquad [1.18]$$

for eccentricities (E) less than 20 degrees, where V is the ganglion cell sampling interval, or M^{-1}, k is the foveal value and S is slope or gradient of the equation 1 + SE which is, therefore, normalized to the foveal value. The values of S were 0.46, 0.50, 0.62 and 0.66 for the temporal, nasal, superior and inferior hemifields respectively. E_2 is simply 1/S, so values of E_2 vary from 1.51 to 2.17°. The validity of his estimates rests on the assumption that there is a direct relationship between M and ganglion cell density - a claim that has been disputed.

Rovamo and Virsu (1978) and Rovamo, Virsu and Näsänen (1979) calculated M in a similar manner to that of Drasdo (1977) and proposed that performance on a contrast sensitivity task would be similar at all eccentricities if

the cortical projection area (number of cortical cells stimulated) was the same. They estimated the value of M for each principal meridian of the visual field indirectly using information on the extent of striate cortex and the density distribution of ganglion cells (data from Rolls & Cowey, 1970) and foveal cones (data from Polyak, 1957). Following Drasdo (1977), they claimed that M^2 was directly proportional to D (density of receptive fields of retinal ganglion cells). However, they disputed Drasdo's value of M_0 because they claimed that his value for centralmost cone density was too high. Rovamo et al. determined M_0 was 7.99 mm/deg for the centralmost fovea and they obtained one equation for each of the principal meridians. Their equation for the temporal meridian, for example, is as follows:

$$M = M_0/(1 + .29E + .000012E^3) \qquad [1.19]$$

This equation is a simple hyperbolic function and yields a reasonably linear relationship between M^{-1} and eccentricity because the cubic component is very small. E_2 values for the principal meridians are 3.45°, 3°, 2.4° and 2.35° for the temporal, nasal, superior and inferior meridians, respectively.

Rovamo et al. (1978) presented subjects unscaled sine wave gratings as well as gratings that were scaled in both size and spatial frequency by the inverse of their calculated M at various eccentricities in the nasal, temporal, superior and inferior visual fields. When gratings were not scaled, the peak of the contrast sensitivity function (CSF) shifted to a lower frequency with increasing retinal eccentricity and absolute contrast sensitivity declined as well because stimuli are not of optimal size for the mechanisms that subserve task performance. When contrast sensitivity was determined using scaled grating patches and spatial frequency was plotted in units proportional to M (cycles/mm), then the CSFs at

all eccentricities assumed a common shape. Unfortunately, later work provided fairly definitive evidence (Dow et al., 1981; Van Essen et al., 1984) that the central visual field has a much greater representation than that implied by a direct proportionality between ganglion cell density and M. This means that their estimate of M was not reliable, but their E_2 values do appear to accurately reflect the rate of change associated with local ganglion cell spacing. It is this latter substrate that appears to limit performance on visual acuity tasks.

Grüsser (1995) reported a very different study of cortical magnification based on migraine phosphenes. The experience of a migraine is sometimes accompanied or preceded by a visual aura (phosphenes) which traverse the visual field. Grüsser plotted the location of scintillating migraine phosphenes as a function of time for his experience of 11 migraines as well as those of two other subjects. In other words, at constant time intervals, the subject indicated where the phosphenes appeared on a polar diagram of the visual field. Grüsser then plotted eccentricity of phosphene appearance as a function of total migraine duration. Two assumptions were made to determine the cortical magnification factor: 1) speed of progression of the pathological process within cortex is constant, and 2) there is regularity in visual processing as expressed by the hypercolumn arrangement (Hubel & Wiesel, 1974; Tootell et al., 1982). The equation which describes the change in visual field location as a function of time is a first-order linear differential equation. This equation can be solved iteratively by varying two parameters to provide the best fit to the data. One then recovers the slope and intercept values that describe M^{-1}. The best-fitting linear regression line was as follows

$$M^{-1} = 0.073°/\text{mm} + 0.059E/\text{mm}. \qquad [1.20]$$

This equation yields $M_0 = 13.70$ mm and $E_2 = 1.24°$.

The decline in the human magnification factor has also been examined using imaging techniques. Horton and Hoyt (1991) correlated magnetic resonance scans with the location of visual field deficits in patients with clearly defined occipital lobe lesions. The representation of the visual field in the human striate cortex was originally studied by Inouye (1909 - cited in Horton & Hoyt). He correlated visual field deficits with the trajectory of missiles that penetrated the occipital cortex and used this information to construct the first retinotopic map of striate cortex. Holmes and Lister and Holmes (1916 & 1917, respectively-cited in Horton and Hoyt) later expanded upon the Inouye's initial work and the Holmes map became a well-known, widely-reproduced standard.

Horton and Hoyt analyzed three clinical cases in detail and concluded that the Holmes map underestimates the relative magnification of central vision. For example, the 30° isoeccentricity contour in the Holmes map was where Horton and Hoyt determined the 12° contour should be. Their equation for the human M was provided in a less typical form as

$$M = 17.3 \text{ mm*deg}^{-1}/(E + 0.75) \qquad [1.21]$$

This equation gives $M_0 = 23.0667$ and $E_2 = .75°$. On the basis of their calculations, Horton and Hoyt modified the Holmes map such that the central visual representation ($M_{0)}$ is expanded by about a factor of two relative to that of the macaque.

Functional magnetic imagery (fMRI) in normal subjects is the latest technique used to determine the mapping from retinal to cortical coordinates. Sereno, Dale, Reppas, Kwong, Belliveau, Brady et al. (1995) recorded fMRI images during phase-encoded retinal stimulation in seven subjects. The eccentricity of presentation was mapped as follows. The observer viewed two concentric expanding annuli presented on a grey background. As the largest

annulus disappeared, a new annulus grew in the centre of the display. Each annulus contained a high-contrast flickering radial checkerboard pattern. As the stimulus slowly expanded, each visual field location alternated between the uniform field and the checkerboard. The time course of this alternation depends upon the visual field location. Neural activity in peripheral regions is systematically delayed relative to that at foveal locations. The fMRI signal, which depends upon venous blood oxygenation, was measured at points along the calcarine sulcus - the site of human primary visual cortex while the observer viewed several periods of the stimulus. Thus, the process involves temporal correlation with a periodic stimulus.

Their data showed that the mapping function is extremely steep near the fovea indicating very large magnification factors near the centre-of-gaze. These magnification factors are significantly larger than those found in the macaque. The mapping function was determined by measuring distances from the most central response zone ($\approx 0.5°$ i.e., closest point measured to the fovea) and the best-fitting equation for the mapping function was given as

$$M = 20.05 \text{ mm}/°(E + 0.08)^{-1.26} \qquad [1.22]$$

In the words of Sereno et al., " The combination of parameters given here fit the cortical distance data very closely but still give unrealistically large estimates of cortical magnification at the exact centre of the fovea" (p. 893). For this reason, a value of E_2 cannot be easily calculated. Nonetheless, the data of Sereno et al. suggest that, in comparison with nonhuman primates, humans have a more prominent emphasis on central vision.

The analyses of Cowey and Rolls (1974), Grüsser (1995) and Horton and Hoyt (1991) all appear to present reliable estimates of E_2 which were 1.09°, 1.24°,

and 0.75°, respectively. Values for the foveal magnification factor (M_0) were 15.1 mm, 13.70 mm and 23.07 mm, respectively. These studies along with that of Sereno et al., (1995) strongly suggest that the centre-of-gaze has a larger representation, in mm, than that of nonhuman primates. This is not surprising because human striate cortex is substantially larger. The average surface area in the macaque is 1200 mm^2 (Van Essen et al., 1984) compared with the average surface area of human striate cortex of 2500 mm^2 (Stensaas, Eddington & Dobelle, 1974) - an area that is greater by a factor of 2.08. If the essential elements of the retinocortical mapping are similar in humans and primates, it is expected that a correction factor of 1.44 ($2.08^{0.5}$) could be applied to M_0 in primates to derive the human value (Horton & Hoyt, 1991). The average value of M_0 from Grüsser, Cowey & Rolls and Horton & Hoyt is 17.3 mm, this is a factor of 1.35 larger than Tootell et al. and Van Essen et al.'s estimates for M_0 of 12.99 and 12.73 mm, respectively, in primates. This value does not differ substantially from the estimate obtained using the correction factor. The rate of decline of the cortical magnification factor appears to be very similar in humans (E_2 average = 1.03° for studies cited above) and primates (e.g., Tootell et al. E_2 = .94°).

Psychophysical studies

M-scaling

Investigation of the representation of visual space in striate cortex clearly indicated that cortical representation of a solid degree of visual angle (M) decreases in a systematic way with increasing eccentricity (e.g., Daniel & Whitteridge, 1961; Hubel & Wiesel, 1974) and that the reciprocal of M rises in a reasonably linear way with increasing retinal eccentricity. The orderly relationship between the size of the cortical projection area and eccentricity

means that it should be possible to make peripheral performance equal to that at the fovea at all eccentricities by simply magnifying stimuli in all dimensions according to the cortical projection area. This notion was originally proposed by Rovamo et al. (1978) and Koenderink, Bouman, Bueno de Mesquita and Slappendel (1978) and came to be known as M-scaling. As mentioned, Rovamo et al. showed that contrast sensitivity could be made equal across the visual field given that grating stimuli were scaled according to a set of preselected scaling factors for each of the four principal meridians of the visual field. These scaling factors were directly proportional to local ganglion cell spacing and thought to reflect the cortical representations of the gratings.[3] In a similar vein, Koenderink et al. (1978) showed that acuity for moving sine wave gratings (4 Hz) could be made equal when scaled in proportion to minimal angle of resolution. This was proportional to local ganglion cell spacing and, they believed, the cortical magnification factor, M.

The idea of M-scaling gained popularity and it was hoped that visual performance on a wide range of tasks could be made equivalent in foveal and extra-foveal vision through application of this procedure. M-scaling was generally successful for visual acuity tasks, such as grating and Snellen acuity (Virsu, Näsänen & Osmoviita, 1987) and several other visual phenomena such as the size of panum's area - a disparity interval that allows binocular fusion (Hampton & Kertesz, 1983) and the magnitude of the tilt after-effect (Harris & Calvert, 1985).

Unfortunately, M-scaling was not successful for all spatial discrimination tasks and failed in particular for those that required the processing of spatial relationships. In one of these studies, Saarinen (1988) presented subjects with

[3] It later became apparent that the foveal representation is greater than that suggested by direct proportionality (Dow et al. 1981; Van Essen et al,. 1984).

clouds of dots at various eccentricities along the horizontal meridian that were either random or symmetrical across the horizontal axis. Stimuli were either unscaled or M-scaled according to an $E_2 \approx 3°$. He reported that the probability of a correct detection declined quite rapidly under the first condition, and that this decline slowed, but was not entirely eliminated through M-scaling. Scaling the stimuli in this way was, therefore, insufficient to remove all eccentricity-dependent variation in performance. These results suggested that further stimulus magnification (i.e., scaling according to a smaller value of E_2) would be required to equate symmetry performance across the visual field. Similarly, Saarinen, Rovamo and Virsu (1989) reported that M-scaling did not successfully equate performance across eccentricities (0 - 12°) for a symmetry detection task in which subjects were presented with sideways S-shaped (⊔⊓) figures on either side of the horizontal meridian. M-scaling has also failed for tasks involving the detection of phase relationships (Bennet & Banks, 1988; Rentschler & Treutwein, 1985; Stephenson, Knapp & Braddick, 1991), bisection acuity (Virsu et al. 1987) and Landolt visual acuity - a type of task in which subject must report the position of a gap in a circular figure (Virsu et al., 1987).

The M-scaling approach was called into question for theoretical as well as practical reasons. Firstly, evidence was mounting from research in humans and monkeys that an $E_2 \approx 3°$ did not really reflect the eccentricity-dependent changes in the cortical magnification factor (e.g., Cowey & Rolls, 1974; Dow et al, 1981; Hubel & Wiesel, 1977; Van Essen et al, 1984). Secondly, it seemed unlikely that a set of preselected scaling factors would be sufficient to equate performance across the visual field for all subjects, given that there are substantial individual differences in cortical representation. For example, Stensaas et al. (1974), in their

analysis of 52 hemispheres, reported that the surface area of human striate cortex shows an approximately two- to three-fold size variation (1284 - 3702 mm^2) - a result recently confirmed by Andrews, Halpern and Purves (1997). A similar range has been found in the macaque (Van Essen et al., 1984). Finally, M-scaling had failed in particular for those tasks that required the discrimination of spatial relationships.

Performance on certain tasks that require the precise encoding of positional relationships is far better than that expected on the basis of cone spacing. Westheimer and McKee (1977) coined the term "hyperacuity" for these tasks because under optimal conditions judgments of relative position are about 10 times finer than the separation of bars at the grating acuity limit. Westheimer (1982) compared the decline in thresholds with increasing eccentricity (0°, 2.5° and 10° on the horizontal meridian) for a grating acuity task with performance on two hyperacuities - orientation discrimination and vernier acuity. The visual acuity task was similar to the one used in the classical study by Wertheim (1894). At each eccentricity, the subject was shown patches of gratings equal to six cycles and having a square aperture. Random deviations were introduced in the length of the aperture to ensure that no cues to grating direction would be provided[4]. The subject's task was to indicate, for each grating stimulus, the direction of the grating lines (horizontal or vertical). Resolution threshold was half the period of the grating whose direction could be identified on 75% of the trials. The vernier stimulus was composed of two dots with a variable inter dot distance and a single line was used as the orientation discrimination stimulus. Subjects were randomly presented with stimuli distributed in the domain in question and

[4] A square piece of grating appears shorter in the direction along the grating lines.

indicated whether the top dot was located to the left or right of the bottom one (vernier task) or whether the line was tilted to the left or right (orientation discrimination). Threshold values were half the distance between those patterns on each side of the mean for which responses were 75% correct. The results for both hyperacuity tasks were similar and indicated that thresholds rose about twice as fast with eccentricity as visual resolution thresholds.

It is interesting to note that data reported by Weymouth (1958), almost thirty years earlier, suggested that performance on various spatial tasks may be limited by different neural mechanisms. Weymouth noted that, for several pattern recognition tasks, there was a remarkably linear increase in the function that fitted threshold size plotted against eccentricity. He suggested that the slope of this curve could be used to relate task performance to a neural substrate. Weymouth noted that there was a comparable rate of increase in both ganglion cell separation (data from Polyak, 1941 - cited in Weymouth) and the minimum angle of resolution (MAR, reciprocal of visual acuity, data from Wertheim, 1894) and remarked "the ganglion cells are the anatomical representatives of the sensory unit and their regional distribution [forms] the basis of the linear relation of the threshold to eccentricity" (p. 109). He noted that vernier thresholds (data of Bourdon, 1902 - cited in Weymouth) had a low intercept, indicating high sensitivity, but a steeper slope than that associated with the MAR, but offered no explanation for this finding.

Levi, Aitsebaomo and Klein (1985) conducted the first study that attempted to relate the rate of decline of performance on hyperacuity and resolution tasks to different neural substrates. They showed that equivalent-to-foveal levels of performance could be achieved across the visual field on vernier acuity tasks by magnifying the stimuli in proportion to the cortical magnification

factor. A value for the inverse cortical magnification (M^{-1}) of 0.77° was derived from Dow et al.'s (1981) data.

Vernier stimuli consisting of two abutting rows of seven vertical lines as well as a more conventional two-line stimulus, were presented at 0°, 2.5°, 5° and 10° in the lower visual field. The stimulus dimensions were "scaled" in proportion to an E_2 of 0.77° by changing the viewing distance. The smallest spatial offset discriminable on 75% of occasions was considered as threshold. When data were plotted in units of cortical distance, the functions obtained at each eccentricity collapsed to a more or less unitary function. This suggested that when scaled according to M^{-1}, vernier discrimination was as good in the periphery as it was foveally. For comparative purposes, grating acuity was measured using the method of adjustment at the same visual field locations. E_2 values ranging from 2.2 to 3° were recovered for this task. These estimates compared favorably with the eccentricity-dependent changes in cone density from data of Rolls and Cowey (1970) for the macaque (E_2 = 3.2° for E = 0 to 10°) and Oesterburg (1931 - cited in Levi et al.) for the human retina (E_2 = 2.9° for E= 0 to 10°). On the basis of their findings, Levi et al. (1985) proposed that visual acuity tasks are limited primarily by retinal factors, whereas position acuity tasks are limited primarily by cortical processing.

The involvement of the cortex in hyperacuity performance had earlier been proposed by Barlow (1981) as well Westheimer (1982). Barlow suggested that the cortical hypercolumns provided the anatomical basis for this type of visual acuity. Theoretically, a neural mechanism, "processing module" or hypercolumn could detect the centre of a group of activated cones and thereby provide localization information even finer than cone separation. Hypercolumns

are roughly equal in area so that performance with stimuli that are sampled by these units might be expected to be directly related to cortical magnification. Levi et al. (1985) provided further support for this notion; they measured vernier thresholds as a function of the separation of flanking bars and found that an elevation of thresholds, or crowding, occurred when interline spacing was less than a cortical distance of one mm - approximately the width of a human cortical ocular dominance column (Hitchcock & Hickey, 1980).

The work of Westheimer (1982) and Levi et al. (1985) suggested the simple and appealing notion that spatial discrimination tasks could be divided into two classes, namely visual or resolution acuity and position acuity, showing quite different eccentricity-dependent changes in performance. This idea would soon be challenged using a valuable new technique in psychophysics.

S-or Spatial scaling

Almost simultaneously, researchers at several laboratories (e.g., Johnston, 1987; Johnston & Wright, 1986; Saarinen et al., 1989; Watson, 1987; Wright, 1987) proposed that E_2 values could be determined solely through size-dependent changes in thresholds; the use of preselected scaling factors was no longer required. Performance is simply measured at various eccentricities over a range of stimulus sizes. Thus, threshold as function of stimulus size curves are recovered at every visual field location. If just a simple shift of spatial scale accounts for eccentricity-dependent variation in performance, then data curves from all eccentricities will reach the same maximum performance levels and they will have the same shape when plotted on logarithmic size axes. The E_2 value is determined by the amount of lateral shift required to superimpose all data. The greater the amount of horizontal shift necessary to align the functions, the smaller the value of E_2. This procedure is known as S or spatial scaling.

In one of the first spatial scaling studies, Watson (1987) obtained contrast thresholds for the detection of a set of Gabor targets having frequencies of 0.25 to 16 cpd in octave increments. Gabors at each eccentricity had a width (1/*e*) equal to the same number of cycles of the underlying sinusoid and were therefore size-scaled versions of each other. The eccentricities tested were 0° and 3° along the horizontal meridian. The technique proved successful for small high-frequency Gabors but failed for the largest, lower frequency ones. The problem was, of course, that large Gabors are spatially extended while the concept of a local spatial scale applies to a point in the visual field. Watson suggested that precedence should therefore be given to the high frequency targets in determining amount of shift required to align the functions. He reported that the high frequency limbs of the functions could be superimposed with a rate of scale change (slope) equal to s = .24. This is equal to an E_2 of 4.17° - a value reasonably similar to Rovamo and Virsu's (1978) E_2 estimate of about 3° for contrast sensitivity.

The technique of spatial scaling gained popularity and has been used to examine a variety of tasks but has been employed most frequently to examine positional acuity using spatially localized broadband stimuli, such as lines and dots. Performance on vernier acuity was one of the so-called "position acuity" tasks examined. The methodology of this study is presented in detail to exemplify the use the spatial scaling technique.

Whitaker, Rovamo, MacVeigh and Mäkelä (1992b) measured thresholds for vernier acuity using two abutting vertical lines as well as vertically separated dot stimuli. All stimuli were simply magnified versions of each other and were presented at eccentricities of 0°, 5°, 10° and 15° along the horizontal meridian. Magnification of a set of stimulus sizes was achieved by varying viewing

distance for each eccentricity of presentation. The subject's task was to indicate, for a single interval presentation, whether the upper vernier element was offset to the left or right of the lower. An adaptive procedure was used to determine the offset for leftward and rightward responses that represented the 75% correct point on the underlying psychometric function; the mean offset was then taken as threshold. To determine the amount by which peripheral data curves were shifted relative to the foveal curves, they first fit psychometric functions to data at each eccentricity. Then, line lengths (stimulus sizes) at a given eccentricity were divided by estimates of the scaling factor in question using an iterative process until the sum of squared deviations between foveal and eccentric data were minimized. Whitaker et al. showed that when all data were divided by the appropriate scaling factors, all size-versus-eccentricity functions superimposed to a more or less unitary function. Once scaling factors were obtained for all eccentricities, a best-fitting linear regression line was plotted through these points to give an estimate of the E_2 for the task.

For two well practiced subjects, E_2s recovered for this task were 1.66° and 1.78° for the vertical line stimuli, and 1.66° and 1.83° for the dot stimuli. It is noteworthy that these E_2 values are about a factor of two larger than Levi et al.'s (1985) estimate of 0.77° for vernier acuity. Levi had, however, used a predetermined scaling factor to superimpose data at eccentricities, thus, it is possible that a different, perhaps somewhat larger, value of E_2 may have more effectively collapsed all data to form a unitary function.

Whitaker, Mäkelä, Rovamo and Latham (1992a), in a follow-up study, used the spatial scaling method to determine E_2 for several tasks: spatial interval discrimination, bisection acuity and displacement detection. Spatial interval discrimination measures the ability of subjects to compare the size of a test gap

or spatial interval with that of a standard. The bisection acuity task examines the observer's ability to bisect or judge the mid-point of the gap between two points or lines. Displacement detection measures the subject's ability to detect whether a stimulus, such as a small square, has moved to the left or right. This can occur gradually or instantaneously and with or without the presence of a stationary reference stimulus. In this experiment, stimuli were placed on an iso-eccentric viewing arc. This method dissociates the effects of eccentricity and feature separation, and is particularly important for the types of tasks described above. The arc was centred at fixation and not visible to the observer. The eccentricity of the stimulus (0°, 2.5°, 5° and 10°) was defined by the radius of the arc. Changes in spatial separation of the stimulus features was achieved by moving the stimulus around the arc.

Whitaker et al. reported that E_2s for spatial interval discrimination ranged from 0.07° to 0.22° and were 0.07° and 0.08° for bisection acuity. The E_2s for the two strictly spatial tasks were therefore in the same range; this is not surprising as both tasks involved making a judgment concerning the spatial extent of the gap. E_2 values for the displacement detection tasks were considerably more variable. E_2s were as small as 1.06° and 1.35° for instantaneous referenced displacement and as large as 18.5° and 13.5° for unreferenced gradual displacement detection. The results of this study emphasized the extremely wide range of E_2s that may be recovered, even for similar tasks, and challenged the assumption that there were only two limitations, retinal and cortical.

Although Whitaker and colleagues had highlighted the range of E_2s that may be recovered, in subsequent studies they showed that certain tasks which are thought to rely on a common process, display similar values of E_2. An average E_2 of 1.95° was recovered for orientation discrimination (Mäkelä,

Whitaker & Rovamo, 1993), E_2s ranging from 1.42 to 2.27° were found for curvature detection and discrimination (Whitaker, Latham, Mäkelä, & Rovamo, 1993) and E_2s from 1.73 to 2.45° were reported for a task that involved the detection of a small amount of geometric change in a human face (Rovamo, Mäkelä, Näsänen, & Whitaker, 1997). With regard to the latter task, Rovamo et al. suggested that, if observers selectively attended to one of the stimuli (i.e., mouth area), then the task would be reduced to a simple discrimination of local features. Mäkelä et al. (1993) and Rovamo et al. (1997) suggested that performance on all of these tasks may be mediated by a similar process, such as orientation discrimination.

In this discussion, certain questions have remained unanswered. Firstly, why do E_2s vary over a considerable range (0.07 to 2.45°), even for strictly spatial tasks? Secondly, what do these E_2s tell us of the functional organization of the visual system? And lastly, why are position acuity E_2s, which presumably reflect cortical processing, often substantially greater than estimates of the E_2 for the human cortical magnification factor?

Local and global processing

One factor to consider in relation to the wide range of E_2s, is that the visual system may rely upon different cues to solve spatial discrimination tasks. A vernier acuity target, for example, can be composed of abutting or more widely separated elements. At small feature separations, correct determination of the displacement of a vernier stimulus may be accomplished through the responses of correctly oriented spatial filters (local processing), whereas at larger separations the two lines must be processed by separate filters and their position labels compared (global processing). Thus, performance of a given task may

draw on different mechanisms which produce quite different E_2 estimates.

Beard, Levi, & Klein (1997) conducted the only psychophysical study that explicitly attempted to determine the E_2 associated with the cortical sampling grain (i.e., the rate of decline associated with the cortical magnification factor). To achieve this, they wanted to ensure that stimulus features would be processed by separate spatial filters. The assumption behind the experiment was that, if the vernier features are adequately separated in time, they will fall outside of the temporal integration span of a single filter - a value of about 100 msec according to Waugh and Levi (1993).

Stimuli were temporally and spatially separated horizontally oriented lines. They used an inter-stimulus interval ranging from 20 to 200 msec between the two vernier features. The test feature was presented after the reference and the subject's task was to determine the offset direction (up or down) of the test line. Stimuli were presented at eccentricities of 0° and 2.5° and viewed from a single distance of 2.2 m (this yielded a line length of 10 min arc). They calculated the rate of decline of thresholds as a function of eccentricity. Beard et al. estimated that vernier thresholds double at about 0.8° ± 0.2°, which they noted is similar to the E_2 associated with the cortical magnification factor. We must, however, give further consideration to their methodology because they did not use a method of spatial scaling. Beard et al. ensured that the line length (10 min arc) was sufficient to optimize foveal thresholds. According to Westheimer and McKee (1977) and Watt (1984), thresholds are independent of line length for lines above 5 min of arc at the fovea. However, we do not know the line length above which thresholds attain a minimal value at 2.5°. Therefore, it is possible that the size of the E_2 that they recovered may be related to the size of foveal standard.

Performance on position acuity tasks, such as orientation discrimination

and vernier acuity with abutting stimulus features, may be accomplished through the operation of local filter responses (i.e., orientation selective mechanisms). As noted earlier, the small, high frequency cells tend to show narrower orientation tuning, meaning that they are more sensitive to stimulus orientation (DeValois, Yund, & Hepler, 1982b; Phillips & Wilson, 1984). This suggests that perhaps orientation discrimination performance is limited by changes in the size of the smallest orientation-selective mechanisms available to encode the stimulus at each eccentricity. Scobey (1982) first suggested that orientation discrimination performance is limited by eccentricity-dependent changes in receptive field sizes at striate cortex. Research in the macaque suggests that the E_2 associated with average receptive field size is somewhat larger than that associated with the cortical magnification factor (Dow et al., 1981; Hubel & Wiesel, 1977; Van Essen et al., 1984). The average E_2 for orientation discrimination performance of 1.95° recovered in the classic spatial scaling study on orientation discrimination of Mäkelä et al. (1993) may therefore reflect changes in the local spatial scale of orientation-selective mechanisms.

Present experiments

It is likely that the wide range of E_2s in the literature results from the fact that the visual system can use different cues and processes to solve the task at hand depending on stimulus characteristics and task demands. It is noteworthy that the stimuli used for positional tasks have been exclusively broadband (e.g., lines). Conversely, narrowband stimuli are generally used for visual-acuity-type tasks (i.e., grating acuity). Therefore, it is of interest to examine the extent to which E_2 may, at least in part, depend on the frequency content of the stimulus. To answer this question, orientation discrimination was tested using both stimulus types within a single task.

The preceding discussion provides the rationale for the first set of experiments. To set the stage for the remainder of the work of this thesis on eccentricity- dependent changes in orientation discrimination performance, it is necessary to consider a recent development in the area of spatial scaling, the technique of double scaling

Double scaling

The tasks that have been discussed to this point have been described as spatially scalable. That is, performance can be made equivalent across the visual field through size scaling changes alone. However, extrafoveal performance on some tasks is poorer irrespective of stimulus magnification. Size scaling cannot equate performance on high-contrast reading (Chung, Mansfield, & Legge, 1998), face discrimination (Melmoth, Kukkonen, Mäkelä & Rovamo, 2000b; Mäkelä, Näsänan, Rovamo & Melmoth et al., 2001) and low-contrast alphanumeric character recognition (Strasburger, Harvey & Rentschler, 1991; Strasburger, Rentschler & Harvey, 1994).

Recently, however, two procedures have been advanced that can potentially normalize performance on numerous tasks not previously considered as spatially scalable. Melmoth et al. (2000b) introduced a technique that has been used to equate foveal and extra-foveal performance on face discrimination by scaling along the contrast as well as the size dimensions. The spatial scaling procedure involves measuring contrast thresholds across a range of eccentricities and stimulus sizes which are all magnified versions of one another. The second technique was proposed by Poirier and Gurnsey (1997, 2002). The Poirier-Gurnsey method involves determining scale thresholds for stimuli having a fixed ratio of size to contrast. Scale thresholds therefore represent the combination of size and contrast that elicit a given fixed level of performance. For both methods,

E_2s for size and contrast are recovered by determining the horizontal and vertical shifts required to superimpose all data.

It is of interest to consider the size-scaling E_2s recovered for tasks such as face discrimination in relation to those of more conventional spatial discrimination tasks such as orientation discrimination and vernier acuity. Similar values of E_2 may suggest that tasks are limited by a common underlying physiological process. It is noteworthy that the E_2s for face identification are often comparatively large. For example, Melmoth et al. (2000b) reported size-scaling E_2s of 2.39° to 25.7° for this task. Mäkelä et al. (2001) reported E_2s for face discrimination of 2.73° and 3.19°. In light of these findings, orientation discrimination performance has been examined in the current set of experiments using the two double scaling methods outlined above as well as a novel technique which attempts to bridge the gap between the original spatial scaling method and the new double scaling techniques. Through the use of different procedures, some important, and unexpected observations were made that suggest contrast-dependent changes in the spatial scaling required to equate orientation-discrimination performance.

CHAPTER 2

ORIENTATION DISCRIMINATION IN FOVEAL AND EXTRA-FOVEAL VISION: EFFECTS OF STIMULUS BANDWIDTH AND CONTRAST

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ABSTRACT

The parameter E_2 is used in many spatial scaling studies to characterize the rate at which stimulus size must increase with eccentricity to achieve foveal levels of performance in detection and discrimination tasks. We examined whether the E_2 for an orientation discrimination task was dependent on the spatial frequency bandwidth of the stimulus used. Two methods were employed. In Experiments 1 and 2 stimuli were presented at a fixed high level of contrast across viewing conditions. In both experiments the E_2s recovered for narrowband stimuli were larger than those recovered for broadband stimuli. In Experiment 3 we controlled for the potentially confounding effects of perceptual contrast by measuring orientation thresholds over a range of stimulus contrast levels. Only thresholds which had reached an asymptotic level, such that increases in stimulus contrast led to no further changes to thresholds, were included in the calculation of E_2. We observed that E_2s recovered in the latter condition were in the range of 1.29° to 1.83° and similar for narrowband and broadband stimuli. We conclude that a failure to consider the role of perceptual contrast may result in inflated estimates of E_2.

Performance in many visual tasks depends upon visual field location and typically declines with increasing retinal eccentricity when a constant stimulus size is used. In many cases, visual performance can be equated in the central and peripheral field by a simple linear change in stimulus size which can be expressed by the function

$$F = 1 + E / E_2 \qquad [2.1]$$

where E_2 indicates the eccentricity (E) in degrees at which the size of a stimulus must be doubled, relative to the foveal standard, to achieve equivalent performance (Levi, Klein & Aitsebaomo, 1984, 1985). Therefore, the smaller the value of E_2 the more rapid the rate of decline in task performance with increasing retinal eccentricity. If peripheral and central performance can be equated by an appropriate size scaling then differences between central and peripheral vision can be considered to be quantitative rather than qualitative. Thus, implicit in the size-scaling literature is the idea that a major limitation on peripheral performance is an eccentricity-dependent change in the spatial scale of the mechanisms required to perform the task at hand.

The decline of performance with eccentricity has been shown to be task dependent, and a wide range of E_2 values has been reported (see Rovamo, Mäkelä, Näsänen & Whitaker, 1997, Table 1). In general, however, contrast sensitivity and grating resolution decline at a slower rate with retinal eccentricity than tasks requiring the assessment of relative position (Levi et al., 1985; Whitaker, Mäkelä, Rovamo & Latham, 1992a). Resolution tasks tend to produce E_2s of three and greater whereas positional tasks elicit E_2s of two or less. Resolution tasks are generally thought to reflect eccentricity-dependent

limitations that are retinal in origin whereas positional tasks are thought to have post-retinal origins (Levi et al., 1985).

Although the task dependence of E_2 appears to be well established, we noted that the stimuli typically used for resolution and positional acuity tasks differ markedly with respect to spatial frequency content. The eccentricity dependence of resolution and contrast sensitivity has been examined using primarily narrowband stimuli (e.g., Koenderink, Bouman, Bueno de Mesquita & Slappendel, 1978; Rovamo & Virsu, 1979; Swanson & Wilson, 1985), whereas those examining positional acuity have used broadband stimuli almost exclusively (e.g., Klein & Levi, 1987; Rovamo et al., 1997; Whitaker et al., 1992a, Whitaker, Rovamo, MacVeigh & Mäkelä, 1992b). Therefore, the starting point for the present investigation is the following simple question: do so-called resolution and positional tasks produce their characteristically different E_2s because of differences in the information necessary to solve the task or because of differences in the bandwidth of the stimuli? To put this question concretely, we could ask, does a particular positional task elicit the same or different E_2s when broadband and narrowband stimuli are used?

We chose to investigate this issue using orientation discrimination because it is one of the classical positional or "hyperacuity" type tasks (Westheimer, 1982). Moreover, orientation performance in the central versus peripheral visual field has been studied extensively using a number of procedures (Mäkelä, Whitaker & Rovamo, 1993; Paradiso & Carney, 1988; Scobey, 1982; Spinelli, Bazzeo & Vicario, 1984; Vandenbussche, Vogels & Orban, 1986; Westheimer, 1982). Mäkelä et al. (1993) were the first to

determine the decline in orientation discrimination performance with retinal eccentricity using a spatial scaling technique (e.g., Johnston, 1987; Johnston & Wright, 1986; Watson, 1987; Wright, 1987) that makes no prior assumptions concerning peripheral magnification factors. In the present study we used the spatial scaling method to examine peripheral versus central orientation discrimination using stimuli that differed with respect to spatial frequency bandwidth (broadband versus narrowband). Broadband stimuli were smoothed line segments and narrowband stimuli were created by filtering the broadband lines with isotropic, frequency selective filters. We used two types of scaling procedures. In Experiment 1 subjects were presented with fixed orientation differences and the probability of a correct discrimination was measured as a function of stimulus size and eccentricity (similar methods have been used by Barrett, Morrill, & Whitaker, 2000; Saarinen, 1988; Saarinen, Rovamo & Virsu, 1989; Sally & Gurnsey, 2001). In Experiments 2 and 3 orientation discrimination thresholds were measured as a function of stimulus size and eccentricity (Mäkelä et al., 1993) for both narrowband and broadband stimuli.

EXPERIMENT 1

METHOD

Subjects.

Two subjects, NW and one of the authors (SS), participated in the experiment. NW had normal vision and SS was a fully corrected myope.

Apparatus.

Stimuli were presented on a Power Mac 7100/80 computer equipped with a 17 inch colour monitor having pixel resolution of 1024 x 768. Pixel

width was 0.27 mm and the refresh rate was 75 Hz. The monitor's colour lookup table (CLUT) was calibrated to be linear using a Minolta CS-100 photometer.

Stimuli.

Stimuli were created using MATLAB (Mathworks Ltd.) and the experiments were run in Pixx (VPixx Technologies *Inc.*). Stimuli were narrowband and broadband line patterns which were tilted either clockwise or counterclockwise (±1.5°) from vertical (see Figure 2.1). The broadband stimulus was a half-cycle cosine (having a wavelength of 10 pixels) modulated by a Gaussian having a standard deviation (σ_G) of 15 pixels. We define nominal line length as including ± $3.5\sigma_G$, or 105 pixels. The narrowband stimulus was created by convolving the broadband stimulus with an isotropic $\nabla^2 G$ filter (Marr & Hildreth, 1980) which has a point-spread function defined as:

$$g(r, \sigma) = 1/\pi^4 (1 - \frac{r^2}{\sigma^2}) e^{-(r^2/2\sigma^2)} \quad [2.2]$$

where σ is the standard deviation of the Gaussian and r is the distance from the centre of the window. This filter has a bandwidth at half power of approximately 1.25 octaves (Marr & Hildreth, 1980). A $\nabla^2 G$ filter with a standard deviation σ will be most sensitive to a spatial frequency, f given by:

$$f(\sigma) = 1/(2^{0.5}\pi\sigma). \quad [2.3]$$

For a line length of 3.20° (i.e., a nominal line length of 105 pixels viewed at 50 cm) σ was 0.034°, corresponding to a peak frequency of 6.6 cycles per degree (see Equation 2.3). The standard deviation of the filter was proportional to the

length of the line such that decreasing the size of the line by a factor of two doubled the peak frequency of the filter.

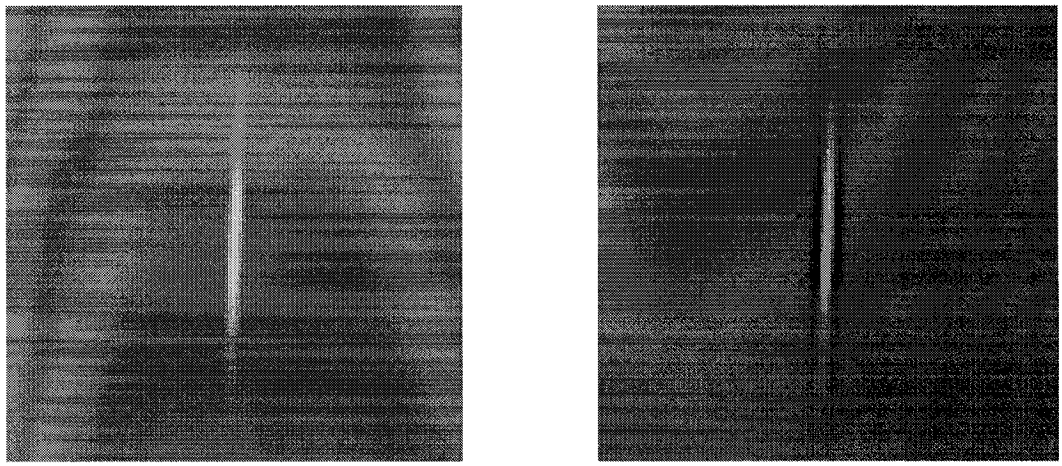

Figure 2.1. Examples of the broadband and narrowband line stimuli (left and right respectively) used in Experiment 1.

The broadband and narrowband stimuli were equated for luminance range from the background to peak luminance. The background and peak screen luminances for both stimuli were 11.9 cd/m^2 and 52.4 cd/m^2 respectively. The minimal screen luminance was the same as the background luminance for the broadband stimulus and 3.62 cd/m^2 for narrowband stimulus. Michelson contrasts for broadband and narrowband stimuli were 0.63 and 0.87 respectively.

Procedure.

Stimuli were presented at 0°, 1°, 2°, 4°, 6° and 8° in the right visual field at line lengths ranging from 3.2 to 0.30° for the broadband stimuli and 3.2 to 0.53° for the narrowband stimuli. Stimulus sizes were manipulated by varying viewing distances. For the broadband stimuli these distances were 50, 100, 200, 400 and 533 cm and for the narrowband stimuli they were 50, 100,

200, 250 and 300 cm. Stimuli were always positioned in the centre of the screen and eccentricity of presentation was controlled by moving a small green fixation dot (6 pixels in diameter) to the left of the screen centre by an appropriate distance. The fixation dot was present for all eccentricities. A red light emitting diode (LED) served as a fixation dot at eccentricities greater than half the screen width.

The task was a single interval forced-choice. A stimulus appeared for 75 msec and subjects reported whether it was tilted to the left or right of vertical using an appropriate key on the keyboard. Subjects pressed a key to initiate each trial. No feedback was given. A block consisted of 50 trials presented at a particular viewing distance and eccentricity. At each viewing distance, eccentricities were tested in the order of 0° to 8°. All eccentricities were tested at one distance before moving to the next. The order in which viewing distances were tested was random.

RESULTS

The probability of a correct detection was calculated for each combination of line length and eccentricity. As expected, at all eccentricities performance improved as line length increased. The raw data for the two subjects are summarized in Figure 2.2. For data obtained with the broadband stimuli (top graphs) the functions at each eccentricity show a fairly gradual decline with decreasing line length. By contrast, functions for the narrowband stimuli (bottom graphs) tend to show a sharper drop with decreasing line length.

To determine E_2 in each condition, we assumed that accuracy (P_{corr}) versus line length (size) functions at fixation could be described by functions

of the form

$$P_{corr}(x) = 0.5 + 0.5 * G_{\mu,\sigma}(x) \qquad [2.4]$$

where

$$G_{\mu,\sigma}(x) = \int_0^x e^{-[\log(x)-\log(\mu)]^2/\sigma} dx \qquad [2.5]$$

is a cumulative Gaussian on a log axis, having a mean of μ and a spread of σ. The mean (μ) of the function corresponds to the 75% probability of a correct detection.

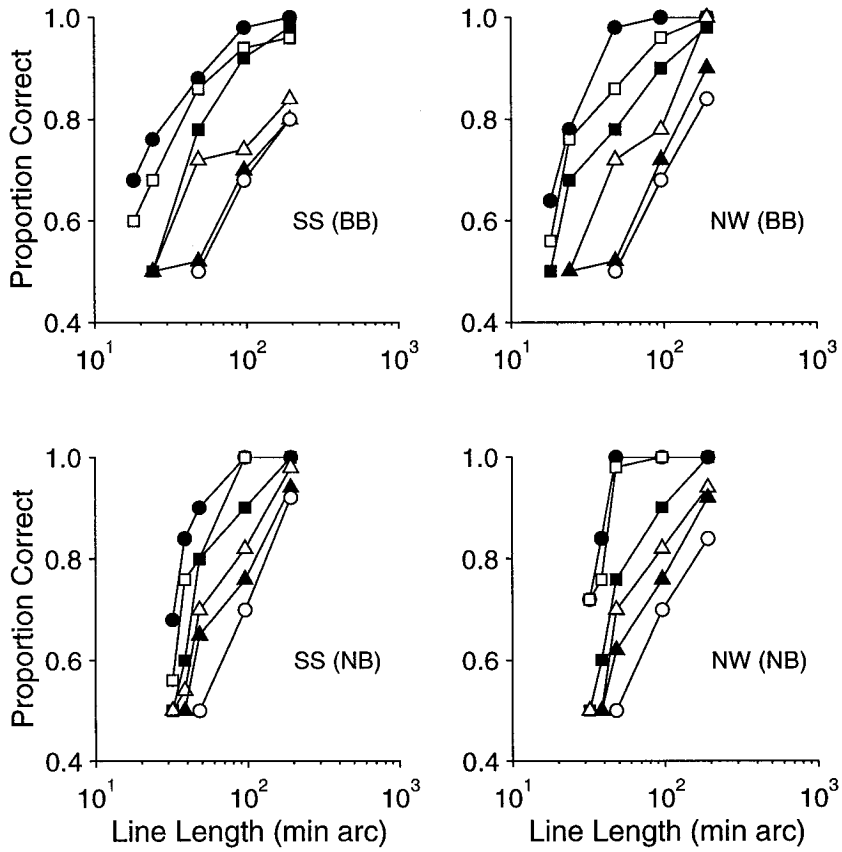

Figure 2.2. Raw data from experiment 1. Proportion correct as a function of stimulus size for broadband (top graphs) and narrowband stimuli (bottom graphs) for subjects SS and NW. Eccentricities from zero to eight degrees: 0° (filled circles) , 1° (unfilled squares), 2° (filled squares), 4° (unfilled up-arrows), 6° (filled up-arrows), 8° (unfilled circles).

Linear scaling theory holds that the data collected at each eccentricity

should conform to psychometric functions that differ only in terms of a shift along the log size axis. That is, data at all eccentricities should collapse onto the same function by scaling the sizes (x) of all stimuli at each eccentricity (E) by an appropriate scaling factor:

$$x_{scaled} = x_E / F \qquad [2.6]$$

where $F = 1 + E / E_2$ as given in Equation 2.1. The entire data set was fit by finding the parameters for μ, σ, and E_2 that minimized the deviation of the parametric curve from the scaled data. Our measure of deviation was the RMS error defined as

$$e_{rms} = \sqrt{\frac{1}{n}\sum_{i}^{n}\left[\frac{Y_{i(est)} - Y_i}{Y_i}\right]^2} \qquad [2.7]$$

n is the number of data points, Y_i is a measured data point and $Y_{i(est)}$ is the value predicted by the parametric function. We express the goodness of the fit as $G = 1 - e_{rms}$ (Melmoth, Kukkonen, Mäkelä, & Rovamo, 2000b). The data were fit using the error minimization routine provided in MATLAB (Mathworks Ltd.); this routine (*fmins*) uses the Nelder-Mead simplex (direct search) method. Numerical solutions found in this way may represent local rather than global minima. Therefore, we ran the minimization routine twenty times for each fit, each run starting from a different randomly chosen initial condition, and we report the best fits obtained.

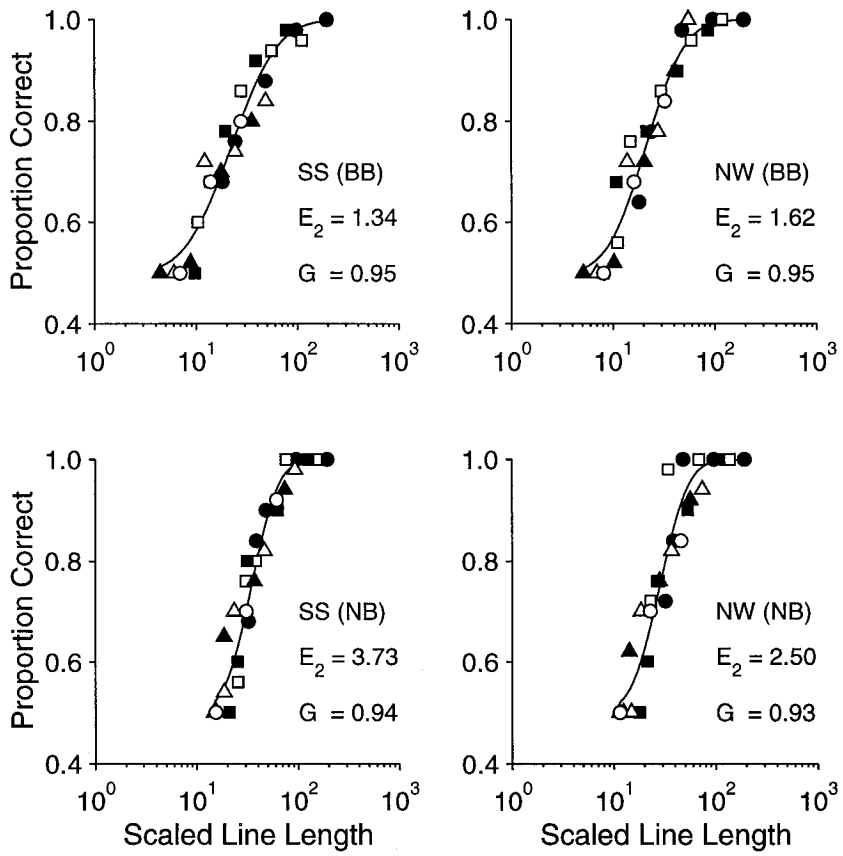

Figure 2.3. Scaled line length data for the broadband (top graphs) and narrowband (bottom graphs) line stimuli. Scaled line length equals the actual line length (in min arc of visual angle) divided by F, where F = 1+ E/E_2. Goodness of fit (G) is indicated.

Figure 2.3 shows the data from all eccentricities plotted as a function of scaled line length. The solid line shows the best fitting psychometric function defined by Equation 2.4. The fits are very good over all with goodness of fit values (G) of 0.93 to 0.95. For the broadband stimuli the average E_2 was 1.48° (1.34° and 1.62° for SS and NW respectively) and for the narrowband stimuli the average E_2 was 3.12° (3.73° and 2.50° for SS and NW respectively). The E_2s found using broadband stimuli are in line with the small E_2s often recovered in other positional acuity tasks such as orientation discrimination E_2 = 1.95° (Mäkelä et al. 1993), vernier acuity $E_2 \approx 0.77°$ (Beard, Levi & Klein, 1997; Levi

et al., 1985), E_2 = 1.06° to 1.96° (Whitaker et al., 1992b) and curvature detection and discrimination E_2 = 1.42° to 2.27° (Whitaker, Latham, Mäkelä, & Rovamo, 1993). The E_2 values (3.73° and 2.50°) obtained for the narrowband stimuli were larger than these estimates, and were more in accord with the E_2s associated with grating resolution tasks (Rovamo & Virsu, 1979; Swanson & Wilson, 1985).

In summary, for both subjects narrowband stimuli elicited larger E_2s than broadband stimuli. This result is consistent with our observation that, in general, large E_2s arise from narrowband stimuli and small E_2s arise from broadband stimuli. That is, the data suggest the possibility that it is not so much the task but the stimuli that determine the size of the recovered E_2.

EXPERIMENT 2

The classic spatial scaling study of orientation discrimination was performed by Mäkelä et al. (1993). Their task differed from our first experiment in a number of respects. Specifically, they measured orientation discrimination thresholds as a function of stimulus size and eccentricity then determined the E_2 that collapsed the threshold *vs* size functions obtained at each eccentricity onto a single function. Experiment 2 was conducted to replicate most of the conditions of the Mäkelä et al. study and to examine the bandwidth manipulation in this context. The main question is whether the bandwidth manipulation would have the same effect in the Mäkelä et al. paradigm as it did in our first experiment.

METHOD

Subjects.

Two subjects, including one of the authors (SS) participated in

Experiment 2. SS and SM were fully corrected myopes and each wore their respective distance correction. Viewing was monocular with the dominant eye (left for both subjects).

Apparatus.

Stimulus images were generated using a Power Mac G4 computer and presented on 21-inch Sony Trinitron CRT colour monitor having pixel resolution of 1600 x 1200. Pixel width was 0.233 mm and the frame refresh rate was 85 Hz. The luminance response of the display was linearized using the gamma correction software available in the VideoToolbox (Pelli, 1997) and absolute luminance levels were determined with a Minolta CS-100 photometer.

Stimuli.

Stimuli were created and the experiments were run in the MATLAB (Mathworks Ltd.) programming environment using functions in the Psychtoolbox (Brainard, 1997) that provide high level access to the routines of the VideoToolbox (Pelli, 1997). Stimuli were again narrowband and broadband line patterns (see Figure 2.4). The broadband stimulus had a Gaussian cross section (with a spread of σ_G) along its minor axis and its nominal width ($\pm 2\sigma_G$) was 11% of its length. [The stimulus dimensions were selected to be similar to those used by Mäkelä et al. (1993).] The narrowband stimulus was created by convolving the broadband stimulus with a $\nabla^2 G$ filter. For a line length of 3°, for example, the standard deviation (σ) of the filter was 0.062°, corresponding to a peak frequency of 3.67 cycles per degree (see Equation 2.3). The standard deviation of the filter was proportional to the

length of the line such that the peak frequency of the filter decreased by a factor of two with each doubling of stimulus size. Bandwidth at half power was approximately 1.25 octaves. The parameters of the filter were chosen somewhat arbitrarily; the qualitative constraint was that the appearance for the stimulus should not be altered dramatically by filtering.

All stimuli were presented against a background luminance of 26.1 cd/m^2. The broadband stimulus had a peak luminance of 79.8 cd/m^2, whereas the narrowband stimulus had luminance values ranging from 68.4 cd/m^2 to 15.9 cd/m^2. Therefore the broadband and narrowband stimuli were approximately equated for luminance range and had Michelson contrasts of 0.51 and 0.62 respectively.

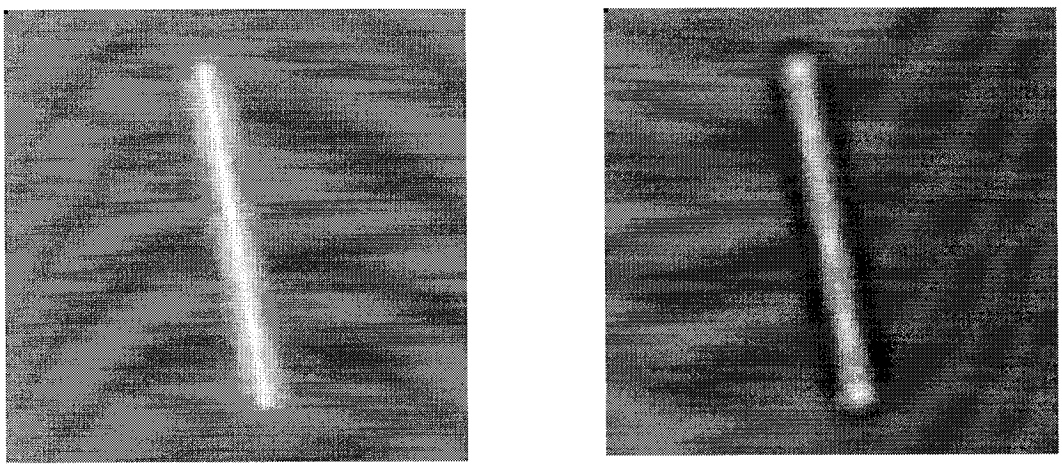

Figure 2.4. An example of the stimulus displays used in Experiment 2. The broadband stimulus (left) has a Gaussian cross section. The narrowband stimulus (right) was created by convolving the broadband stimulus with a small isotropic bandpass filter.

Procedure.

Orientation thresholds were measured over a range of sizes at 0°, 2.5°, 5°, 10° and 15° in the right visual field (temporal retina). Stimulus sizes ranging from 3° to 0.375° were manipulated by varying viewing distances.

These distances were 50, 100, 200 and 400 cm. The smallest stimulus size (0.1875°) was achieved by decreasing stimulus extent by a factor of two (112-56 pixels; i.e. 2.6-1.3 mm) at the furthest viewing distance. The largest stimulus sizes were created by changing pixel resolution to 800 x 600 and increasing the number of pixels composing the stimulus. This produced a maximal size of 15.6 mm (18° when viewed from 50 cm). Stimulus sizes larger than 12° were not tested for the narrowband stimulus because the convolution prohibited the generation of very large displays in real time. The experiment was conducted in a dimly lit room and the horizontal stimulus location was jittered by 5% of the stimulus size from trial to trial.

A trial consisted of the sequential presentation of two line stimuli. Each pattern was presented for 200 msec separated by an inter-stimulus interval of 300 msec. One of the lines was vertical and the other was tilted counter-clockwise. The subject's task was to report via the mouse which interval contained the tilted stimulus, i.e. a two-interval forced choice (2IFC).

Thresholds were obtained using an adaptive procedure (QUEST, Pelli, 1987; Watson & Pelli, 1983) which assumes an underlying Weibull function. The 82% correct detection level was taken as threshold. Auditory feedback was provided after each response. To avoid fatigue the data were collected in a large number of sessions lasting approximately 25 minutes each. All threshold estimates resulted from approximately 75 trials and the final threshold represents the mean of 2 to 4 estimates. The subjects received extensive practice with the task before data collection began.

RESULTS

Figure 2.5 shows orientation discrimination thresholds plotted against

line length for each of the five eccentricities. At each eccentricity thresholds show an initial rapid decrease followed by a more gradual change, and finally reach a plateau at long line lengths. Thresholds appear to approach the same minimal value across eccentricities and do not appear to differ substantially for broadband and narrowband stimuli. Minimum average orientation thresholds were 0.56° for both the broadband and narrowband stimuli for subject SS and were 0.55° and 0.53° for subject SM.

Following Mäkelä et al. (1993) the orientation threshold versus line length data at all eccentricities were assumed to be well described by the function

$$\theta = \theta_{min} * (1 + L_{crit} / x)^n \qquad [2.8]$$

where θ is the orientation threshold, θ_{min} refers to the smallest discriminable orientation difference, L_{crit} refers to the critical line length marking the transition between the decreasing and constant parts of Equation 2.8, n determines the slope of the line and x refers to scaled line length. According to linear scaling theory, thresholds at all eccentricities should fall onto a single curve when line length is scaled (divided) by an appropriate constant; i.e., $F = 1 + E / E_2$. The entire data set was fit by finding parameters for θ_{min}, L_{crit}, n, and E_2 that minimize the deviation of the data from the parametric curve. The data fitting method used here was exactly as in Experiment 1 except that the error measure was defined as in Equation 2.9, which, according to Melmoth et al. (2000b) is appropriate when the data are expressed on a logarithmic scale (e.g., Figure 2.5).

$$e_{rms} = \sqrt{\frac{1}{n}\sum_{i}^{n}\left(\log Y_{i(est)} - \log Y_i\right)^2} \qquad [2.9]$$

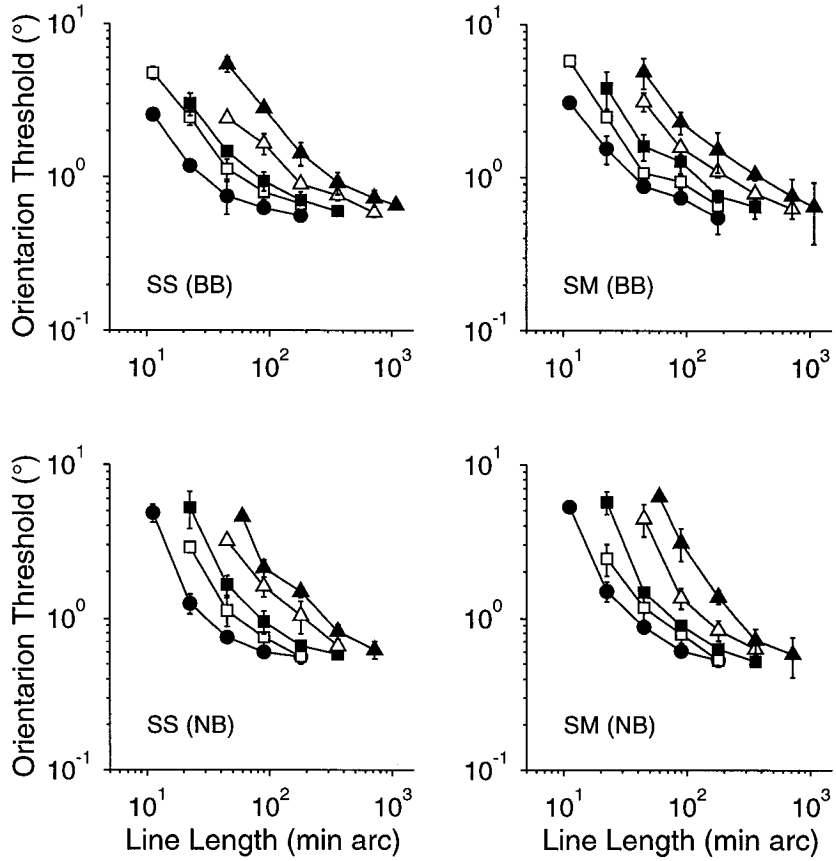

Figure 2.5. Orientation discrimination thresholds (in degrees of rotation) at each eccentricity plotted against line length for broadband (top graphs) and narrowband (bottom graphs) line stimuli for subjects SS and SM. The standard errors are shown for each point. Eccentricities from zero to sixteen degrees: 0° (filled circles) , 2.5° (unfilled squares), 5° (filled squares), 10° (unfilled up-arrows), 15° (filled up-arrows).

Scaled line length data for broadband and narrowband stimuli for the two subjects are shown in Figure 2.6 with best-fitting functions indicated as solid curves. Goodness of fits values were G = 0.95 for broadband stimuli (both subjects) and G = 0.93 and 0.94 for narrowband stimuli. For the broadband stimuli the average E_2 was 2.36° (2.08° and 2.64° for SS and SM respectively). These values of E_2 are close to those reported by Mäkelä et al.

(1993) using similar broadband stimuli (E_2 = 1.95°). The average E_2 recovered using the narrowband stimuli was 3.2° (3.25° and 3.15° for SS and SM respectively). We note that E_2s were on average 36% larger for the narrowband than the broadband stimuli (56% larger for SS and 19% larger for SM).

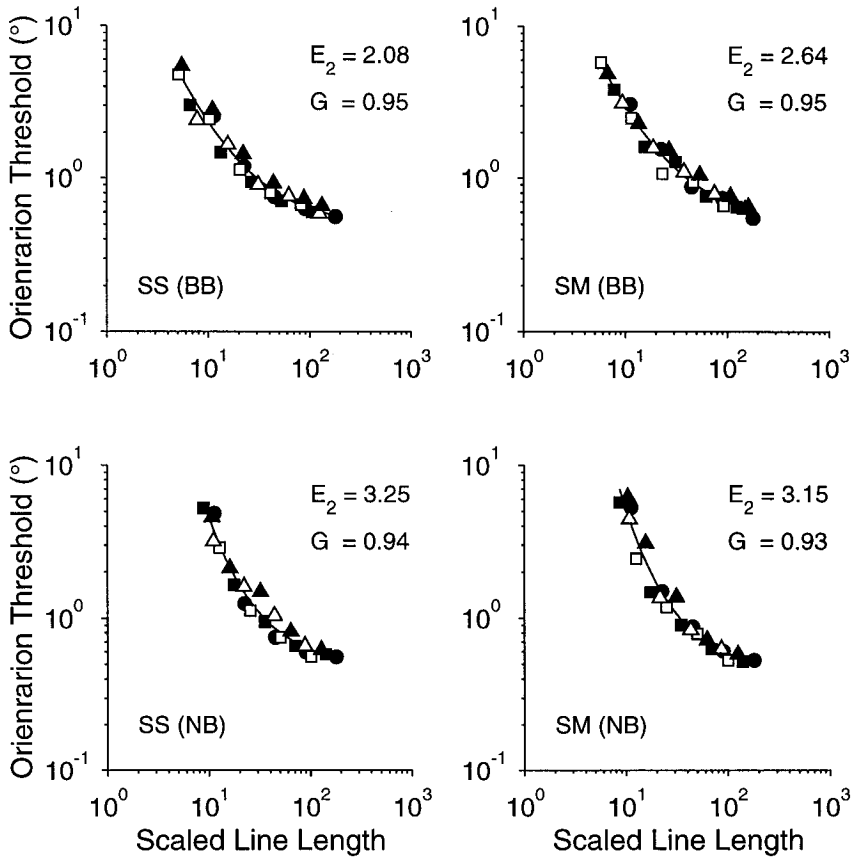

Figure 2.6. Scaled line length data for the broadband (top graphs) and narrowband (bottom graphs) line stimuli. Goodness of fit (G) is indicated.

Experiments 1 and 2 show that E_2s recovered for broadband stimuli are smaller than those for narrowband stimuli. We note that the same pattern of results has been found in several other experiments. For two subjects (SS and CP) tested binocularly under the conditions of Experiment 2 we found average E_2s of 2.21° and 3.20° for broadband and narrowband stimuli

respectively (Sally & Gurnsey, 2000). In a symmetry detection experiment (similar in design to Experiment 1), average E_2s for three subjects were 2.23° and 3.68° for broadband and narrowband stimuli respectively (Sally & Gurnsey, 1999). Therefore, these results are consistent with our observation that stimulus characteristics rather than task demands *per se* may determine the recovered E_2.

Why do narrowband and broadband stimuli produce their characteristically different E_2s? There is an interesting pattern in the results of Experiments 1 and 2 that might suggest an uncontrolled performance limitation that inflates the E_2s associated with narrowband stimuli. If one considers the bottom two panels of Figure 2.2 [SS(NB) and NW(NB)] it is clear that the shift required to align the data at low performance levels is less than the shift required to align that data at higher performance levels. This means that if E_2s are calculated at low performance levels they should be larger than those calculated at high performance levels; the results of these and subsequent calculations are shown in *endnote 1*. A similar analysis may be conducted on the results of Experiment 2. In this case low performance is associated with large orientation thresholds and high performance with small orientation thresholds. For subject SS(NB) [but not for SM(NB)] a greater shift is required to align the high-performance parts of the curves than the low performance parts. A similar pattern was found by Sally and Gurnsey (2000) in the data of subjects SS and CP. Thus in five of six cases stimuli producing poor foveal performance elicit larger E_2s than those producing good foveal performance. Put differently, E_2 appears to depend on the size of the foveal stimulus that serves as the standard, against which peripherally presented

stimuli are size scaled to match for elicited performance.

It is likely that reducing the size of narrowband stimuli reduces the stimulus contrast transferred through the visual system. (As one would expect, contrast thresholds for detection of these stimuli increase with reductions in stimulus size.) We speculate that very small narrowband stimuli elicit lower perceptual contrast than large narrowband stimuli. Reductions in perceptual contrast are likely to have the same effect as reductions in physical contrast; viz., reduced accuracy and increased orientation discrimination thresholds (Reisbeck & Gegenfurtner, 1998; Webster et al., 1990; Westheimer, Brincat & Wehrhahn, 1999). At small stimulus sizes then there may be two limits on performance; viz., a mismatch between the size of the stimulus and smallest mechanism available to encode it, and sub-optimal perceptual contrast. It is possible that for relatively large stimuli perceptual contrast does not play a role in limiting performance. This idea is consistent with the finding that orientation discrimination thresholds become asymptotically low at high contrasts (Webster et al., 1990). Thus, the relative contribution of different factors to orientation discrimination thresholds may change as a function of stimulus size leading to our observed size--or performance--dependent E_2s The excellent fits achieved by a single shift (as in Figures 2.3 and 2.6) may disguise multiple eccentricity-dependent limitations in the data.

In the foregoing discussion we considered narrowband stimuli only. However, the same analysis may be applied to broadband stimuli. For all broadband stimuli in Experiments 1 and 2 the shifts required at low performance levels are less than the shifts required at high performance levels. However, this effect was not found by Sally and Gurnsey (2000) for

broadband stimuli in subjects SS and CP. Furthermore, the effect was arguably present in only one of the three subjects in the Mäkelä (1993) study. Thus, in only four of the nine cases just mentioned E_2 was larger for small stimuli than for large stimuli.

These results suggest that perceived contrast may vary with stimulus size and in some cases inflate E_2. Such inflation would seem more likely to occur when stimulus contrast is close to detection threshold. This might explain why the broadband stimuli in Experiments 1 and 2 elicit the effect whereas it is not found in the results of Mäkelä et al. (1993); their Methods section suggests that stimuli were presented at much higher contrasts than ours[1]. In any case, there is reason to believe that performance may be limited by sub-optimal perceptual contrast in addition to a mismatch between the size of the stimulus and smallest mechanism available to encode it. If this is the case then effects of perceptual contrast should be controlled when comparing the size scaling required for broadband and narrowband stimuli. If uncontrolled differences in perceptual contrast are responsible for the characteristically different E_2s found for broadband and narrowband stimuli in Experiments 1 and 2 then controlling for effects of perceptual contrast should reduce this difference.

EXPERIMENT 3

The subjects, apparatus, data collection, stimulus displays and viewing conditions were identical to those used in Experiment 2. Experiment 3 differed from Experiment 2 only in that orientation thresholds had to have reached a saturation or asymptotic level with increases in stimulus contrast to

[1] We have no explanation for why this effect should have been shown for SS under conditions of monocular testing but not under conditions of binocular testing. It may be that the effect is more tenuous for the broadband stimuli.

be used in the calculation of E_2.

METHOD

Stimulus sizes/viewing distances were selected in pilot experiments as follows. Orientation discrimination thresholds were measured for a range of stimulus sizes at stimulus contrasts that were usually 50 to 100% of the maximum available contrast. Orientation thresholds had to remain constant from at least 75% to 100% of the maximum contrast for the data points to be used in the calculation of E_2. Two thresholds were measured at 50, 75, 85 and 100% of the highest available contrast. Average orientation thresholds consisted of 3 or 4 measurements of threshold taken at maximal contrast levels. The resulting stimulus sizes were 18° to 0.25° for the broadband stimulus and 12° to 0.375° for the narrowband stimulus.

RESULTS

Figure 2.7 shows orientation discrimination thresholds as a function of line length for each of the five eccentricities. Similar to Experiment 2, orientation thresholds decreased with increasing line length and minimum thresholds were fairly similar across eccentricities. Minimum average orientation thresholds were similar for the two types of stimuli (0.60° and 0.52° for the broadband and narrowband stimuli respectively for subject SS and 0.76° and 0.80° degrees for subject SM). The requirement that orientation thresholds remain constant with changes in stimulus contrast effectively eliminated the smallest stimulus sizes at each eccentricity and reduced the largest orientation thresholds.

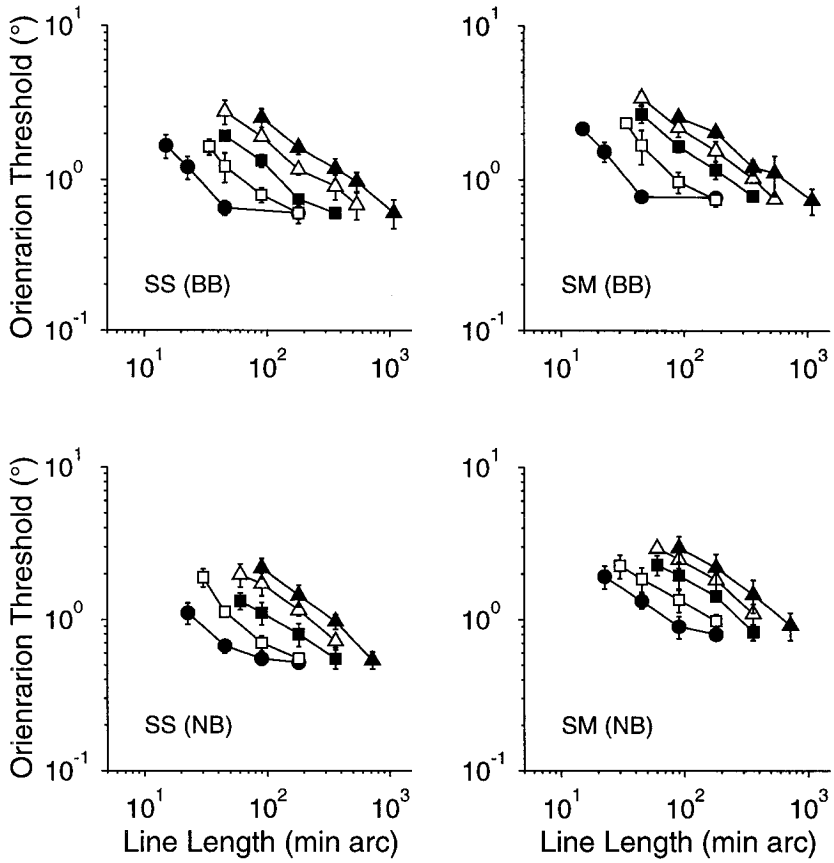

Figure 2.7. Orientation discrimination thresholds (°) at each eccentricity plotted against line length for broadband (top graphs) and narrowband (bottom graphs) line stimuli for subjects SS and SM. Standard errors are indicated. Eccentricities from zero to fifteen degrees: 0° (filled circles), 2.5° (unfilled squares), 5° (filled squares), 10° (unfilled up-arrows), 15° (filled up-arrows)

We calculated E_2 using the same fitting equation and procedure employed in Experiment 2. The scaled data are shown in Figure 2.8. Goodness of fit values ranged from 0.95 to 0.97. For the broadband stimuli the average E_2 was 1.38° (1.29° and 1.47° for SS and SM respectively) and for the narrowband stimuli the average E_2 was 1.64° (1.44° and 1.83° for SS and SM respectively). Interestingly, the observed performance level dependent E_2s were found in three of the four conditions. In other words, controlling for perceptual contrast did not completely eliminate the performance level

dependent E_2 effect; see *endnote* 2. Note, however, that E_2s recovered for all performance levels were generally less than 2 over all (1.46° on average) consistent with the results of Mäkelä et al. (1993).

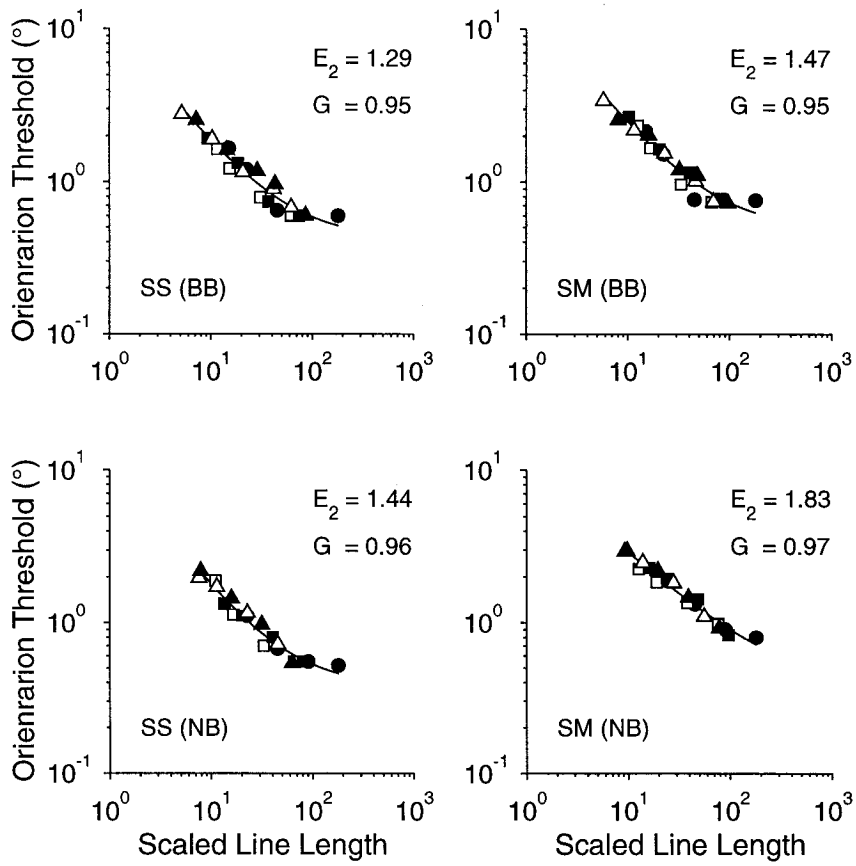

Figure 2.8. Scaled line length data for the broadband (top graphs) and narrowband (bottom graphs) line stimuli for subjects SS and SM. Goodness of fit (G) is indicated.

The results of Experiments 2 and 3 were submitted to a 2 (Experiments) by 2 (bandwidths) analysis of variance with E_2 as the dependent variable. The analysis revealed a main effect of Experiment indicating that E_2s in Experiment 3 were significantly smaller than those of Experiment 2 [$F(1, 1) = 67081$, $p < .005$], as predicted. The effect of bandwidth was not significant at the 0.05 level [$F(1, 1) = 19.5$, $p > .14$]. We expected that E_2 would vary as a function of bandwidth in Experiment 2 but less so, or not at all in Experiment 3, and

thus predicted a significant Experiment by bandwidth interaction. This trend is clearly evident in the data for the two subjects but is not statistically significant [$F(1, 1) = 19.5$, $p > 0.37$]. However, we note the low power of our statistical test.

GENERAL DISCUSSION

Experiments 1 and 2 showed that E_2s for broadband stimuli were greater than for narrowband stimuli. When effects of perceptual contrast on orientation discrimination thresholds were controlled in Experiment 3 the difference between the broadband and narrowband conditions was greatly attenuated. This result is consistent with the idea that it is "possible to equate foveal and peripheral performance by spatial scaling for certain tasks as long as contrast is high" (Mäkelä et al., 2001, p. 600).

Mäkelä et al. (2001; see also Melmoth et al., 2000a,b and Strasburger, Rentschler & Harvey, 1994) have argued that size scaling may be insufficient to explain all eccentricity-dependent variance when stimulus contrast is low. Mäkelä et al. performed a face discrimination task in which they measured contrast sensitivity as a function of stimulus size [i.e., contrast sensitivity functions (CSFs)] at a range of eccentricities. Classically, the shift along the size axis (horizontal shift) necessary to collapse the CSFs obtained at each eccentricity on to a single function specifies E_2. In many cases, however, the CSFs were found to asymptote at different maximal sensitivities; often peak sensitivity drops with eccentricity. In such a situation a single shift is insufficient to collapse all CSFs onto a single curve. To do so requires both a horizontal shift (representing the size scaling associated with the task) and a vertical shift (representing the contrast scaling associated with the task).

When the CSFs were aligned with only a horizontal shift, relatively large shifts (E_2s of 1.43° and 1.87° for two subjects) were needed (and a substantial amount of variability in the data remained unexplained). When the horizontal shift was accompanied by a vertical shift then smaller horizontal shifts (E_2s 2.73° and 3.19° for two subjects) were required to align the curves.

Our results and those of Mäkelä et al. (2001) indicate that a failure to control for perceptual contrast can result in erroneous estimates of E_2. Yet the direction (smaller or larger) of this difference appears to depend upon the level of contrast at which discrimination performance is evaluated. This raises a question about the size of E_2s that might be recovered in an orientation discrimination task using the method described by Melmoth et al. (2000b) and Mäkelä et al. (2001).

Sally, Gurnsey, and Poirier (2002) performed just such a study using broadband stimuli identical in structure to those shown in the left panel of Figure 2.4. One stimulus was vertical and the other was tilted 1.5° counterclockwise. A two-interval forced-choice procedure was used in which subjects were to report the interval containing the tilted stimulus. We determined the contrast required to make this discrimination at a range of stimulus sizes and eccentricities. We simultaneously solved for the size and contrast scaling necessary to collapse the CSFs onto a single parametric curve. Size-scaling E_2s for the two subjects of Experiment 3 were 4.51° and 5.69° for SS and SM respectively. The contrast scaling E_2s were 25.86° and 10.10° respectively. Even when contrast was not scaled our E_2s were quite large (3.51° and 3.12° for SS and SM respectively).

Our original observation was that broadband and narrowband stimuli

tend to be associated with different E_2s and these different E_2s were thought to reflect different kinds of eccentricity-dependent changes in visual processing. The results of the present study combined with those of Sally et al. (2002), suggest that it is not the difference in bandwidth *per se* that produced the characteristically different E_2s in previous studies. Rather, the difference seems to result from the fact that narrowband stimuli are typically employed at threshold level contrasts, whereas broadband stimuli are most often employed at contrasts that are vastly greater than threshold. It may be that higher level cortical limitations are only revealed when perceptual contrast is sufficiently high.

We conclude that large E_2s will be recovered when orientation sensitivity is measured at contrasts close to detection threshold and small E_2s will be recovered when orientation sensitivity is measured well above contrast detection threshold. This result is consistent with our analysis of E_2 as a function of performance level. It is interesting to note that recent psychophysical (Mareschal, Henrie & Shapley, 2002) and physiological (Kapadia, Westheimer & Gilbert, 1999; Sceniak, Ringach, Hawken & Shapley, 1999) data suggest that cortical receptive field sizes change as a function of stimulus contrast. If this increase is relatively greater at the fovea than in the periphery, this may explain why large E_2s are recovered for low-contrast stimuli.

When perceptual contrast was controlled in Experiment 3, E_2s associated with orientation discrimination are all less than 2 (Figure 2.8) Therefore, our results are generally consistent with those of Mäkelä et al. (1993). As mentioned, their stimuli appear to have been of higher contrast

than those used in Experiments 2 and 3. This may explain why their data do not show the same performance-level-dependent E_2s that we found in Experiment 2. The fact that three of the four panels of Figure 2.7 show that the slopes of the threshold by size functions change as a function of eccentricity is intriguing. These changes cannot be attributed to uncontrolled differences in perceptual contrast. Should such results be found consistently, it would mean that the form of the psychometric function changes at each eccentricity indicating that a single scaling factor is insufficient to account for all eccentricity-dependent variability in the data. Adaptations of the methods of Poirier and Gurnsey (2002) or Melmoth et al. (2000b) could be employed to test multiple limitations at high stimulus contrasts.

Endnote 1. The numerical results of the computations described in the text are provided in this footnote. For each experiment we indicate the subject and condition, and the low and high performance levels tested in brackets [e.g., SubjCond(low, high)]. Following this are the respective E_2s and their ratio (in bold).

Experiment 1.
SSBB(0.68, 0.80) = 1.83, 1.32, **1.39**;
NWBB(0.64, 0.84) = 2.34, 1.45, **1.62**;
SSNB(0.68, 0.92) = 5.55, 2.87, **1.94**;
NWNB(0.72, 0.84) = 3.93, 2.15, **1.82**.

Experiment 2.
SSBB(2.0, 0.8) = 2.14, 1.36, **1.57**;
SMBB(3.0, 0.8) = 3.07, 1.93, **1.59**;
SSNB(3.0, 0.8) = 3.81, 1.86, **2.05**;
SMNB(3.0, 0.8) = 3.30, 3.26, **1.01**.

Sally and Gurnsey (2000).
SSBB(3.0, 1.0) = 2.52, 2.79, **0.90**;
CPBB(2.0, 0.8) = 1.29, 1.86, **0.69**;
SSNB(2.0, 0.8) = 4.21, 2.27, **1.86**;
CPNB(2.0, 0.8) = 2.85, 2.12, **1.35**.

Mäkelä et al. (1993).
PM(3.0, 0.8) = 1.75, 2.95, **0.59**;
DW(3.0, 0.8) = 2.02, 1.90, **1.06**;
KL(3.0, 0.8) = 1.68, 1.30, **1.29**.

Endnote 2. For Experiment 2.3 we indicate the subject and condition, and the low and high performance levels tested in brackets [e.g., SubjCond(low, high)]. Following this are the respective E_2s and their ratio (in bold).

Experiment 3.
SSBB(2.0, 0.8) = 1.60, 0.86, **1.86**;
SMBB(2.0, 1.0) = 1.55, 0.91, **1.71**;
SSNB(2.0, 0.8) = 1.77, 1.28, **1.38**;
SMNB(2.0, 1.0) = 1.66, 2.04, **0.81**.

PREFACE TO CHAPTER 3

In the preceding chapter Sally and Gurnsey (2003a) determined E_2s for orientation discrimination using broadband and narrowband stimuli within a spatial scaling paradigm. The results indicated that failure to control for the effects of perceptual contrast on orientation thresholds can result in inflated estimates of E_2, particularly for narrowband stimuli. Once perceptual contrast was controlled at high levels of stimulus contrast, E_2s for both types of stimuli were similar and in the range of 1.29° to 1.83°. These E_2s are far smaller than those that have been recovered for the tasks of face discrimination (Mäkelä, Näsänen, Rovamo, & Melmoth, 2001, average E_2 = 2.96°; Melmoth, Kukkonen, Mäkelä, & Rovamo, 2000b, average E_2 = 8.81°) and detection of distortions in face and grating stimuli (Melmoth, Kukkonen, Mäkelä, & Rovamo, 2000a, average E_2 = 4.99°) using a recently developed spatial scaling technique that involves measuring contrast thresholds. This observation suggested that either E_2s are larger at low contrasts or task differences were responsible for the observed variations in E_2s.

In the experiments which follow, E_2 is determined for orientation discrimination using stimuli and subjects identical to those used at high contrasts. Two primary questions were asked: 1) would E_2s be larger than those recovered at high contrasts? and 2) would double scaling be required? Two different double scaling procedures were used - the Melmoth et al. (2000a,b) and Poirier-Gurnsey (2002) methods. The procedures differ in terms of how data are collected and their models of psychophysical performance. A secondary objective was to compare the two methodologies.

CHAPTER 3

ORIENTATION DISCRIMINATION ACROSS THE VISUAL FIELD: SIZE ESTIMATES AT CONTRAST THRESHOLD

by

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ABSTRACT

Performance in detection and discrimination tasks can often be made equal across the visual field through appropriate stimulus scaling. The parameter E_2 is used to characterize the rate at which stimulus dimensions (e.g., size and contrast) must increase to achieve foveal levels of performance. We compared two data collection and data fitting methods that provide estimates of size and contrast E_2s for orientation discrimination at near threshold levels of stimulus contrast. One data collection method involved measuring contrast sensitivity for a range of fixed stimulus sizes. The second method involved measuring thresholds for combinations of stimulus size and contrast having a constant ratio. Threshold data were then scaled using both fitting procedures. Overall, the pattern of results was reasonably consistent across collection and fitting methods. Size-scaling E_2s ranged from 3.71° to 6.86°. These E_2 values are substantially larger than those recovered in an orientation discrimination task using similar stimuli at high levels of stimulus contrast (E_2 = 1.95, Mäkelä, Whitaker, & Rovamo, 1993; E_2 = 1.29° to 1.83°, Sally & Gurnsey, 2003a). E_2s associated with contrast were large (9.0° to > 100°) indicating that little or no contrast scaling was required. We conclude that the size scaling required at low contrasts may be larger than that required at high contrasts even when no contrast scaling is needed.

Performance in many spatial vision tasks declines when a stimulus of a constant size is presented at greater retinal eccentricities (e.g., Rovamo, Virsu, & Näsänen, 1978; Rovamo & Virsu, 1979; Weymouth, 1958). However, performance can often be made equal across the visual field by magnifying peripherally presented stimuli in all dimensions according to

$$F = 1 + E / E_2 \qquad [3.1]$$

where E_2 indicates that eccentricity (E) in degrees at which the size of a stimulus must be doubled relative to the foveal standard to achieve equivalent performance (Levi, Klein, & Aitsebaomo, 1984, 1985).

The suggestion that performance could be equated across the visual field through an appropriate choice of scaling factors was originally put forth by Rovamo et al., (1978), and Koenderink, Bouman, Bueno de Mesquita and Slappendel (1978). Stimuli were scaled in inverse proportion to the size of the proposed cortical neural projection area, a procedure known as M-scaling. It was assumed that performance across eccentricity for all tasks could be made equal through the use of a single set of predetermined scaling factors, one for each principal meridian of the visual field. Later research, however, suggested that the amount of peripheral size scaling required to equate task performance depends on task demands (Klein & Levi, 1987; Levi et al., 1985; Westheimer, 1982). To overcome limitations associated with M-scaling, a procedure known as spatial scaling or S-scaling, was introduced (Johnston, 1987; Johnston & Wright, 1986; Saarinen, Rovamo, & Virsu 1989; Watson, 1987; Wright, 1987). The technique makes no prior assumptions concerning the size of peripheral magnification factors. Task performance is measured for a set of stimulus sizes at each eccentricity, and is then plotted as a function of

stimulus size. If size scaling alone is sufficient to overcome the peripheral decline in performance, then threshold versus size curves at all eccentricities will have a similar shape on logarithmic axes and will be laterally shifted versions of each other. The amount by which the peripheral curves must be shifted on the size axis in order to superimpose all data determines size scaling.

Implicit in spatial scaling theory is the assumption that achieving optimal performance at each eccentricity requires an appropriate match between stimulus dimensions and the mechanisms they engage. The major limitation on peripheral performance is assumed to be an eccentricity-dependent variation in the spatial scale of the underlying neural mechanisms. According to Watson (1987) this amounts to assuming that visual processing is homogeneous throughout the visual field apart from a change in the scale of the local mechanisms at each peripheral location; the parameter E_2 is thought to reflect this eccentricity-dependent scale change.

In one of the first spatial scaling studies, Watson (1987) computed contrast thresholds for a set of Gabor stimuli at eccentricities of 0° and 3° then determined the horizontal shift on the spatial frequency axis required to align all data[1]. However, the majority of spatial scaling studies have been conducted at very high stimulus contrasts and spatial discrimination thresholds (e.g., curvature detection, vernier acuity, orientation discrimination) have been measured. Typically, size scaling successfully equates performance across eccentricities under these circumstances (e.g, Mäkelä, Whitaker, & Rovamo; 1993; Whitaker, Latham, Mäkelä, & Rovamo, 1993; Whitaker, Rovamo, MacVeigh &, Mäkelä; 1992;). For some tasks, however, performance cannot

[1] The technique proved successful for high but not low frequencies.

be made equal across the visual field through spatial scaling alone. For example, reading high contrast stimuli does not appear to be spatially scalable (Chung, Mansfield, & Legge, 1998), and the procedure has also failed for various tasks conducted at very low contrasts. For example, spatial scaling alone cannot normalize low-contrast alphanumeric character recognition (Strasburger, Harvey, & Rentschler, 1991; Strasburger, Rentschler, & Harvey, 1994) or contrast sensitivity for face discrimination (Mäkelä, Näsänen, Rovamo, & Melmoth, 2001; Melmoth, Kukkonen, Mäkelä, & Rovamo, 2000b). Melmoth and colleagues have shown that contrast scaling in addition to size scaling is required to equate face discrimination across eccentricities (Mäkelä et al., 2001; Melmoth et al., 2000b).

Mäkelä et al. (2001) argued that size-scaling estimates may be erroneous if one fails to consider the role of stimulus contrast. They had subjects perform a face discrimination task and measured the contrast required to perform the task as a function of stimulus size at a range of eccentricities. The identification sensitivity vs. size curves at each eccentricity reached different asymptotic levels indicating that a shift along the size axis was insufficient to bring all curves into alignment. The curves had to be shifted along the contrast axis as well as the size axis to superimpose all the data. When identification sensitivity curves were aligned with a single lateral shift, relatively large shifts were required, the resulting values of E_2 were small (1.43° and 1.87°) and substantial variability in the data remained unexplained. When data were shifted along the size and contrast axes (i.e., *double scaling*) smaller lateral shifts were required to align the functions, and hence the size E_2s recovered were significantly larger (E_2s of 2.73° and 3.19°).

In a related study, Sally and Gurnsey (2003a) concluded that a failure to control for perceptual contrast may influence the size of the recovered E_2 in an orientation discrimination task. Initial experiments revealed that the size scaling required to equate orientation discrimination performance at high levels of contrast was related to the spatial frequency content of the stimuli. Orientation discrimination was assessed with narrowband and broadband line-type stimuli using two methods. In the first experiment, line-type stimuli were oriented ±1.5° from vertical and we measured the proportion of correct responses as a function of stimulus size and eccentricity. Narrowband stimuli yielded relatively large E_2s (3.75° and 2.50°), whereas the E_2s recovered using broadband stimuli were smaller (1.34° and 1.62°). We obtained a similar pattern of results in a second experiment using a more conventional orientation discrimination task in which orientation thresholds were measured for a range of stimulus sizes and eccentricities (average E_2s were 3.2° and 2.36° for narrowband and broadband stimuli, respectively for two subjects). This observation led us to consider that both size and perceptual contrast might jointly determine orientation thresholds but they may not exert an equivalent influence across viewing conditions. As stimulus size is reduced, it is likely that there are concomitant reductions in perceptual contrast which would have effects similar to reductions in physical stimulus contrast (e.g., increased orientation thresholds). To eliminate the influence of perceptual contrast we presented stimuli at physical contrasts that were sufficiently high that orientation thresholds had reached an asymptotic level. The size E_2s--particularly those for narrowband stimuli--were thereby reduced considerably, and both types of stimuli yielded similar size-scaling estimates

(E_2 = 1.29° - 1.83°).

Two questions arise from the contrasting results of Sally and Gurnsey (2003a), in which it was concluded that controlling contrast leads to smaller E_2s, and those of Melmoth et al. (2000b), in which it was concluded that controlling contrast leads to larger E_2s. The first question is whether both size scaling and contrast scaling are required in an orientation discrimination task conducted at low contrast. The second is whether the size-scaling E_2s recovered in an orientation discrimination task conducted at low contrast would be similar to those recovered at high contrasts.

Melmoth, Kukkonen, Mäkelä and Rovamo (2000a) argued that contrast scaling may only be required when the task is "complex." Both contrast scaling and size scaling were necessary when the task was face discrimination but only size scaling was necessary when the task was to detect phase-distortions. These were considered to be complex and simple tasks respectively. Complex tasks are assumed to rely on high-level computations. It may be that contrast scaling is unnecessary for orientation discrimination because it may have more in common with phase-distortion detection than with face discrimination. Regardless of whether contrast scaling is required in an orientation discrimination task conducted at low contrasts, it is important to know if size-scaling E_2s for orientation discrimination tasks are similar when obtained at high and low contrasts. This question is the principal focus of the present study.

A second focus of the present study is to compare two recently proposed procedures for assessing the question of double scaling. The procedures differ in terms of how data are collected and their models of

psychophysical performance limits. The procedure used by Melmoth et al. (2000a,b) (henceforth *the Melmoth procedure*) involves measuring contrast thresholds for fixed stimulus sizes at various eccentricities. In essence, contrast sensitivity functions (CSFs) are measured at a range of eccentricities, and E_2s for size and contrast are recovered by determining the horizontal and vertical shifts required to align these CSFs. The procedure used by Poirier and Gurnsey (2002) (henceforth *the Poirier-Gurnsey procedure*) involves measuring *scale*-thresholds for stimuli having a fixed ratio of size to contrast; each such ratio is referred to as a *configuration*. Each configuration defines a straight line emanating from the origin of a space of sizes and contrasts; a scale threshold, therefore, represents a combination of stimulus size and stimulus contrast that elicits a fixed level of performance. As in the Melmoth procedure, E_2s for size and contrast are recovered by determining the horizontal and vertical shifts required to align the data[2] .

METHOD

Subjects

Two subjects, including one of the authors (SS) participated in the experiment. SS and SM were fully corrected myopes and both wore their respective distance correction during testing.

[2] Previous work has fixed contrast and varied size and orientation differences (e.g., Mäkelä et al., 1993) whereas we have fixed the orientation difference and varied size and contrast. It is possible to compute three dimensional response surfaces (performance as a function of size, contrast and orientation difference) but it is difficult as a practical matter to recover such a large data set. We therefore addressed the more focused question of the joint contributions of size and contrast to orientation discrimination because there is a base of empirical literature (e.g., Melmoth, Kukkonen, Mäkelä and Rovamo, 2000a,b; Melmoth and Rovamo, 2003) against which the results can be compared.

Apparatus

Stimulus images were generated using a Power Mac G4 computer and presented on a 21-inch Sony Trinitron CRT colour monitor having pixel resolution of 1600 x 1200. Pixel width was 0.233 mm and the frame refresh rate was 85 Hz. The background luminance of displays was 13.0 cd/m^2. Luminance resolution was increased by combining colour channels with a video summation device (Pelli & Zhang, 1991) which allows contrast resolution of up to 12-bit accuracy. Software available in the VideoToolbox (Pelli, 1997) was used to calibrate the device and correct for display non-linearities. Absolute luminance levels were determined with a Minolta CS-100 photometer.

Stimuli

Stimuli were created and experiments were run in the MATLAB (Mathworks Ltd.) programming environment using Psychtoolbox code (Brainard, 1997). Stimuli were line patterns (see Figure 3.1) having Gaussian cross sections along their minor axes. One of the line patterns was vertical and the other was tilted 1.5° from vertical. The width of each line ($\pm 2\sigma$) was 11% of its length. These stimuli were identical to those used to measure orientation thresholds at high levels of stimulus contrast (Sally & Gurnsey, 2003a). The fixed orientation difference of 1.5° was selected because we had determined in pilot testing that this was approximately the smallest angular difference at which correct discriminations could be made for a reasonable range of stimulus sizes and eccentricities. We note that the average minimum discriminable orientation difference at high contrasts for the two subjects was 0.56° and 0.55° for SS and SM respectively (Sally & Gurnsey, 2003a).

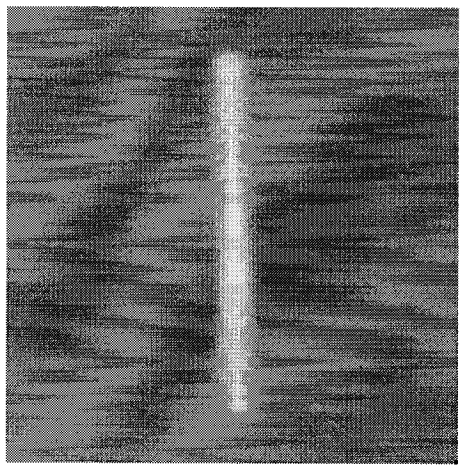

Figure 3.1. Example of the stimuli used in the Experiment. The stimulus is broadband and has a Gaussian cross section along its minor axis.

Procedure

The following details were common to both data collection procedures. Stimuli were presented at 0°, 2.5°, 5° and 10° eccentricity along the horizontal meridian in the right visual field. Eccentricity was defined as distance from fixation to the centre of the stimulus. A fixation spot (6 pixels) was presented for all eccentricities except 0° and auditory feedback was provided after each response. Viewing was binocular.

A trial consisted of the sequential presentation of two line stimuli; one was vertical and the other was tilted. Each was presented for 200 ms separated by an inter-stimulus interval of 300 ms. The subject reported via the mouse which interval contained the tilted stimulus, i.e., a two-interval forced choice (2IFC). The experiment was conducted in a dimly lit room and stimulus location was jittered from trial to trial by 5% of its height.

Thresholds were obtained using an adaptive procedure (QUEST, Watson & Pelli, 1983; Pelli, 1987) which assumes an underlying Weibull function. The 82% correct detection level was taken as threshold. Each

threshold estimate resulted from approximately 75 trials and the final threshold represents a mean of 2 to 4 estimates.

The Melmoth Procedure

Data Collection Method. Contrast thresholds for identification of the target stimulus were obtained for a range of logarithmically-spaced stimulus sizes at each eccentricity. Retinal sizes of 0.375° - 24° were achieved by varying viewing distance and/or changing the stimulus dimensions on the screen. Stimulus sizes of 3°, 1.5°, 0.75° and 0.375° were obtained by fixing stimulus size on the screen and varying viewing distance from 50 cm to 400 cm. Stimulus sizes of 6°, 12°, 18°, and 24° were generated at a viewing distance of 50 cm by increasing stimulus dimensions from 112 to 448 pixels. Pixel resolution was also changed to 800 x 600 to create the three largest sizes (12°, 18° and 24°). All eccentricities were tested for one stimulus size before moving to the next. The order in which stimulus sizes were tested was random.

Melmoth et al., (2000a,b) and Mäkelä et al., (2001) have assumed that CSFs at all eccentricities can be captured by the function

$$S = S_{max}[1 + (S_{crit} / x)^{p}]^{-n} \qquad [3.2]$$

where S is identification sensitivity, S_{max} is the maximum contrast sensitivity, S_{crit} refers to the critical image size marking the transition between the steeply and more gradually ascending parts of Equation 3.2, x is line length (size). The product of the exponents (pn) indicates the slope of the increasing part of the function. We use the reciprocal of Equation 3.2 to facilitate comparison with the Poirier-Gurnsey method. The left panel of Figure 3.2 summarizes underpinnings of the method employed by Melmoth

et al., (2000a,b). The curved lines represent hypothetical contrast thresholds for a range of stimulus sizes (indicated by the vertical lines) at two eccentricities (the left curve represents foveal data and the right curve represents 5° in the periphery). Collecting contrast thresholds may be described as *sampling* along lines that are parallel to the contrast axis.

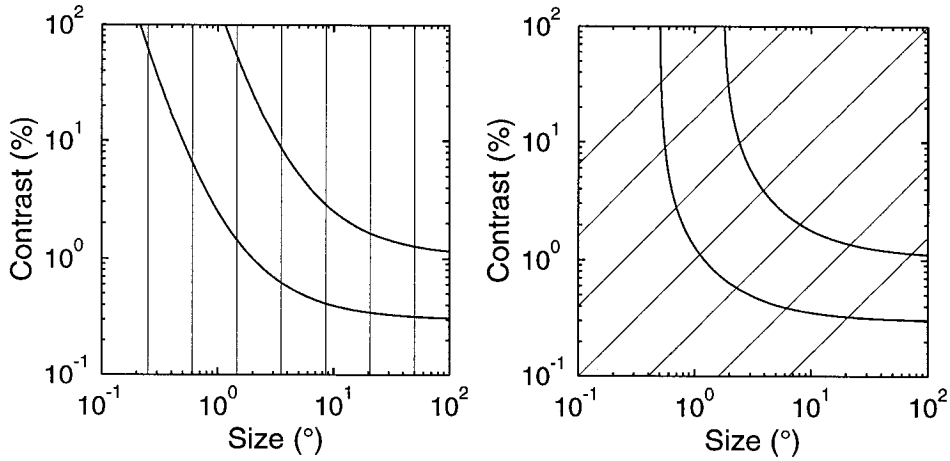

Figure 3.2. Illustration of conceptual frameworks of Melmoth et al. (2000a,b) and Poirier and Gurnsey (2002). In the Melmoth sampling method (left panel), contrast thresholds are determined for a range of stimulus sizes at several eccentricities. In the Poirier sampling method (right panel), stimuli vary simultaneously in size and contrast such that stimulus size is proportional to stimulus contrast. Each diagonal line represents a different *configuration*; i.e., ratio of size to contrast. Stimulus *scale* increases as one moves out along a configuration line. For each configuration line, threshold represents the scale that elicits 82% correct responses.

Data Fitting Method. Size scaling theory holds that data at all eccentricities should collapse onto the same function by scaling the sizes (x) of all stimuli at each eccentricity (E) by an appropriate factor:

$$x_{scaled} = x_E / F \qquad [3.3]$$

where $F = 1 + E / E_2$ as given in Equation 3.1. In addition, contrast scaling involves shifting peripheral data with respect to the contrast axis in an identical manner. In our analysis, the entire data set for each subject was

scaled by finding parameters for S_{crit} and $E_{2contrast}$, E_{2size}, p and n that minimize the deviation of the data from the parametric curve. Following Melmoth et al. (2000a,b) the measure of deviation used was RMS error defined as

$$e_{rms} = \sqrt{\frac{1}{n}\sum_{i}^{n}\left(\log Y_{i(est)} - \log Y_i\right)^2} \qquad [3.4]$$

where n is the number of data points, Y_i is a measured data point and $Y_{i(est)}$ is the value predicted by the parametric function. Goodness of the fit is expressed as G = 1 - e_{rms}. The data set was also scaled by finding the parameters that minimize the squared deviation (r^2) of the data from the parametric curve. These two measures yielded virtually identical E_2s. We therefore report results obtained using the latter method because it is the measure of deviation used in the Poirier-Gurnsey method.

The data were fit using the error minimization routine provided in MATLAB (Mathworks Ltd.); this routine (*fmins*) used the Nelder-Mead simplex (direct search) method. Numerical solutions found in this way may represent local rather than global minima. Therefore, we ran the minimization routine twenty times for each fit, each starting from a different randomly chosen initial condition, and we report the best fits (highest r^2 values) obtained in this way.

The Poirier-Gurnsey Procedure

Data Collection Method. The right panel of Figure 3.2 summarizes the underpinnings of the Poirier-Gurnsey method. The curved lines represent combinations of stimulus size and stimulus contrast that elicit threshold

level performance. The left curve represents foveal data and the right curve represents 5° in the periphery. A notable feature of these curves is that they become asymptotic with respect to the size and contrast axes. For the present stimuli, this means that thresholds are determined by an asymptotically low contrast for large stimulus sizes. And, for very high contrasts, there is an asymptotic limit to stimulus size. The diagonal lines depict combinations of size and contrast having a constant ratio. We refer to these combinations as having the same *configuration*. In a linear space these configuration lines emanate from the origin. Stimuli are said to increase in *scale* as one moves from the origin outward. In our experiments we determined scale thresholds for a number of configurations at each eccentricity. Computing thresholds in this way may be referred to as sampling along configuration lines. We use the terms "data collection method" and "sampling method" interchangeably.

The initial set of configurations was determined in pilot experiments by measuring the minimum size at which stimulus identification could be made across eccentricities when contrast was maximal. The maximum size was chosen such that stimulus size at contrast threshold would not exceed the limits of the display. Configuration lines were then selected to be at equal logarithmic steps within this space. For each configuration, line length was a fixed *multiple* of stimulus contrast; for example, a contrast of .1 and multiplier of 64 corresponds to a line that is 6.4° in length. Nine different configurations were tested at all eccentricities. These configuration were defined by line lengths (in degrees) that were 5.1, 10.2, 20.4, 40.8, 81.6, 163.2, 326.4, 652.9 and 1305.8 times stimulus contrast. A configuration of 2.55 was tested at eccentricities of 0°, 2.5° and 5° and a configuration of 1.28 was tested

at 0°. A viewing distance of 100 cm was used for all but the smallest and largest multipliers. The viewing distance was decreased to 50 cm for the largest multipliers (652.9 and 1305.8). The maximum stimulus presentation size was set at 24° for these two conditions; all thresholds were below this limit. Viewing distance was increased to 200 cm for multipliers that yielded the smallest stimulus sizes on the screen. All eccentricities were tested for one multiplier (configuration) before moving to the next. The order in which multipliers were tested was random.

Data Fitting Method. Poirier and Gurnsey (2002) proposed that scale thresholds at each eccentricity conform to a rectangular parabola (Serway, 1992; Strasburger et al., 1994) which has the form

$$(s - s_{min})(c - c_{min}) = \Omega^2 \qquad [3.5]$$

where s and c represent combinations of size and contrast at orientation discrimination threshold. s_{min} and c_{min} are size and contrast limits such that thresholds have reached a plateau or saturation level with respect to these variables. Ω^2 determines the curvature of the function at intermediate values of s and c; the curves in the right panel of Figure 3.2 are defined by Equation 3.5. Shifting the peripheral curves down to the left in log-log space corresponds to dividing the parameters (s and c) of the rectangular parabola by linear scaling factors associated with size and contrast (i.e., $F_{size} = 1 + E / E_{2size}$ and $F_{contrast} = 1 + E / E_{2contrast}$ as given in Equation 3.1). The scaling for parameter Ω^2 is equal to the product of F_{size} and $F_{contrast}$ (see Poirier and Gurnsey, 2002). The entire data set was scaled by finding parameters for s_{min}, c_{min}, Ω^2, E_{2size} and $E_{2contrast}$ that minimize the squared deviation of the data from the parametric curve along the configuration lines. The error

minimization routine was as described earlier. We report the best fits (highest r^2 values) obtained from 20 runs with different initial conditions.

RESULTS

Figure 3.3 shows combinations of stimulus size and contrast that elicit threshold level performance. The data obtained using the two sampling methods reach similar minimum Michelson contrasts; viz., 0.0096 and 0.0079 for SS and SM respectively using the Melmoth sampling method, and 0.0105 and 0.0084 for SS and SM respectively using the Poirier-Gurnsey sampling method. On the other hand, the functions become parallel to the contrast axis when the Poirier-Gurnsey sampling method was used, but not when the Melmoth sampling method was used. In other words, thresholds decline more gradually with increases in stimulus size when data are obtained with the Melmoth sampling method than with the Poirier-Gurnsey sampling method.

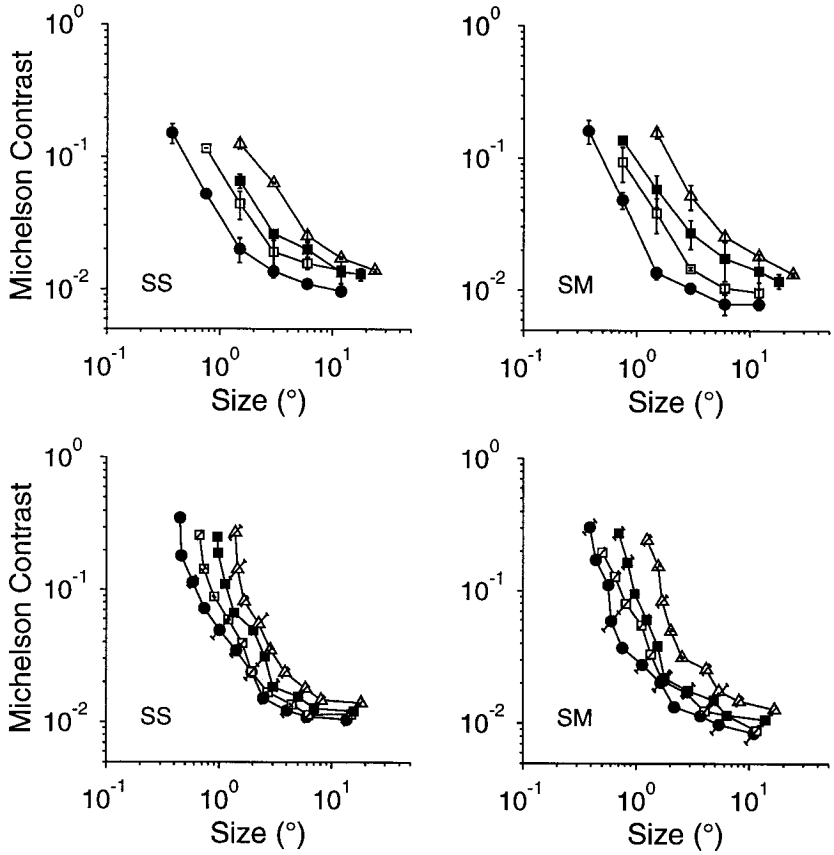

Figure 3.3. Data obtained for subjects SS and SM using the Melmoth sampling method (top graphs) and Poirier-Gurnsey sampling method (bottom graphs). In the top graphs, contrast thresholds are indicated for correct stimulus identification. In the bottom graphs, combinations of size (line length) and contrast at identification threshold are shown. In all graphs, eccentricity is plotted against line length and standard errors are shown for each point. Eccentricities from zero to 10 degrees: 0° (filled circles) , 2.5° (unfilled squares), 5° (filled squares), 10° (unfilled triangles).

The size versus contrast functions obtained using the Melmoth sampling method (Figure 3.3, top panels) are similar in form to those observed for recognition of numeric characters (Strasburger et al., 1991, 1994), face discrimination (Mäkelä et al., 2001; Melmoth et al., 2000b), and the detection of distortions in a polar grating and bandpass filtered face (Melmoth et al., 2000a). The scale thresholds in the bottom two panels of Figure 3.3 resemble the size versus wavelength functions observed by Poirier and

Gurnsey (2002) in a subjective contour discrimination task. Thus, the sampling method can influence shape of the recovered functions; we return to this point in the General Discussion.

Data Fitting: data collected using the Melmoth sampling method.

Figure 3.4 shows data obtained using the Melmoth sampling method that have been scaled using the Melmoth fitting method (top graphs) and the Poirier-Gurnsey fitting method (bottom graphs). Fits in all cases were excellent. r^2 values were very similar for both fitting methods; viz, 0.97 and 0.96 for SS and SM respectively using the Melmoth fitting method and 0.96 for both subjects using the Poirier-Gurnsey fitting method.

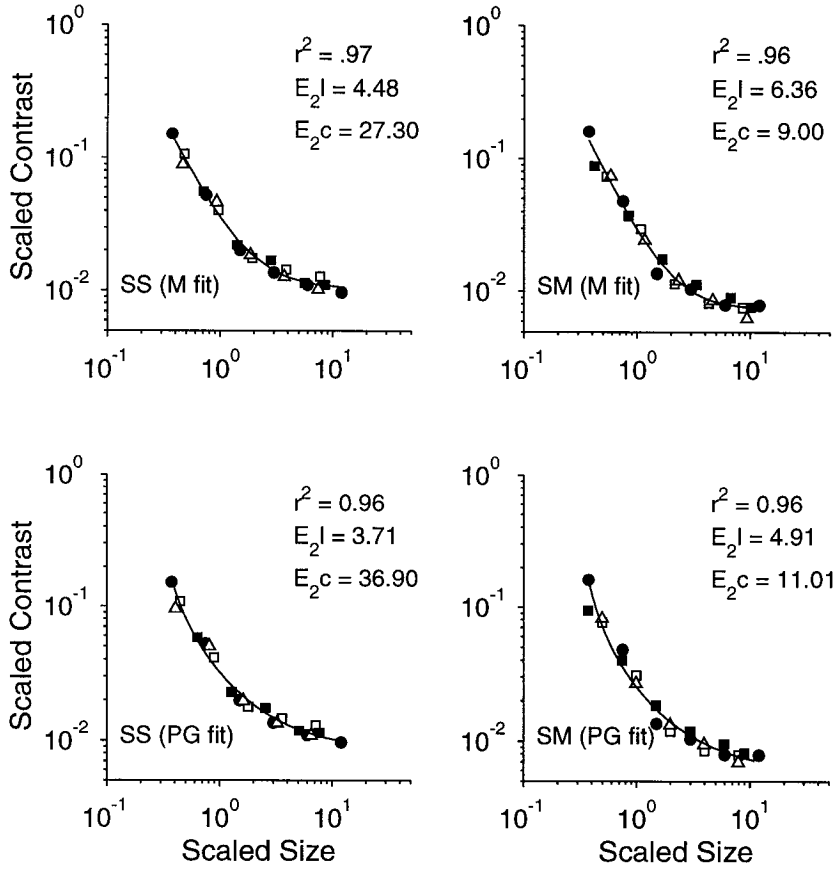

Figure 3.4. Data obtained using the Melmoth sampling method. The data have been scaled using the Melmoth fitting method (top graphs) and Poirier-Gurnsey fitting method (bottom graphs). E_2 values and fits (r^2) are as shown.

The average E_{2size} obtained with the Melmoth fitting method was 5.42° (4.48° and 6.36° for subjects SS and SM respectively). The average E_{2size} obtained with the Poirier-Gurnsey fitting method was 4.31° (3.71° and 4.91° for SS and SM respectively). Averaged over all four fits, E_{2size} was 4.87° with a standard error of 0.56°.

The average $E_{2contrast}$ obtained with the Melmoth fitting method was 18.15° (27.30° and 9.00° for SS and SM respectively). The average $E_{2contrast}$ obtained with the Poirier-Gurnsey fitting method was 23.96° (36.30° and 11.01° for SS and SM respectively). Averaged over all four fits, $E_{2contrast}$ was

20.90° with a standard error of 6.57°. It is interesting to note that $E_{2contrast}$ was about 3 times larger for SS than for SM using both fitting methods.

The two fitting methods produce similarly good fits yet systematically different E_2s. For both subjects E_{2size} was greater when the Melmoth fitting method was used (Equation 3.2) than when the Poirier-Gurnsey fitting method was used (Equation 3.5). Conversely, for both subjects $E_{2contrast}$ was smaller when the Melmoth fitting method was used than when the Poirier-Gurnsey fitting method was used. The choice of fitting method appears to affect the recovered E_2. On the other hand, under both regimes, E_{2size} is smaller than $E_{2contrast}$ indicating that sensitivity loss attributable to stimulus size increases more quickly with eccentricity than sensitivity loss attributable to stimulus contrast.

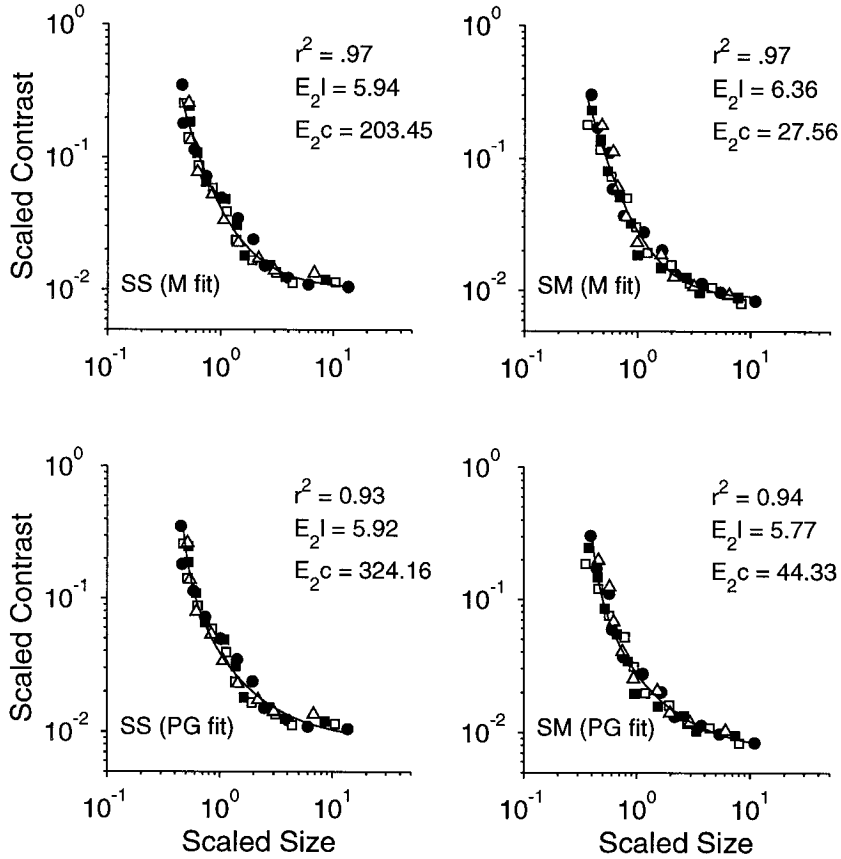

Figure 3.5. Data obtained using the Poirier-Gurnsey sampling method. The data have been scaled using the Melmoth fitting method (top graphs) and the Poirier-Gurnsey fitting method(bottom graphs) . *E2* values and fits (r^2) are as shown.

Data Fitting: data collected using the Poirier-Gurnsey sampling method.

Figure 3.5 shows data obtained using the Poirier-Gurnsey sampling method that have been scaled using the Melmoth fitting method (top graphs) and the Poirier-Gurnsey fitting method (bottom graphs). r^2 values were 0.97 for both subjects using the Melmoth fitting method. The r^2 values were 0.93 and 0.94 for SS and SM respectively when data were fit using the Poirier-Gurnsey fitting method. We note that when residual error is assessed by the vertical distance from the parametric curve (as in the Melmoth fitting method) the r^2s obtained using the Poirier-Gurnsey fitting method increase to

0.99.

The average E_{2size} for size obtained with the Melmoth fitting method was 6.15° (5.94° and 6.36° for subjects SS and SM respectively). The average E_{2size} obtained with the Poirier-Gurnsey fitting method was 5.85° (5.92° and 5.77° for SS and SM respectively). Again, E_{2size} was similar across fitting methods. Averaged over all four fits, E_{2size} was 6.0° with standard error of 0.127°.

The average $E_{2contrast}$ obtained with the Melmoth fitting method was 115.51° (203.45° and 27.56° for SS and SM respectively). The average $E_{2contrast}$ obtained with the Poirier-Gurnsey fitting method was 184.24° (324.16° and 44.33° for SS and SM respectively). Both fitting methods indicate that the E_2s for contrast were 7.3 times larger for SS than SM. Averaged over all four fits, the average $E_{2contrast}$ value was 149.88° with a standard error of 70.32°.

In the present experiments we find a reasonably consistent pattern of results across sampling methods and fitting methods. The E_2s for size ranged from 3.71° to 6.36°. These E_2s are substantially larger than those generally recovered for orientation discrimination at very high stimulus contrasts. In these cases an E_2 of 2 or less generally equates performance across eccentricities (Mäkelä et al., 1993, average E_2 =1.95°; Sally & Gurnsey, 2003a, average E_2 = 1.51°). The E_2s for contrast were smaller when the Melmoth sampling method was employed and were on average 20.90° and 149.88° for data obtained with the Melmoth and Poirier-Gurnsey sampling methods respectively. This suggests that relatively little or no contrast scaling was required.

GENERAL DISCUSSION

Previous studies have shown size-scaling E_2s for orientation discrimination for high contrast stimuli to be less than 2 (average E_2 = 1.95°, Mäkelä et al., 1993; E_2 = 1.29° - 1.83°, Sally & Gurnsey, 2003a). In our "high-contrast" experiment Sally and Gurnsey (2003a) controlled for the effects of perceptual contrast on orientation thresholds by including in the calculation of E_2 only those thresholds that had reached a saturation level such that increases in stimulus contrast led to no further changes to thresholds. In the present study, using low contrast stimuli, we found size-scaling E_2s that averaged 5.43° when contrast was simultaneously scaled. This seems to agree with the conclusions of Mäkelä et al. (2001) who argue that when contrast scaling is required, doing so increases the estimates of size-scaling E_2s. On the other hand, the finding that values of $E_{2contrast}$ are generally large raises the question of whether contrast scaling was necessary to fit the present data.

Large E_2s indicate that stimulus size must be increased only modestly with eccentricity in order to match foveal performance. Across all analyses described above, size-scaling E_2s (range = 3.71° to 6.36°) were consistently far smaller than contrast-scaling E_2s (range = 9.0° to 324°). When the data were fit without including contrast scaling, size-scaling E_2s averaged 5.82° (range = 2.83° to 9.93°) with little drop in explained variance (3% reduction on average). Because $E_{2contrast}$ tends to be large (indicating that little contrast scaling is required) and because E_{2size} remains large in the absence of contrast scaling, we conclude that contrast scaling has little effect on the size scaling required for orientation discrimination in the present experiments. In other

words, the size E_2s found at threshold contrasts are not attributable to the need to scale contrast.

In fact, size-scaling E_2s recovered at threshold contrasts are often large whether or not contrast scaling is required. For example, Melmoth et al. (2000b) reported size-scaling E_2s for face discrimination ranging from 2.39° to 25.7° with an average across subjects of 8.81°. Contrast-scaling E_2s ranged from 1.92° to 7.51° with an average of 5.53°. Mäkelä et al. (2001) found size-scaling E_2s for face perception of 2.73° and 3.19° for two subjects with corresponding contrast-scaling E_2s of 5.26° and 14.5°. Melmoth et al. (2000a) observed that size scaling E_2s of 3.60° and 6.38° equated performance across eccentricities for phase-distortion detection in both polar grating and bandpass filtered face stimuli. The authors reported that contrast scaling was not required. [We reanalyzed their data using a data fitting method that solves for an E_2 for contrast simultaneously and recovered E_2s for size ranging from 5.05° to 33° and E_2s for contrast ranging from 10.36°to 694°]. Thus, size-scaling E_2s are often fairly large at low contrast. These observations are consistent with the suggestion of Sally and Gurnsey (2003a) that low-contrast stimuli will generally elicit large size E_2s whereas high-contrast stimuli will elicit small size E_2s.

The two sampling and data fitting methods used in this study yielded comparable results. There was, however, one notable difference attributable to sampling method. The Melmoth sampling method involves measuring contrast thresholds for stimuli of fixed sizes, whereas the Poirier-Gurnsey sampling method involves determining scale thresholds for stimuli having

different configurations. Contrasts at threshold for small stimuli were larger when data were obtained using the Poirier-Gurnsey sampling method. One possible reason for this difference is that the Melmoth sampling method allows the observer to selectively attend to a stimulus of one particular size and perhaps as a consequence, more effectively engage mechanisms optimally tuned to that stimulus. There is considerable evidence that spatially-directed attention can modulate neural processing at the attended location (i.e., Huk & Heeger, 2000; Kastner & Ungerleider, 2001). With the Poirier-Gurnsey sampling method, stimuli vary in contrast and size from trial to trial. The observer may have to distribute attention across several mechanisms to perform the task. This process may be most disruptive for the smallest stimuli. Such a disruption is not seen for large stimuli; for large stimuli, contrast at threshold was very similar across sampling methods.

The size-scaling E_2s were similar for the two sampling methods. The E_2s averaged across subjects and fitting procedures were 4.89° and 6.0° for data obtained with the Melmoth and Poirier-Gurnsey sampling methods respectively. These E_2s compare with an average across the same two subjects of 1.51° obtained in our previous experiment in which contrast was controlled at very high levels (Sally & Gurnsey, 2003a).

One might argue that our results do not reflect the orientation selectivity of the cortex but reflect contrast sensitivity of pre-cortical mechanisms. After all, some have measured grating contrast sensitivity using a methodology where the forced-choice component is to distinguish between horizontal and vertical gratings, and this cannot be considered an orientation discrimination task. Furthermore, our recovered E_2s are in the range

normally associated wth grating resolution. Therefore, we have to address the claim that the orientation component of our stimulus serves only as a useful measure by which a forced-choice methodology can be used to establish contrast thresholds.

First, it is unrealistic to consider discriminating a 90° difference as qualitatively similar to discriminating a 1.5° difference. Horizontal and vertical gratings activate populations of units with non-overlapping sensitivities. It is precisely because of this that orthogonal gratings can be used to assess contrast sensitivity of pre-cortical mechanisms; the task can hardly be seen as challenging the ability of the cortex to resolve orientation differences. Put another way, discriminating horizontal from vertical can be seen as involving labelled lines (e.g., Watson & Robson, 1981) whereas discriminating a 1.5° difference clearly does not. Again, the cortex imposes no limitation on performance when there is a 90° orientation difference.

Second, it is true that at low contrasts both contrast and orientation differences combine to determine accuracy. Consider any level of contrast in Figure 3.3. A 1.5° orientation difference represents the orientation discrimination threshold *for that level of contrast:* increase or decrease the orientation difference and accuracy will change. All data points (interpolated or otherwise) in Figure 3.3 having contrast *c* tell us how stimulus size must be increased with eccentricity to maintain threshold performance. Therefore our method and task are appropriate to assessing size scaling and orientation sensitivity cortical mechanisms at low stimulus contrasts.

Sally and Gurnsey (2003b) recently recovered converging evidence for the conclusion that size-scaling E_2s for orientation discrimination depend on

stimulus contrast. We repeated the classic Mäkelä et al. (1993) study at low contrasts; subjects matched the perceived contrast of all stimulus sizes at all eccentricities to a 3° reference stimulus presented at fixation that was 2 just noticeable differences above detection threshold. E_2s of 3.42° and 3.50° were recovered for the same two subjects who had performed the high contrast version of this experiment (Sally & Gurnsey, 2003a, Experiment 3). These E_2s were on average, a factor of 2.3 times larger than those recovered at high contrasts. Therefore, all available evidence suggests that size-scaling E_2s for orientation discrimination depend on stimulus contrast; large E_2s are recovered at low contrasts and small E_2s are recovered at high contrasts.

It is possible that large size-scaling E_2s were recovered at low contrasts because of differences in the structure of orientation selective mechanisms across eccentricities at high and low stimulus contrasts. Kapadia, Westheimer, and Gilbert (1999) and Sceniak, Ringach, Hawken, and Shapley (1999) have recently shown that receptive fields of VI neurons can increase substantially as stimulus contrast is reduced. Psychophysical evidence of this phenomenon has been provided as well (Mareschal, Henrie, & Shapley, 2002; Mareschal & Shapley, 2003). If we assume that orientation selectivity is determined by a match between stimulus size and the smallest mechanism available to encode it, then changes in receptive fields at low contrasts may alter E_2 estimates if the contrast-dependent changes in receptive field sizes were relatively greater at the fovea than in the periphery; i.e., less spatial scaling would therefore be required to equate task performance across eccentricities. This possibility remains to be evaluated in psychophysical studies.

We conclude that the size-scaling E_2 for orientation discrimination

depends critically on stimulus contrast. When contrast level has been controlled, size-scaling E_2s are large for low-contrast stimuli and small for high-contrast stimuli. The conclusion may generalize to other spatial discrimination tasks. To the extent that orientation discrimination (Mäkelä et al., 1993), curvature discrimination (Whitaker et al., 1993) and discrimination of vernier offsets (Whitaker et al., 1992) depend on the same mechanisms, then all should show increases in size-scaling E_2s as stimulus contrast is reduced. This suggests that replicating some of this earlier work using high and low contrasts would be useful. Ideally, one would like to measure spatial discrimination thresholds that are not contaminated by size-dependent changes in perceptual contrast (Sally & Gurnsey, 2003a,b).

PREFACE TO CHAPTER 4

In the preceding chapter two different methods (Melmoth, 2000a,b and Poirier-Gurney, 2002) were used to recover size- and contrast-scaling E_2s for orientation discrimination at near threshold levels of stimulus contrast. Both procedures yielded a similar pattern of results, with size-scaling E_2s ranging from 3.71° to 6.86° and little to no contrast scaling required. It was noted that the size-scaling E_2s were far larger than those recovered in the high contrast experiment (Sally & Gurnsey, 2003a, average E_2 = 1.51°) as well as those obtained in the classic spatial scaling study on orientation discrimination of Mäkelä et al. (1993, average E_2 =1.95°), also conducted at high stimulus contrasts. The present experiment is identical to the high contrast orientation discrimination experiment (Sally & Gurnsey, 2003a) in all respects except for the near-threshold levels at which stimuli were presented. Stimulus contrasts are determined using a procedure by which subjects match the perceived contrast of all stimuli to a standard stimulus presented at fixation. Contrast detection thresholds are also determined for all stimuli. The primary focus of the study is to compare E_2s for the same task and subjects at high and low levels of stimulus contrast. A secondary objective is to determine whether there is a direct relationship between contrast thresholds and suprathreshold perceived contrast, as indicated by the matching procedure. This question is pertinent because a commonly used technique to equate for perceptual contrast is to present all stimuli at equal multiples of their respective detection thresholds.

CHAPTER 4

ORIENTATION DISCRIMINATION ACROSS THE VISUAL FIELD: MATCHING PERCEIVED CONTRAST NEAR THRESHOLD

by

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ABSTRACT

Performance can often be made equal across the visual field by scaling peripherally presented stimuli according to $F = 1 + E / E_2$ where E_2 is the eccentricity at which stimulus size must double to maintain foveal performance levels. Previous studies suggest that E_2 for orientation discrimination is in the range of 1.5° to 2° when stimuli are presented at high contrasts. Recent psychophysical and physiological evidence suggests spatial reorganization of receptive fields at low contrasts. Such contrast-dependent changes in receptive field structure might alter the amount of size scaling necessary to equate task performance across the visual field. To examine this question we measured orientation discrimination thresholds for a range of stimulus sizes and eccentricities (0° - 15°). We used the same procedure previously employed except that stimuli were presented at low contrasts. We controlled for the effects of perceptual contrast on thresholds through a matching procedure. A standard line of 3° in length presented at fixation was set to two just noticeable differences above detection threshold. The perceived contrast of all other stimuli was adjusted by the subject to match this one. Orientation discrimination thresholds were then obtained at these matching contrasts for all stimulus sizes and eccentricities. E_2s of 3.42° and 3.50° were recovered for two subjects; these values were about a factor of two larger than E_2s previously found for this task when stimuli were presented at high contrasts.

Performance on many spatial vision tasks depends on visual field location and tends to decline with increasing retinal eccentricity. Thresholds can often be made equal, however, when stimuli are scaled in all spatial dimensions according to

$$F = 1 + E / E_2 \qquad [4.1]$$

where E_2 indicates the eccentricity (E) in degrees at which stimulus size must double to maintain equivalent-to-foveal performance levels (Levi, Klein & Aitsebaomo, 1984, 1985). The smaller the value of E_2, the faster stimulus size must increase in the periphery in order for thresholds to remain constant. The magnitude of E_2 is often thought to reflect eccentricity-dependent changes in the spatial scale of the mechanisms required to perform the task at hand. It was therefore hoped that this psychophysically-derived measure would reveal something about the neural mechanisms that subserve performance on different tasks (Toet & Levi, 1992). Ideally, tasks could be classified according their E_2 value.

There is at least some evidence that E_2 can provide information about the functional organization of the visual system. Mäkelä, Whitaker and Rovamo (1993) pointed out that tasks such as curvature detection, vernier acuity and orientation discrimination probably rely on similar cortical mechanisms (i.e., orientation selective mechanisms) and it has been shown that these tasks elicit E_2s within a similar range; viz., curvature detection, E_2 = 1.42° to 2.27° (Whitaker, Latham, Mäkelä, & Rovamo, 1993); vernier acuity, E_2 = 1.06°to 1.96° (Whitaker, Rovamo, MacVeigh, & Mäkelä, 1992b); orientation discrimination, E_2 = 1.95° (Mäkelä et al., 1993) and E_2 = 1.29° to 1.83° (Sally &

Gurnsey, 2003a). In contrast, grating detection tasks are often associated with E_2s of 2.5° or more and are assumed to be limited by retinal mechanisms (e.g., Levi et al., 1985; Wilson, Levi, Maffei, Rovamo, & DeValois, 1990).

Unfortunately, E_2 values even for the same task (e.g., vernier acuity) can vary widely from laboratory to laboratory (see Table 2, Beard, Levi, & Klein, 1997) Also, E_2 values can vary greatly across tasks (from less than 0.1° to greater than 10°, Whitaker, Mäkelä, Rovamo, & Latham, 1992a). This has raised doubts that E_2 provides a reliable indication of visual functional organization (Beard et al., 1997).

Melmoth, Kukkonen, Mäkelä and Rovamo (2000b) and Mäkelä, Näsänen, Rovamo and Melmoth (2001) have suggested that the 100-fold range of E_2 values reported in the literature may reflect--at least in part--the use of experimental procedures that do not explicitly consider eccentricity-dependent limitations associated with stimulus contrast. They argued that contrast may need to be scaled with eccentricity in much the same way that size must be scaled, in order to capture all eccentricity-dependent variability in the data. Melmoth et al. (2000b) and Mäkelä et al. (2001) measured contrast sensitivities for target identification or detection as a function of image size at various eccentricities in the visual field. An E_2 for size (E_{2Size}) and an E_2 for contrast ($E_{2Contrast}$) were determined by computing the amount of horizontal shift (size scaling) and vertical shift (contrast scaling) required to superimpose contrast thresholds obtained at all sizes and eccentricities. Mäkelä et al. (2001) obtained values for E_{2Size} of 1.43° and 1.87° for two subjects in a face discrimination task when size scaling alone was used to scale the data. The values were larger (E_{2Size} = 2.73° and 3.19°) and more eccentricity-dependent

variance was explained, when both size and contrast scaling was performed.

Sally and Gurnsey (2003a) arrived at a similar conclusion concerning the need to control perceptual contrast, yet from a different perspective. We determined E_{2Size} for orientation discrimination using high-contrast stimuli and included in our calculations of E_{2Size} only orientation thresholds that remained at an asymptotic level over a range of stimulus contrasts (Sally & Gurnsey, 2003a). The values of E_{2Size} recovered in this way tended to be somewhat smaller (E_{2Size} = 1.29° - 1.83°) than those obtained using identical stimuli but without the requirement that thresholds reach an asymptotic level with respect to variations in contrast (E_{2Size} = 2.08° - 3.25°). Therefore, our results as well as and those of Mäkelä et al. indicate that estimates of E_{2Size} may be erroneous when the contrast dimension is not taken into account. These findings also suggested that E_{2Size} may depend on the contrast level at which discrimination performance is evaluated; viz., E_{2Size} may be small when obtained with high-contrast stimuli and large when obtained with low-contrast stimuli.

On the other hand, orientation discrimination and face discrimination may rely upon quite different processes. Therefore, to assess the suggestion that E_{2Size} is relatively larger for low-contrast stimuli, it would be best to compare the effect of contrast within a single task. With this in mind, Sally, Poirier and Gurnsey (2002) determined E_{2Size} for orientation discrimination using a broadband stimulus identical to that used by Sally and Gurnsey (2003a) using two methods (Melmoth et al., 2000a,b; see also Strasburger, Harvey, & Rentschler, 1991 and Poirier & Gurnsey, 2002) that control for

contrast at near-threshold levels. The subject's task was to discriminate between a vertical line and one oriented 1.5° from vertical. We found that both procedures yielded comparable size-scaling estimates (E_{2Size}) that averaged 5.44° (range 3.71° to 6.36°). These values are far larger than those recovered in our high-contrast experiment in which an average E_{2Size} of 1.51° equated orientation discrimination performance across eccentricities (Sally & Gurnsey, 2003a). We also found that the average $E_{2Contrast}$ was very large, indicating that very little or no contrast scaling was required to capture all eccentricity-dependent variation in the data.

Taken together, the results of Sally and Gurnsey (2003a) and Sally et al. (2002) suggest that small values of E_{2Size} are recovered at high contrasts and large values of E_{2Size} are recovered at low contrasts. However, the conditions of the two experiments were quite different so it would be useful to replicate most of the conditions of Sally and Gurnsey (2003a) using stimuli that are equated for perceptual contrast. This is the objective of the present research.

To achieve this, we selected a 3° line presented at fixation to serve as a reference stimulus. The reference was then set to a contrast level two just noticeable differences (JNDs) above detection threshold and the perceived contrast of all other stimuli at all eccentricities was adjusted by the observer to match that of the standard. Once the perceived contrast of all line stimuli was equated we determined orientation discrimination thresholds for all line sizes at all eccentricities. The amount by which peripheral curves had to be shifted laterally to superimpose all data determined the E_{2Size} for orientation discrimination.

METHOD

Subjects

Two subjects, SM and one of the authors (SS), participated in all phases of the experiment. Both subjects were moderate myopes and wore their distance correction during testing. Viewing was monocular with the dominant eye (left for both subjects) and stimuli were presented to the temporal retina.

Apparatus

Stimulus images were generated using a Power Mac G4 computer and presented on a 21-inch Sony Trinitron CRT colour monitor having a pixel resolution of 1600 x 1200. Pixel width was 0.233 mm and the frame refresh rate was 85 Hz. Background luminance of displays was 13.0 cd/m^2. Luminance resolution was increased by combining color channels with a video summation device (Pelli & Zhang, 1991) which allows contrast resolution of up to 12-bit accuracy. Software available in the VideoToolbox (Pelli, 1997) was used to calibrate the device, and correct for display non-linearities. Absolute luminance levels were determined with a Minolta CS-100 photometer.

Stimuli

Stimuli were created and the experiments were run in the MATLAB (Mathworks Ltd.) programming environment using routines provided in the Psychtoolbox (Brainard, 1997) that permit access to the routines in VideoToolbox (Pelli, 1997). Stimuli were broadband line patterns (see Fig. 1) having Gaussian cross sections (with a spread of σ_G) along their minor axes. The nominal line width ($\pm 2\sigma_G$) was 11% of its length. These stimuli were identical to those we used previously in orientation discrimination tasks by

Sally and Gurnsey (2003a) and Sally, et al., (2002) and similar to stimuli used by Mäkelä et al. (1993).

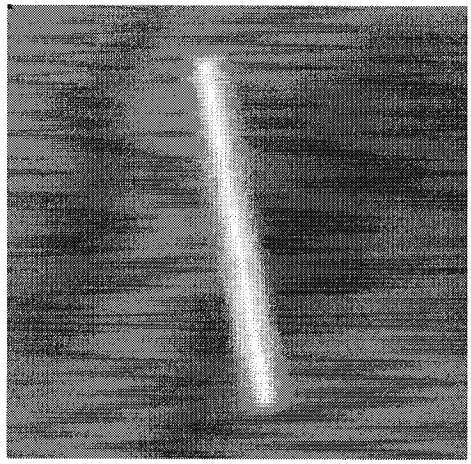

Figure 4.1. Example of the broadband line stimulus used for all tasks.

Procedure

The following details of the procedure were common to all tasks. Thresholds were obtained using an adaptive procedure (QUEST, Pelli, 1987; Watson & Pelli, 1983) which assumes an underlying Weibull function. All tasks were 2IFC and the 82% correct detection level was taken as threshold. Auditory feedback was provided after each response. To avoid fatigue the data were collected in a large number of sessions lasting approximately 25 minutes each. All testing was conducted in a dimly lit room. Threshold estimates resulted from approximately 60 to 65 trials and the final threshold represents the mean of three estimates. The subjects received extensive practice with all tasks before data collection began.

1) Selecting the contrast level of reference stimulus

The reference was a 3° vertical line stimulus identical to that to be used in the orientation discrimination task and within the range of stimulus sizes that were tested (0.1875° - 12°). The stimulus was presented at fixation and

preceded by a fixation dot (6 pixels in diameter). The QUEST procedure was used to determine contrast detection threshold for the reference stimulus. Each stimulus interval was 200 ms in duration with an inter stimulus interval (ISI) of 300 ms. Each interval was signaled by an auditory tone as well as a square frame (2 pixel line width at 17.25 cd/m^2, 5.8 degrees in diameter) centred at the location of the test stimulus. A frame was only provided for this part of the experiment and was required because of the brief duration of test and inter-stimulus intervals. The subject's task was to indicate, via the mouse, the interval in which the stimulus had appeared.

A similar 2IFC adaptive procedure was used to determine contrast increment thresholds (JNDs) for the reference stimulus. Stimulus interval and ISI duration were as indicated above. A trial consisted of the sequential presentation of the two, 3° vertical line stimuli. One interval contained the stimulus set to a fixed predetermined level of contrast (contrast threshold or one JND above threshold) and the contrast of the test stimulus in the other interval was varied. The subject's task was to indicate the interval containing the stimulus with the highest contrast.

2) Matching perceived contrast / Measuring contrast detection thresholds

The 3° reference line was set to two JNDs above detection threshold for each subject. The contrast of this line was used as a standard against which the contrast of all line sizes at all eccentricities was matched using the method of adjustment. The reference and test stimulus were presented simultaneously for 500 ms at all eccentricities except fixation. (The 500 ms presentation duration was found to produce less variable matches than the 200 ms presentation duration.) For foveal presentations, the reference and test

stimuli were presented sequentially with an inter-stimulus interval of 600 ms. Subjects matched the perceived contrast of the test stimulus with that of the reference by pressing the up and down arrow keys on the computer keypad. While the arrow keys were depressed no stimulus appeared. When the arrow keys were released the stimulus immediately reappeared on the screen for 500 ms. The subject repeated the adjustment process until satisfied with the match (usually about 10-20 presentations were required). The subject then terminated the trial using a key on the keyboard.

Stimulus sizes were manipulated by varying viewing distance and/or changing the size of the stimulus on the display. Stimulus sizes ranged from 0.1875° to 12° in logarithmic steps. Stimuli from 3° to 12° were viewed from 50 cm. The largest stimulus size was created by changing pixel resolution to 800 x 600 and doubling the spatial extent of the image (in pixels) horizontally and vertically; i.e., this quadrupled the number of pixels per stimulus. Stimuli smaller than 3° (1.5°, 0.75°, 0.375° and 0.1875°) were viewed from successively greater distances. The smallest stimuli were viewed from a distance of 375 cm and pixel number was reduced (line length changed from 112 to 53 pixels). All eccentricities were tested at one stimulus size before moving to the next size. The order in which stimulus sizes were tested was random.

The adjustment procedure described above was modified to obtain contrast detection thresholds for all of the viewing conditions. The test stimulus was presented in a single interval of 200 ms signaled by the presence of a tone. A fixation dot was provided for all eccentricities except the fovea. The subject's task was to adjust the contrast of the test stimulus using up and

down arrow keys until the presence of contrast could be just detected. As in the contrast matching task, the stimulus did not appear on the screen while arrow keys were depressed. The adjustment process was terminated once the subject was satisfied with the contrast level selected (usually about 8-12 stimulus presentations).

3) Orientation discrimination experiment

The task was designed to be similar in all respects except stimulus contrast to the orientation discrimination experiment previously reported by Sally and Gurnsey (2003). The contrasts of the test stimuli were set to the level determined from the matching procedure. Orientation thresholds were measured over a range of sizes at 0°, 2.5°, 5°, 10° and 15° in the right visual field (temporal retina). The viewing sizes / distances were as indicated for the contrast matching task. A fixation dot (6 pixels in diameter) was present for all eccentricities except at fixation. All eccentricities were tested at one stimulus size before moving to the next size. The order in which stimulus sizes were tested was random. The horizontal stimulus location was jittered by 5% of the stimulus size from trial to trial so that absolute stimulus location could not provide an orientation cue.

A trial consisted of the sequential presentation of two line stimuli. Each pattern was presented for 200 ms separated by an inter-stimulus interval of 300 ms. One of the lines was vertical and the other was tilted counter-clockwise. The subject's task was to report via the mouse which interval contained the tilted stimulus.

RESULTS

Contrast matching and contrast detection thresholds

Figure 4.2 shows contrast matching (top graphs) and contrast detection thresholds (bottom graphs) plotted against line length for each of the five eccentricities. At each eccentricity thresholds show an initial rapid decline followed by a more gradual change, and finally reach a plateau at very long line lengths. Also, for both tasks, average minimal values (i.e., thresholds or matching contrasts) are essentially identical at all eccentricities. Because of this we did not use a double scaling procedure (e.g., Melmoth et al., 2000a,b; Poirier & Gurnsey, 2002) to fit the data (see below). In other words, only size scaling was used in the fits. Therefore, all E_2s reported are size-scaling E_2s and E_2 should be read as E_{2Size}.

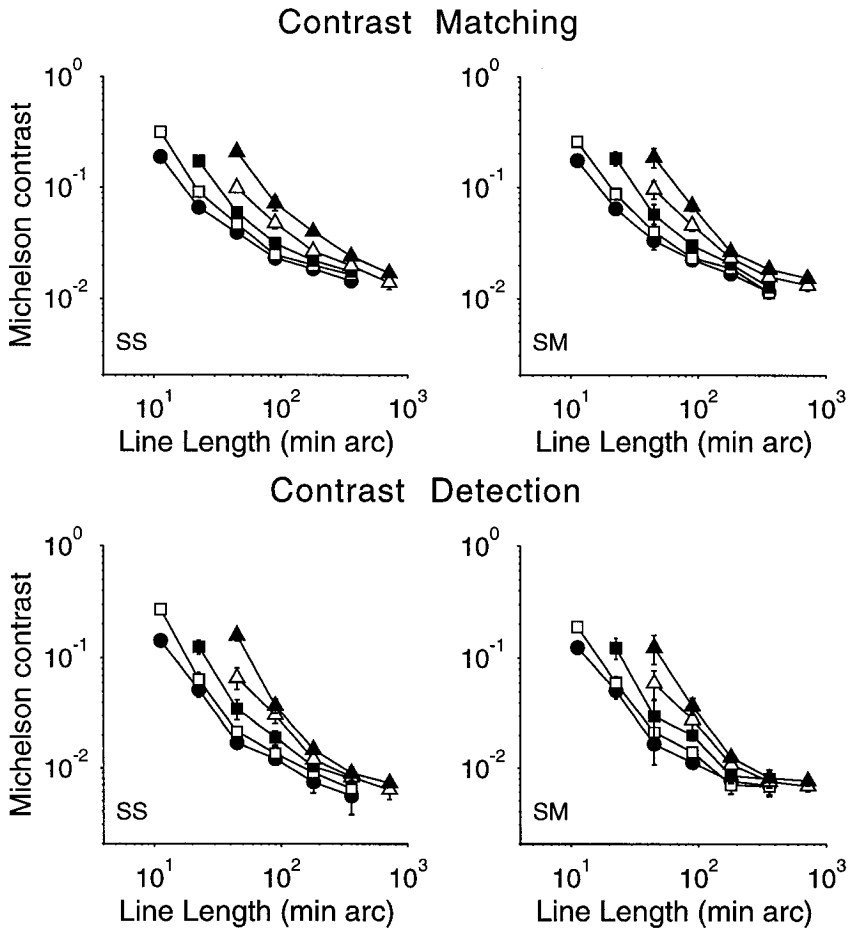

Figure 4.2. Michelson contrast thresholds at each eccentricity plotted as a function of line length for contrast matching (top graphs) and contrast detection (bottom graphs) for subjects SS and SM. Standard errors are shown for each point. Eccentricities from zero to fifteen degrees: 0° (filled circles) , 2.5° (unfilled squares), 5° (filled squares), 10° (unfilled up-arrows), 15° (filled up-arrows).

We assumed the relationship between line length and contrast threshold would be well described at all eccentricities by the function

$$C = C_{min}(1 + L_{crit} / x)^n \qquad [4.2]$$

where C is the contrast threshold, C_{min} refers to the minimum contrast threshold, L_{crit} refers to the critical line length marking the transition between the decreasing and constant parts of Equation 4.2, n determines the slope of the line and x refers to scaled line length. (We also assumed that this function

would well describe the contrast matching data.) According to linear scaling theory, thresholds at all eccentricities should fall onto a single curve when line length is scaled (divided by) by an appropriate constant; i.e., $F = 1 + E / E_2$. For each subject, the entire data set was fit by finding parameters for C_{min}, L_{crit}, n, and E_2 that minimize the deviation of the data from the parametric curve. Our measure of deviation was the RMS error defined as

$$e_{rms} = \sqrt{\frac{1}{n}\sum_{i}^{n}\left(\log Y_{i(est)} - \log Y_i\right)^2} \qquad [4.3]$$

where n is the number of data points, Y_i is a measured data point and $Y_{i(est)}$ is the value predicted by the parametric function. We express the goodness of the fit as $G = 1 - e_{rms}$ (Melmoth et al., 2000a,b). The data were fit using the error minimization routine provided in MATLAB (Mathworks Ltd.); this routine (*fmins*) used the Nelder-Mead simplex (direct search) method. Numerical solutions found in this way may represent local rather than global minima. Therefore, we ran the minimization routine twenty times for each fit, each starting from a different randomly chosen initial condition, and we report the best fits obtained in this way.

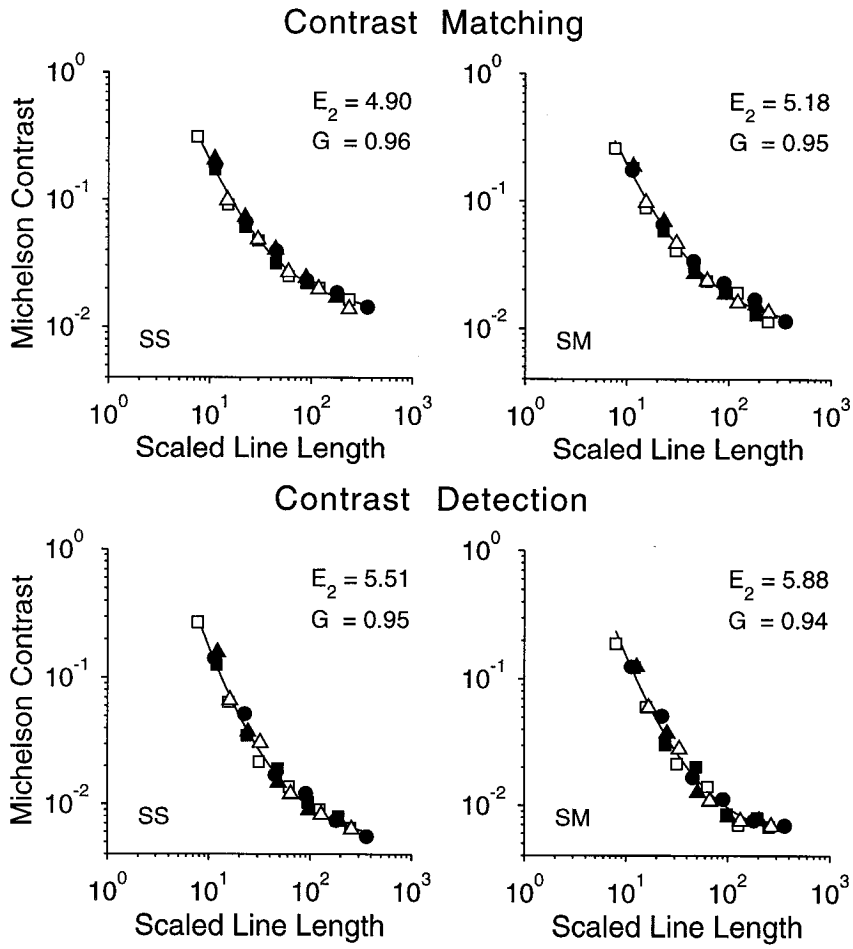

Figure 4.3. Scaled line length data for the contrast matching (top graphs) and contrast detection (bottom graphs) tasks. Scaled line length equals the actual line length (in minutes of visual angle) divided by F, where $F = 1 + E / E_2$.. Goodness of fit (G) is indicated.

Scaled line length data for the contrast detection and contrast matching tasks are shown in Figure 4.3. Best-fitting functions are indicated as solid curves. Goodness of fits values ranged from G = 0.94 to 0.96 and were similar across the two tasks and subjects. The average E_2 for the contrast detection task was 5.7° (5.51° and 5.88° for SS and SM respectively) and was 5.04° (4.90° and 5.18° for SS and SM respectively) for the contrast matching task. E_2s were therefore in the same range for both tasks and on average only 13% larger for contrast matching. The similarity of E_2s for contrast matching and contrast

detection is not unexpected; it is likely that comparable low-level mechanisms subserve performance on both tasks.

Orientation discrimination thresholds

Orientation discrimination versus line length functions (see Figure 4.4, top panels) have the same general form at all eccentricities. Thresholds show an initial steep decline, followed by a more gradual decrease with increasing line length and appear to approach a plateau at very long line lengths. The average minimum thresholds were 1.32° and 1.29° for subjects SS and SM respectively. At high contrasts these subjects achieved minimal orientation thresholds of 0.56° and 0.55° for SS and SM respectively, for the same stimuli (Sally & Gurnsey, 2003a).

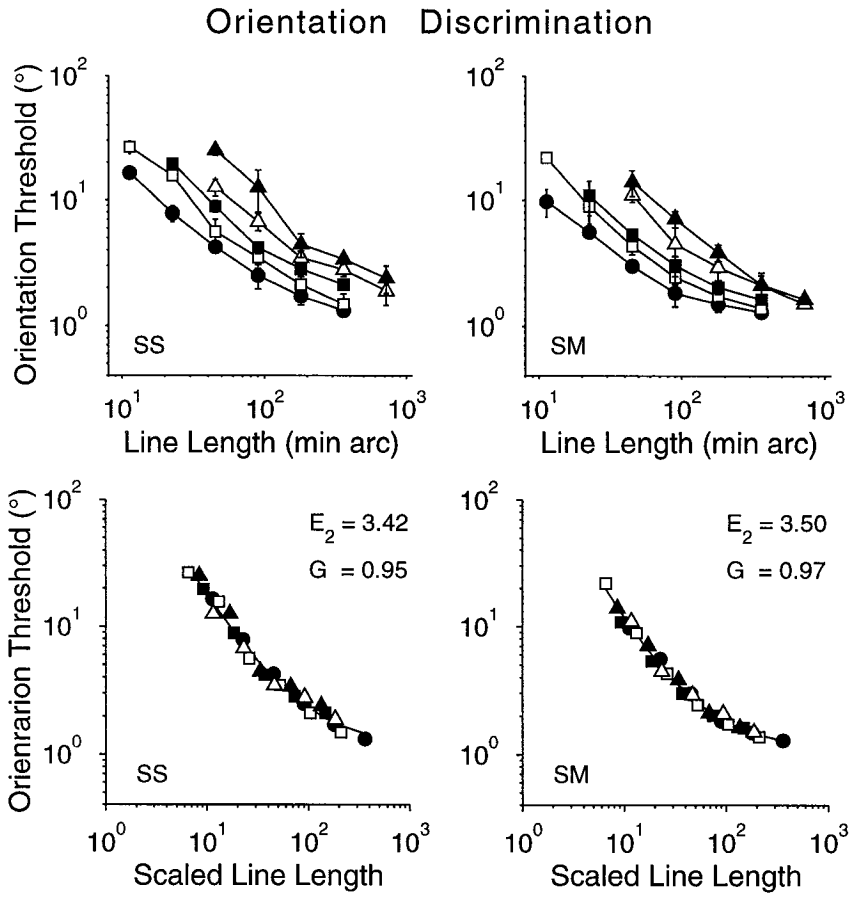

Figure 4.4. Orientation discrimination thresholds (°) at each eccentricity plotted against line length for subjects SS and SM. Standard errors are shown for each point. Eccentricities from zero to fifteen degrees: 0° (filled circles), 2.5° (unfilled squares), 5° (filled squares), 10° (unfilled up-arrows), 15° (filled up-arrows) (top graphs). Scaled line length data for orientation discrimination. Goodness of fit (G) is indicated (bottom graphs).

We fit the orientation threshold versus line length data using Equation 4.4

$$\Delta\theta = \theta_{min}(1 + L_{crit} / x)^n \qquad [4.4]$$

where $\Delta\theta$ indicates orientation threshold, θ_{min}, the smallest discriminable; L_{crit}, x and n have the same interpretation as in Equation 4.3. Details of fitting procedure were as described above for the contrast detection and contrast matching tasks. Scaled line length data for two subjects are shown in Figure

4.4 (bottom graphs). Goodness of fits values were G = 0.95 and 0.97 for subjects SS and SM respectively. These values compare favourably with those obtained previously at high contrasts (G = 0.95 for SS and SM). Thus, a substantial amount of eccentricity-dependent variability was removed from the data using a single scaling function. The average E_2 recovered for this task was 3.46° (3.42° and 3.50° for SS and SM respectively). These values are considerably larger than those obtained using an identical stimulus at high contrasts (Sally & Gurnsey, 2003a). We previously reported an average E_2 for this task of 1.51°. Therefore, the present results indicate that E_2 increases by a factor of 2.29 at low contrasts. The E_2 values for orientation discrimination in the present experiment are also substantially larger than those obtained by Mäkelä et al. (1993) using a similar stimulus at high contrasts. The authors reported an average E_2 of 1.95° for this task. [We derived E_2 estimates of 1.77° to 1.85° for their data using our present fitting procedure]. We can therefore conclude that E_2s for orientation discrimination are significantly larger when stimuli are presented at near-threshold levels of contrast.

GENERAL DISCUSSION

In the present study the average size-scaling E_2 for orientation discrimination at low contrasts was 229% larger than those we obtained previously at high contrasts using identical stimuli, subjects and threshold measuring procedure (Sally & Gurnsey, 2003a). Thus, the contrast level at which stimuli are presented is a critical determinant of E_2 .

These results are generally consistent with those of Sally et al. (2002) who reported size-scaling E_2s for orientation discrimination ranging from 3.71° to 6.86° with an average of 5.44°. This value is larger than the present size-scaling estimate of 3.46°, perhaps because there were methodological differences between the two studies; i.e., orientation discrimination thresholds were measured in the present study and a fixed orientation difference was used in Sally et al. (2002). Most importantly, however, both studies found that large size-scaling E_2s for orientation discrimination are required for low-contrast stimuli. These findings agree with the results of other spatial scaling studies conducted at near-threshold contrasts. For example, size-scaling E_2s of 2.73° and 3.19° for two subjects have been reported for face discrimination (Mäkelä et al., 2001) and E_2s of 3.60° and 6.38° have been obtained for detection of phase-distortions in bandpass filtered faces and polar grating stimuli (Melmoth et al., 2000a).

In addition to the size-scaling estimates for orientation discrimination, we determined the size-scaling E_2s required to equate for perceived contrast as well as contrast detection across eccentricities. Results were very similar for the two cases; 5.7° and 5.04° for the contrast matching and detection tasks, respectively. Presumably, E_2 values for both tasks are similar because they rely

on the same mechanisms.

To our knowledge, no other studies have determined size-scaling E_2s associated with contrast (detection and matching) using a broadband stimulus. Tasks that assess the detection of stimulus contrast generally employ narrowband stimuli. In an early study, Rovamo and Virsu (1979) measured contrast sensitivity across the visual field and showed that performance could be made approximately equal at all eccentricities when stimuli were scaled in proportion to local ganglion cell spacing, which corresponds to an E_2 of about 3°. Thibos, Cheney and Walsh (1987a, 1987b) pointed out the importance of distinguishing between resolution limits (i.e., limits on the ability to perceive a grating stimulus veridically) and detection limits (i.e., the limits on the ability to correctly report the presence of a stimulus). Thibos et al. (1987a, 1987b) and Anderson, Mullen and Hess (1991) provided further evidence that resolution of achromatic and chromatic sine wave gratings is limited by the density of beta (midget) retinal ganglion cells. Thibos et al. (1987b) and Anderson and Hess (1990) also showed that, in the periphery, gratings may be detected at frequencies beyond the resolution limit. In this case, the stimuli are perceived non-veridically because they arise from aliasing. Thibos et al. (1987b) report that "At a given eccentricity, the very finest pattern which produces aliasing has a spatial period which approaches the smallest anatomical dimension: the diameter of a single photoreceptor." (p. 2193, data from Polyak, 1941). Our analysis of these limited data (Figure 3, Thibos et al., 1987a) suggests that eccentricity-dependent changes in cone size are associated with E_2s of 10° or more. Our size-scaling E_2s for contrast detection and matching of about 5 to 6° likely reflect retinal limitations, but

whether these are associated with changes in cone size, ganglion cell density or some other retinal source (e.g., receptive field size or scatter) is not clear.

Sally et al. (2002) recovered *contrast-scaling* E_2s that averaged 85.5°, which might seem inconsistent with the *size-scaling* E_2s for contrast thresholds (or contrast matches) recovered in the present experiment. Of course, there is no inconsistency. The size-scaling E_2s for contrast in the present study reflect the *horizontal shifts* required to equate perceived contrast and contrast detection across eccentricities. The contrast-scaling E_2s reported in Sally et al. reflect the *vertical shifts* required to equate average minimal contrast thresholds at each eccentricity. Sally et al. found that little or no contrast scaling was required because all contrast sensitivity functions reached approximately the same asymptotic level at sufficiently long line lengths. Similarly, in the present experiment, the average minimal contrast thresholds or matching contrasts were essentially identical at all eccentricities. Thus, size scaling was required to equate contrast detection and perceived contrast across the visual field, but contrast scaling was not.

We note that contrast detection thresholds show a more rapid rise with reductions in stimulus size than do thresholds for contrast matching (see Figure 4.2). This means that perceived contrast did not change as dramatically as detection thresholds over the same range of line lengths. Thus, there was not a multiplicative relationship between contrast detection threshold and level of perceived stimulus contrast (Gurnsey, Sally & Ball, 2002). This is a significant point because a common procedure to equate for stimulus 'visibility' is to present stimuli at a fixed multiple above detection threshold across viewing conditions. To determine if there is a systematic relationship

between contrast threshold and perceived contrast, we examined these measures as a function of line length and eccentricity. The pattern of results was consistent across eccentricities and similar for the two subjects. At each eccentricity, the contrast value obtained through contrast matching represented the highest multiple of contrast threshold at the longest stimulus sizes and the smallest multiple at the smallest stimulus sizes. The perceived contrast value was an average of 2.14 multiples of detection threshold for the two largest sizes at each eccentricity and decreased to 1.53 for the two smallest sizes. This means that if we had set all stimuli to the same multiple of contrast threshold (e.g., 2.14 times threshold), the smallest stimuli at every eccentricity would have had higher physical contrast than that determined in the matching procedure.

The primary aim of this study was to determine whether size-scaling E_2s for orientation discrimination at near-threshold contrasts are larger than those obtained at high stimulus contrasts. We have shown that this is clearly the case. Although there may be numerous explanations for this finding, we suggest that this effect is related to changes in the structure of neuronal receptive fields at low stimulus contrasts. Recent physiological studies indicate that areal summation of V1 neurons can increase by a factor of at least two as stimulus contrast is reduced (Kapadia, Westheimer, & Gilbert, 1999; Sceniak, Ringach, Hawken, & Shapley, 1999). Psychophysical evidence also supports the notion of contrast-dependent changes in receptive field structure (Mareschal, Henrie, & Shapley, 2002; Mareschal & Shapley, 2003). A relatively greater increase in areal summation at the fovea than periphery would result in larger E_2s for low-contrast stimuli. In general, larger receptive

fields permit higher sensitivity (Derrington & Lennie, 1982; Enroth-Cugall & Shapely, 1973; Sceniak et al., 1999). Changes in spatial structure may be more adaptive for neurons at the fovea because peripheral receptive fields are already comparatively large.

CHAPTER 5

Summary and conclusions

This section briefly summarizes the results of the studies presented in this thesis and examines what this research reveals of the eccentricity-dependent limitations on orientation discrimination performance. Also discussed, is the way in which perceptual contrast can influence E_2 estimates for tasks that rely on orientation discrimination processes.

E_2 for orientation discrimination and spatial frequency bandwidth

The first series of experiments examined whether the E_2 for orientation discrimination is dependent upon spatial frequency bandwidth of the stimulus. Sally and Gurnsey (2003a) observed that different types of stimuli are typically used for resolution or visual acuity and position acuity tasks. Narrowband stimuli, such as gratings, are used to test visual acuity and typically yield E_2s of about 3° or more (e.g., Rovamo & Virsu, 1979; Swanson & Wilson, 1985). Broadband stimuli have been used almost exclusively for tasks such as the discrimination of vernier offsets and orientation discrimination; E_2s typically recovered for these tasks are generally less than 2° (e.g., Levi, Klein & Aitsebaomo, 1985; Mäkelä, Whitaker & Rovamo, 1993; Whitaker, Rovamo, MacVeigh & Mäkelä, 1992). It is therefore possible, that E_2 is dependent not on the task, but on the spatial frequency bandwidth of the stimuli that are typically employed. In other words, that it is not so much the task but the stimuli that determine E_2. To study this issue, E_2 was calculated using the two types of stimuli within a single task.

E_2 was determined as a function of stimulus bandwidth using two orientation discrimination tasks. For both tasks, orientation discrimination

performance was examined as a function of stimulus size and eccentricity using broadband and narrowband stimuli. In the first experiment, orientation discrimination stimuli had a fixed difference of ±1.5° from vertical and the proportion of correct responses was measured. In the second experiment, orientation discrimination thresholds were obtained. The latter experiment was similar to the classic spatial scaling study on orientation discrimination of Mäkelä et al. (1993).

E_2s recovered for the narrowband stimuli were substantially larger than those for the broadband stimuli. Average E_2s for two subjects were 1.48° and 3.12° for the broadband and narrowband stimuli, respectively in the first experiment. Average E_2s of 2.36° and 3.2° for the broadband and narrowband stimuli, respectively, were recovered for the second. These results suggested that the stimulus not the task determined E_2 values.

Although overall the fits were quite good, with goodness of fit values ranging from 0.93 to 0.95 in the two experiments, a systematic pattern in the results suggested the presence of an uncontrolled performance limitation. The horizontal shift along the size axis required to align or "match" the data at lower levels of performance (i.e., small stimulus sizes) was less than that required to align those data at higher performance levels (i.e., large stimulus sizes). A larger amount of lateral shift yields a smaller E_2. This effect was also noted for a binocular version of this experiment (Sally & Gurnsey, 2000) and was particularly evident in all cases for the narrowband stimuli. Contrast thresholds increase dramatically with reductions in stimulus size for narrowband stimuli. Therefore, small stimulus sizes are more likely than large stimulus sizes to have reduced perceptual contrasts. Sub-optimal perceptual contrast would be expected to have the same effect as decreased

physical stimulus contrast, namely elevations in thresholds (Reisbeck & Gegenfurtner, 1998; Webster, DeValois & Switkes, 1990). Thus, E_2s may have been larger for narrowband stimuli because of multiple eccentricity-dependent limitations on performance.

Controlling for perceptual contrast at high levels of stimulus contrast

Orientation discrimination thresholds become asymptotically low at high stimulus contrasts (Webster et al., 1990). This suggested a means of controlling for the effects of perceptual contrast on orientation thresholds. Orientation thresholds were measured over a range of physical stimulus contrasts; thresholds were only included in the calculation of E_2 if performance had reached asymptotic level such that further increases in contrast led to no further changes to orientation thresholds. The results of this study indicated that, once there was experimental control of perceptual contrast, there was relatively little difference between E_2s for narrowband and broadband stimuli. The average E_2s for the two subjects were 1.38° and 1.64°, for broadband and narrowband stimuli, respectively. This represents an average difference of only 19%. Further, the results of a statistical analysis revealed that overall E_2s were significantly smaller in the experiment in which perceptual contrast was controlled (average E_2 of 1.51°) than the uncontrolled version of the same experiment (average E_2 of 2.78°).

These experiments make an important contribution to the scaling literature because they emphasize the degree to which E_2s can vary at high contrasts when perceptual contrast is not controlled. This set of experiments also demonstrated that excellent fits achieved by single shifts along the size-scaling axis may disguise multiple eccentricity-dependent limitations in the data. Further, the experiments provide an estimate of the E_2 for orientation

discrimination which can be used to infer something of the neural substrate(s) that limit performance on this task.

Anatomical/physiological basis of orientation discrimination performance

The average E_2 of 1.5° for orientation discrimination obtained in the high-contrast experiment (Sally & Gurnsey, 2003a, Experiment 3) was reasonably similar to that recovered by Mäkelä et al. (1993) in their classic spatial scaling study on orientation discrimination, also conducted at high stimulus contrasts (average E_2 = 1.95°). What do these E_2s suggest concerning the factors that limit orientation discrimination performance across the visual field? Striate cortex is the first site at which orientation-selective cells appear, thus orientation discrimination must rely on cortical processing. However, the E_2s obtained by Sally and Gurnsey and Mäkelä et al. at high contrasts are somewhat larger than the estimate of the E_2 associated with the cortical magnification factor in humans (i.e., Beard et al., 1997, E_2 = 0.8°; Cowey & Rolls, 1970, E_2 = 1.09°; Grüsser, 1995, E_2 = 1.24°; and Horton and Hoyt, 1991, E_2 = 0.75°). This suggests that the rate of change associated with the cortical sampling grain does not limit orientation discrimination performance. It is, however, possible that stimulus orientation may be signaled by correctly oriented spatial filters, and that orientation discrimination performance reflects changes in the local spatial scale of orientation-selective mechanisms. This may be expressed by eccentricity-dependent variations in the receptive field size of striate cortical neurons. The rate of change associated with this parameter in humans is not known. Physiological studies in the macaque have, however, suggested that receptive fields change more slowly with increasing eccentricity than the cortical magnification factor, particularly near the fovea (Dow et al., E_2 = 6.0° for E =

0.08 to 2.67°). As noted in the Introduction, there is considerable uncertainty associated with changes in average receptive field size with a tremendous amount of vertical scatter at each eccentricity (Dow et al., 1981; Van Essen et al., 1984)[1]. Also, it is more likely that eccentricity-dependent limitations on orientation-discrimination performance reflect changes in the spatial scale of the smallest orientation-selective mechanisms available to encode the stimulus rather than changes in average receptive field size.

Low contrast stimuli: Double scaling

Melmoth, Kukkonen, Mäkelä and Rovamo (2000) and Mäkelä, Näsänen, Rovamo and Melmoth (2001) reached a conclusion similar to that of Sally and Gurnsey (2003) regarding the importance of controlling for stimulus contrast, yet from a somewhat different perspective. Mäkelä et al. (2001) measured contrast thresholds for identification of face stimuli as a function of stimulus size [i.e., contrast sensitivity functions (CSFs)] at a range of eccentricities. CSFs for face discrimination reach an asymptotic level at different levels of sensitivity with eccentricity and must be shifted along both the size and contrast axes to superimpose data at all eccentricities. Mäkelä et al. showed that when data were shifted only on the size axis, relatively large shifts were required and E_2s were fairly small (average E_2 of 1.65° for two subjects). When CSFs were double scaled (i.e., along the contrast and size axes) smaller shifts were required, resulting in larger E_2s (average E_2 of 2.96°) and more eccentricity-dependent variance in the data was explained.

The observations of Mäkelä et al. that controlling for contrast produces *larger* E_2s appeared to conflict with the conclusions of Sally and Gurnsey (2003). The two studies were, however, conducted at near threshold and high

[1] One possible reason for this is that electrophysiological studies record from single neurons as well as small clusters of neurons.

levels of stimulus contrast, respectively. This suggested the possibility that E_2s may be larger when stimuli are presented at low levels of contrast. Alternatively, E_2s may have differed because the tasks of orientation discrimination and face discrimination rely on quite different processes. Orientation discrimination (fixed orientation difference of 1.5°) was therefore examined at low contrasts using stimuli and subjects identical to those used at high contrasts. Two primary questions were asked: 1) would E_2s be larger than those recovered at high contrasts? and 2) would double scaling be required? Two different double scaling procedures were used - the Melmoth et al. (2000) and Poirier-Gurnsey (2002) methods. The procedures differ in terms of how data are collected and in their models of psychophysical performance. A secondary objective was to compare the two methodologies.

A reasonably consistent pattern of results was found across the two data collection and fitting methods. Average E_2s for size were 4.87° and 6.0° recovered with the Melmoth et al. and Poirier-Gurnsey sampling procedures, respectively. Little to no contrast scaling was required, with corresponding E_2s for the two data collection procedures of 20.9° and 149.9°, respectively. The average E_2 for size scaling across subjects and data collection procedures of 5.43° was significantly larger than the average E_2 for orientation discrimination of 1.51° recovered for the same two subjects at high contrasts. The size E_2s found at threshold contrasts were not attributable to the need to scale contrast. Indeed, it was noted that size-scaling E_2s were large regardless of whether contrast scaling was performed. This experiment provided convincing evidence that E_2s for orientation discrimination vary as a function of stimulus contrast.

Low contrast stimuli: Matching perceived contrast

The final experiment presented in this thesis was designed to be identical to the high-contrast orientation discrimination experiment (Sally & Gurnsey, 2003) in all respects except for the near-threshold levels at which stimuli were presented. To determine the levels of contrast for orientation discrimination stimuli, the subjects matched the perceived contrast of all stimuli at all eccentricities to a foveal standard presented at fixation. The standard was a 3° line at two JNDs above detection threshold. Contrast thresholds were also obtained using an adjustment procedure.

The orientation discrimination data obtained in this experiment resembled those obtained at high stimulus contrasts; orientation threshold as a function of size curves and average minimal orientation threshold values were essentially identical at all eccentricities. The average E_2 recovered for the two subjects was 3.46°. This is a factor of 2.29 larger than the average E_2 of 1.50° recovered for same subjects when orientation discrimination thresholds were measured at high contrasts. Therefore, both this study and the double scaling experiments provide converging evidence that size-scaling E_2s for orientation discrimination are larger at low contrasts. Thus, E_2 for this task depends critically on the level of stimulus contrast.

The role of perceived contrast

For the experiments that involved matching perceived contrast, it was noted that there was no multiplicative relationship between contrast detection threshold and level of perceived stimulus contrast. Other studies of perceived contrast in the fovea and periphery are in accordance with this conclusion. The perceived contrast of suprathreshold sine wave gratings presented at the fovea tends toward equivalence across spatial frequencies and

does not show the marked attenuation at high and low spatial frequencies that characterizes the threshold contrast sensitivity function (Blakemore, Muncey & Ridley, 1973; Bowker 1983; Cannon, 1985; Georgeson & Sullivan, 1975). Cannon (1985) examined the perceived contrast of sine wave gratings with a 2° circular aperture in the periphery using a magnitude estimation procedure. Sine wave gratings of 2°, 4°, 8° and 16° were presented at eccentricities of 0° to 40° in 10° increments at contrasts up to 0.8. Subjects assigned numerical ratings to these gratings based on perceived contrast. Contrast detection thresholds for all stimuli were obtained using an adjustment procedure.

Data at each eccentricity were fit with contrast response functions (R) of the form

$$R = k(C - T)^m \qquad [5.1]$$

where C is the stimulus contrast, T is the contrast threshold and k and m are fitted constants.

The data and contrast response functions indicated that, although contrast thresholds increased substantially with eccentricity for all gratings, the differences in perceived contrast tended to disappear as physical contrast increased. This occurs because the perceived contrast of stimuli with high thresholds rises more steeply with physical contrast than the perceived contrast of stimuli with low thresholds. Therefore, the result is that the low- and high-threshold perceived contrast functions "catch up" to each other at sufficiently high levels of physical contrast. Georgeson and Sullivan (1975) have referred to this phenomenon as contrast compensation. A further consequence of the rapid increase in the contrast response curves in the periphery is that a sine wave grating can, at certain equivalent levels of

physical contrast, have a higher perceived contrast in the periphery than at the fovea (Cannon, 1985; Georgeson, 1991; Georgeson & Sullivan, 1975). Georgeson (1991) refers to this as contrast overconstancy.

Taken together, these studies provide strong evidence that the perceptual magnitude of a stimulus does not increase at a rate that is proportional to its detection threshold (Gurnsey, Sally & Ball, 2002). Thus, the multiple-of-contrast- threshold approach to controlling contrast is inappropriate. Control of perceptual contrast is essential; the high-contrast experiment of this thesis (Sally & Gurnsey, 2003a) and the work of Mäkelä et al. (2001) have demonstrated that failure to control for contrast can result in significant variation in E_2 values.

Equivalent noise and efficiency

Whereas little to no contrast scaling was required for orientation discrimination, there are certain tasks, such as face discrimination, for which data must be scaled in both size and contrast dimensions. We can therefore ask what factors underlie the inferiority of peripheral processing for this task even after size scaling. To answer this question, we consider that visual sensitivity can be partitioned into two components that represent the observer's efficiency (η) and equivalent noise (N_{eq}) - the amount of internal noise (Legge, Kersten & Burgess, 1987; Nagaraja, 1964). Equivalent noise is calculated by measuring 1) threshold for a target on a blank background and 2) threshold on a background of visual white noise. Threshold contrast for both conditions is then converted to energy units. Contrast energy (E) is the square of the contrast function summed over the dimensions along which the stimulus varies. Threshold contrast energy on a blank background and in white noise are designated E_0 and E_n, respectively.

Threshold contrast energy (E_n) is linearly related to the display noise power spectral density (N) (Pelli, 1990, 1999). Because there is a linear relationship between these parameters, the N_{eq} can be calculated from the amount of threshold elevation on a background of noise as follows.

$$N_{eq} = \frac{E_0}{E_n - E_0} N \qquad [5.2]$$

Efficiency is the ratio of threshold energies of mathematically defined ideal and human observers.

$$\eta = \frac{E_{ideal}}{E_n} \qquad [5.3]$$

The ideal observer makes decisions based on the available information, so as to maximize the probability of a correct response. In Pelli's (1999) words " Efficiency (η) rates the computations underlying our perceptual decisions on the absolute performance scale defined by the ideal observer, while equivalent noise (N_{eq}) specifies how much noise the observer's visual system (including transduction) adds to the display" (p. 649).

Mäkelä et al. (2001) calculated equivalent noise and efficiency for optimally size scaled face stimuli. The task and observers were as described above for the primary experiment. The ideal observer in the task was a template matching observer which searches for the shortest Euclidian distance between the signal and a set of internal templates. They found that equivalent noise remained the same with increasing eccentricity, but there was a decline in efficiency. According to Mäkelä et al., for the task of face discrimination, shifting data along the contrast axis compensates for the decline in efficiency.

A very recent study reported a relationship between efficiency and stimulus contrast. Simpson, Findlay and Manahilov (2003) measured

performance in terms of reaction time for the detection of Gabors in dynamic Gaussian white noise. They reported that internal noise remained constant but sampling efficiency increases as signal contrast increases. Simpson et al. suggested that the observer develops a more accurate template (Burgess, 1990) for the higher contrast signals.

Why are E_2s large at low stimulus contrasts?

The E_2s that were recovered in all orientation discrimination experiments conducted at near threshold contrasts in this thesis were substantially larger than those obtained in the high-contrast experiment (Sally & Gurnsey, 2003a). One possible reason why E_2s are larger at low contrasts is because the cells of the M pathway, which are more sensitive to contrast than those of the P pathway, are preferentially involved in task performance at low stimulus contrasts. This appears unlikely, however. Firstly, it is generally felt that neurons of the P pathway,with on average, smaller receptive fields, are required for acuity tasks (Wilson, Levi, Maffei, Rovamo & DeValois, 1990). Secondly, as mentioned in the Introduction, Merigan and Eskin (1986) and Merigan (1989) showed that when P_β retinal ganglion cells were selectively destroyed, contrast thresholds for stationary and counterphase modulated gratings at the lowest rate of temporal modulation were elevated substantially at all spatial frequencies. This finding suggests that neurons of the P pathway play an important role in the detection of contrast at low temporal frequencies.

Sally and Gurnsey (2003) suggested that large E_2s for orientation discrimination at low stimulus contrasts may result from dynamic changes in the spatial structure of receptive fields. Kapadia, Westheimer and Gilbert (1999) measured changes in receptive field size centre area as a function of

stimulus contrast at different levels of contrast (20-70%) in awake, behaving macaques. They plotted the number of spikes per unit time elicited as a function of length of bars; the extent of the excitatory receptive field was defined as the stimulus length that produced the maximal response at each contrast. Kapadia et al. reported that on average the length of the excitatory receptive field was 4-fold greater for low contrast stimuli[2]

Sceniak, Ringach, Hawken and Shapley (1999) also reported variations in areal summation of receptive fields in VI of anesthetized macaques with changes in stimulus contrast. They measured neuronal responses as a function of stimulus area using circular and rectangular sine wave gratings that were optimally tuned to the cell's spatial frequency, temporal frequency and orientation. The extent of areal summation was defined as the radius at the peak neural response and was measured at two contrast levels in each cell - near the low and high ends of the sloping region of the cell's contrast response function. They reported that on average the excitatory part of the receptive field increased in area and length by a factor of 2.8 and in width by a factor of 2.

Mareschal, Henrie and Shapley (2002) examined this phenomenon psychophysically using a contextual orientation discrimination task. A sine wave grating stimulus (2 cpd) with a circular aperture of 3.1° was embedded in a surround of a similar spatial frequency. Orientation thresholds obtained with this type of stimulus are typically elevated. As the gap width between the centre and surround increases, the masking effect of the surround on orientation thresholds decreases. They hypothesized that if receptive field size

[2] They noted a similar amount of change in receptive field size when a high contrast stimulus was embedded in a textured surround. The observation that receptive fields in primary visual cortex are dynamic and can vary as a function of surround stimulation had been reported previously in cat (Pettet & Gilbert, 1992; Sengpiel, Sen & Blakemore, 1997).

of neurons is increased at low contrast, then the effect of the surround would extend over longer gap distances. Two contrast levels, 5% and 30%, were tested using a 2-alternative temporal forced-choice experimental design. Grating stimuli in the central patch were presented at a range of orientations and the subject's task was to determine whether the stimulus in the second interval was shifted clockwise or counterclockwise relative that in the first. In accord with their assumption, the surround's masking effect on orientation thresholds persisted over greater distances (from a gap width about 1.5° to 2°) at low contrasts.

Studies on perceived contrast have also indicated differences in areal summation at low contrasts. Cannon (1985), using a magnitude estimation procedure as described above, showed that foveal perceived contrast depended on grating area at low contrast but was independent of area at high contrasts. Subjects estimated the perceived contrast of a 1.25 cpd grating which was presented alternately with a 2° or 4° aperture at seven contrast levels from 0.01 to 0.8. Although detection thresholds were quite different (0.0052 and 0.013 for the 2° and 4° aperture, respectively), at high levels of physical stimulus contrast perceived contrast was approximately equal. Cannon states "Whereas a reduction in the stimulus area produces an increase in contrast threshold, presumably because of spatial summation effects, it produces almost no change in contrast perception for contrasts above 0.1"(p. 1767). Other studies have also suggested different spatial summation processes at low and high stimulus contrasts. Legge and Foley (1980) showed that a model with a strong dependence on spatial summation at low but not high contrasts was required to explain their contrast discrimination data. Also, data of Swanson, Wilson and Giese (1984) indicated that contrast perception was

dependent on the number of grating cycles at low levels but not high levels of physical stimulus contrast.

Sally and Gurnsey (2003) proposed that increases in areal summation of receptive fields at low contrasts may be relatively greater at the fovea than in the periphery. This would result in larger E_2s for low contrast stimuli. The type of contextual stimuli used by Mareschal et al. (2002) and the work on perceived contrast as a function of stimulus area (e.g., Cannon, 1985) provide two psychophysical methods with which the contrast-dependent changes in receptive field size with eccentricity can be investigated.

Concluding remarks

In the Introduction, the following question was posed. Why do E_2 values vary widely, even for the same task (i.e., vernier acuity see Table 1, Beard, Levi & Klein, 1997)? The work presented in this thesis suggests that at least part of the reason is that, in most instances, there has been no explicit control of stimulus contrast. The results of the first series of experiments showed convincingly that failure to control for perceptual contrast at high levels of physical stimulus contrast can result in inflated E_2s. Further, even when some attempt to control for contrast has been made, the multiple-of-detection-threshold method is generally used (e.g., Barrett, Morrill & Whitaker; Beard et al., 1997). Evidence was provided in this thesis that this method is less than satisfactory.

The present set of experiments have indicated that size-scaling E_2s for orientation discrimination are critically dependent on stimulus contrast. When perceptual contrast is controlled, E_2s are small for high-contrast stimuli and large for low-contrast stimuli. It can be predicted that this conclusion should generalize to other tasks such as vernier acuity (Whitaker

et al., 1992b) and curvature discrimination (Whitaker, Latham, Mäkelä & Rovamo, 1993) that are believed to rely on similar orientation selective processes. It is likely that if some of the earlier work on spatial discrimination performance is replicated at high at low levels of stimulus contrasts under controlled conditions of perceptual contrast, then the degree of heterogeneity of E_2 values in the current scaling literature will be reduced considerably.

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