

UNDERSTANDING THE MECHANISMS OF VISUAL
ORIENTATION DISCRIMINATION

By

NICOLE D. ANDERSON

A Thesis

Submitted to the School of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree
Doctor of Philosophy

McMaster University

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VISUAL ORIENTATION DISCRIMINATION

DOCTOR OF PHILOSOPHY (2003)

McMaster University

(Psychology)

Hamilton, Ontario

TITLE: Understanding the Mechanisms of Visual Orientation Perception

AUTHOR: Nicole D. Anderson, B.A. Hons (University of Western Ontario)

SUPERVISOR: Professor Kathryn M. Murphy

NUMBER OF PAGES: xi, 123.

Abstract

Most studies of orientation detection and discrimination have focussed on the ability to detect oriented stimuli at low contrast or to discriminate small differences in stimulus tilt. In this thesis, I present a new orientation-in-noise stimulus that is high contrast and broadband in spatial frequency and is designed to assess orientation discrimination. Thresholds were measured as the minimum amount of oriented signal required to accurately discriminate the underlying orientation. In Chapter 2, the nature of orientation discrimination was explored using two versions of this novel stimulus. Discrimination thresholds were better for a Local stimulus, where the orientation signal was spatially limited, than for a Global stimulus, where the orientation signal extended across the entire stimulus. Performance improved with increasing stimulus area and reached a limit of about 11% orientation signal. In Chapter 3, the temporal aspects of orientation discrimination were measured with the orientation-in-noise stimulus. Discrimination thresholds were better with a dynamic stimulus, containing multiple independent samples over time, than with a static stimulus presented for an equal duration. Furthermore, increasing the presentation time resulted in even better performance with the dynamic stimuli. These psychophysical results, along with results from a computational model, suggest that human orientation discrimination is mediated by pooling the local responses of low-level neural mechanisms over space and time, and is limited by two stages of intrinsic neural noise. The effects of an oriented context on discrimination in noise thresholds are presented in Chapter 4. Discrimination thresholds increase two-fold when an oriented center is surrounded by a parallel texture. Thresholds with an orthogonal surround are the same as thresholds with no surround, and slightly

better than thresholds with an unoriented noise surround. The effects of a surround on orientation discrimination are reduced when the center size is increased, a gap is increased between the center and the surround, or the surround signal strength is reduced. These results are captured by a computational model based on orientation-specific inhibition and pooling. When the center and surround components are presented either dichoptically or in depth, the effect of a parallel surround on orientation discrimination is not eliminated (Chapter 5). These results suggest that context effects are mediated by early cortical mechanisms. Together, the behavioural and computational results provide novel insights into the nature of orientation perception, and lay the foundation for future research probing the neural mechanisms of orientation discrimination.

Preface

This thesis is partly comprised of two papers (Chapters 2 and 3) that are published and submitted to *Vision Research* and the *Journal of Vision*, respectively. Both chapters were a collaborative effort between myself, David Jones, and Kathryn Murphy. I was extensively involved in designing and programming the experiments, conducting the analyses and preparing the manuscripts for publication.

Acknowledgements

First and foremost, I extend my deepest gratitude to my supervisors, Kathryn Murphy and David Jones. Both of you have provided me with a tremendous amount of knowledge and support, both on and off the field. I leave your lab knowing that I am the best scientist I can be. Many thanks to my committee members, Pat Bennett and Lorraine Allan, for their comments and suggestions throughout the development of my thesis.

Throughout my time in the lab, I have worked with many people who have contributed to my development as well. Thanks to Brett Beston, whose sense for female fashion far surpasses my own, for being a source of friendship and advice. The lab wouldn't have been the same without you. To the research assistants, Sandra Hessels and Phil Boley, and various undergrads, thanks for all your hours as psychophysical subjects. Also, sorry about that. I owe you.

Life as a graduate student at McMaster has certainly been a social one. I cannot list everyone's name here (except you Aimee Skye and Fil Cortese), but please know I that I appreciate meeting every one of you.

Thank-you Homer Simpson and Ralph Wiggum for being a source of constant one-liners.

To my extended NASA family, Sandra Hessels (you're in here twice buddy!), Christine Tsang (my bizarro world twin), Lynne Honey (Corky), Amy Eaton (dancin' Pete), Vicki LeBlanc (Easter Cream Egg sicko), Nikie Conrad (\$35 pie), and Carrie Sniderman (In rod we trust), thank you for your unwavering support. We did it guys.

Finally, for my family. Ryan, thank-you for being such a large part of my life for the past several years. I hope your graduate school experience will be as fruitful as mine. Mom and Dad, I could never have finished this journey without you there by my side. I am so lucky to have such great parents. This is for you.

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Chapter 1

General Introduction

In 1959, David Hubel and Torsten Wiesel published their landmark study showing that neurons in primary visual cortex respond selectively to oriented bars of light. When a bar of light is passed through the receptive field of a visual cortical neuron, the strength of the neural response depends upon a variety of spatial characteristics, including the eye of stimulation, the direction of movement, and the orientation of the stimulus (Hubel & Wiesel, 1959; 1962; 1968). Most neurons respond to these visual dimensions in a bandpass manner, suggesting that even in the earliest stages of the visual pathway, a form of rudimentary information processing is occurring for basic visual features. The discovery of spatially selective receptive fields revolutionized research in vision sciences, as it suggested a direct role for V1 neurons in the perception of basic attributes of the visual scene.

One of the most striking features of V1 neurons is their selectivity to orientation. The nature of orientation selectivity in V1 neurons has received a great deal of research attention for the past several decades and, as such, the neurophysiological properties of orientation selectivity are well characterized. The orientation selective properties of visual neurons are best described through a response tuning function, where the strength of the neural response is plotted as a function of stimulus orientation (Fig. 1). Most V1 neurons are optimally tuned to one orientation, reflected by the peak of the orientation tuning curve. As the stimulus tilts away from the preferred orientation, the strength of the neural response is reduced. The rate at which the response strength drops away from the optimal response denotes the sensitivity of the neuron and is characterized by the bandwidth of the tuning function: the broader the bandwidth (half-width at half-

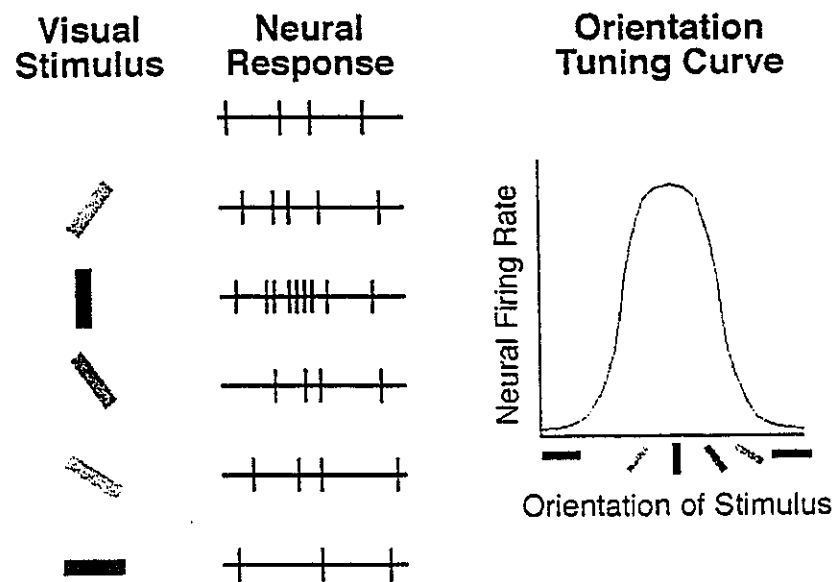


Figure 1. A hypothetical orientation tuning curve. When an orientation-selective neuron is presented with a bar of light the neuron will respond most to one orientation, and less to other orientations. The tuning curve presents the neural response strength as a function of orientation. The preferred orientation is characterized as the location of the peak of the tuning curve, and the sensitivity is the bandwidth (half-width and half-height) of the curve. In this example, the neuron responds best to a 90° orientation.

height), the less sensitive the neuron is to changes in orientation. In Macaque V1, the narrowest bandwidth observed in orientation-selective neurons is 5° , while bandwidths as narrow as 2° have been recorded in cat cortex (Bradley, Skottun, Ohzawa, Sclar, & Freeman, 1987).

Hubel and Wiesel (1959; 1962; 1968) also discovered that orientation selective neurons are arranged in a highly organized manner within the visual cortex. When a microelectrode is advanced perpendicular to the cortical surface, all of the neurons encountered share a similar orientation preference. When the microelectrode is advanced tangentially to the cortical surface, neurons exhibit a gradual progression through orientation preferences. Over approximately 1 mm of cortex, orientation preferences systematically shift through 180° . This pattern of orientation preference is best observed using recently developed techniques in Optical Imaging, a high resolution imaging technique that takes advantage of changes in the optical properties of active cortical tissue. When orientation-dependent activity is measured in visual cortex, a regular pattern with fields of slowly changing orientation preferences is observed (Blasdel, 1992). This pattern is continuously repeated over V1, with the exception of local orientation discontinuities that occur periodically. Interestingly, neurophysiological and anatomical evidence suggests that non-adjacent cortical regions that share the same orientation preference are connected via long-range intrinsic connections (Gilbert & Wiesel, 1979; 1989; Malach, Amir, Harel & Grinvald, 1993). Taken together, these results demonstrate that orientation selectivity is a feature that is exquisitely organized in a functional manner in early cortical regions.

In the perceptual domain, orientation is a visual property that has also received a great deal of research attention. Human observers are very sensitive to

changes in orientation tilt, and can resolve tilt differences that are smaller than the spacing of photoreceptors, an ability commonly referred to as a hyperacuity (Westheimer, 1981). The most common stimuli used for measuring orientation discrimination and detection are tilted lines or gratings, where the threshold is measured as the minimum amount of tilt required to detect or discriminate a change in orientation. With long lines, human observers can discriminate a tilt difference as small as 0.5° of visual angle (Andrews, 1967a,b; Westheimer, Shimamura & McKee, 1976). With shorter lines, discrimination thresholds are poorer (Scobey, 1982; Vogels & Orban, 1984, Westheimer & Ley, 1997). Orientation discrimination thresholds also depend upon stimulus contrast: when stimulus contrast is near-threshold, tilt discrimination thresholds can be as high as 10° (Watson and Robson, 1981). Other research concerned with orientation discriminations involve the use of low contrast gratings, where thresholds are determined as the lowest contrast at which subjects can accurately report the orientation of the grating (Blakemore & Campbell, 1968; Movshon & Blakemore, 1973).

A fundamental goal for vision science is to establish links between the neural mechanisms and the perceptual performance of the organism. The orientation system appears to be an ideal system for exploring links between physiology and behaviour because both responses are well characterized in the orientation domain. Making that link, however, has proven to be difficult. Very few orientation-selective neurons possess tuning bandwidths sufficiently narrow to support perceptual performance (Bradley, et al, 1987; Vogels and Orban, 1990). If orientation perception is directly mediated by the tuning properties of V1 neurons, then perceptual decisions for stimuli presented at threshold are dictated

by integrating over a sparse neural code. Furthermore, the overall map of orientation preference is surprisingly normal (Kim & Bonhoeffer, 1994) in animals that have extremely poor vision (Murphy & Mitchell, 1986). Finally, the responses of orientation-selective neurons are profoundly affected by changes in stimulus contrast and spatial frequency (Movshon, Thompson & Tolhurst, 1978), whereas perceptual discrimination thresholds are relatively unaffected (Burbeck & Regan, 1983; Paradiso, Carney & Freeman, 1989). Taken together, these discrepancies have made it difficult to develop precise models of orientation perception based on underlying orientation-sensitive mechanisms in primary visual areas.

Although the details of the link between the neural mechanisms and orientation perception have remained elusive, more success has been achieved with respect to motion perception. In 1992, Britten, Shadlen, Newsome and Movshon published their remarkable findings that the sensitivities of neurons in Macaque MT can match the psychophysical sensitivities of the animal. In their paradigm, performance was measured using a motion-in-noise stimulus, where the threshold was measured as the minimum proportion of moving dots required to correctly discriminate the direction of motion (Fig. 2). Neural response rates and behavioural responses were simultaneously recorded. The neurometric and psychometric functions recorded under these conditions were very similar, both in terms of the overall shape of the curves and the absolute thresholds. Moreover, from trial-to-trial the response rate of individual neurons was correlated with the behavioural response of the animal, *even in the absence of a coherent motion signal* (Britten, Newsome, Shadlen, Celebrini & Movshon, 1996). These results were the first to demonstrate that the responses of single MT neurons can support the overall discrimination capabilities of the animal in the motion domain, and laid

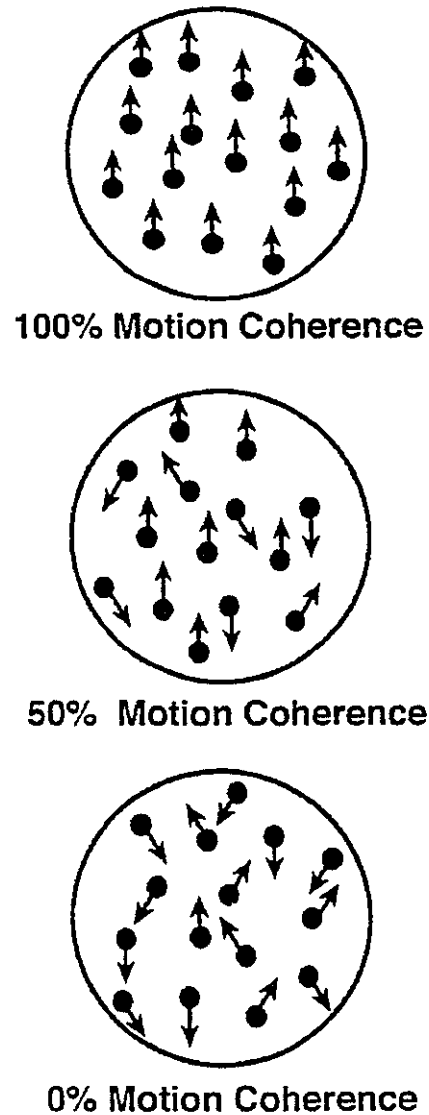


Figure 2. Examples of motion-in-noise stimuli. The stimulus in the top panel contains a strong (100%) motion signal. In the middle panel, 50% of the moving dots carry the motion signal, and in the bottom panel, 0% of the moving dots carry the motion signal. Motion discrimination thresholds are measured as the minimum number of signal dots required to correctly discriminate the direction of motion.

the foundation for researchers to develop similar links in other visual domains.

Visual motion-in-noise stimuli have also been successful in elucidating the perceptual correlates of abnormal neural function in the motion processing system. Animals and patients with deficits in neural mechanisms that underlie the perception of motion can make motion judgements in a noise-free situation. For example, cats with a reduced number of directionally-selective neurons can accurately discriminate opposite motions using random dot kinematograms containing no visual noise (Pasternak, Albano, & Harvitt, 1990). Their performance drops precipitously, however, when even a small number of 'noise' dots are added to these displays. Likewise, the motion-blind patient L.M. exhibits only mild-to-moderate deficits in motion discrimination tasks using noise-free stimuli but adding even a small amount of visual noise to the display renders the motion virtually invisible to L.M. (Baker, Hess & Zihl, 1991). These observations are thought to reflect a difference in the processing of relevant neural circuits to distinguish the neural signal from noise.

These experiments on motion perception illustrate the advantages of using signal-in-noise stimuli to link perceptual thresholds with the underlying neural mechanisms. One advantage of the signal-in-noise paradigm is that the strength of the visual signal can be manipulated without changing the contrast of the stimulus. In many other psychophysical tasks, signal strength is reduced by lowering the contrast of the stimulus and the threshold is then measured as the minimum contrast at which the stimulus dimension can still be discriminated. This technique for making a task more perceptually challenging has the unfortunate consequence of confounding the effects of low contrast with the stimulus dimension of interest. This is especially problematic when recording

neural responses because there is an interaction between stimulus contrast and the response rate and properties of V1 neurons. For example, the size of the classical receptive field of V1 neurons is larger when measured using low contrast stimuli than with high contrast stimuli (Kapadia, Westheimer, & Gilbert, 1999). As a result, it has been difficult to develop paradigms to measure behavioural and neural performance that probe the characteristics of spatial processing using low contrast stimuli. Using high contrast signal-in-noise stimuli allows for neural and behavioural thresholds to be measured for visual dimensions independent of stimulus contrast.

A second major advantage of signal-in-noise stimuli is that discrimination thresholds for large stimulus differences can be determined. Another common method for measuring threshold performance is to reduce the stimulus difference in the dimension being measured, where thresholds are evaluated as the smallest difference that can be discriminated. The neural mechanisms that underlie these fine discriminations likely differ from those that underlie coarser discriminations since fine discriminations will depend on mechanisms that share similar tuning characteristics. Perceptual discriminations of large differences, on the other hand, likely depend upon activity from largely non-overlapping populations of visual cortical neurons. Establishing links between behaviour and neural processing should be easier when studying populations of neural mechanisms that are largely separable in function. Therefore, determining the populations that contribute to perceptual decisions should therefore be easier with larger stimulus differences. Taken together, these advantages suggest that, in order to establish links between neurons and behaviour in other visual domains, the use of signal-in-noise stimuli may be a more effective approach.

In this thesis, I present a novel orientation-in-noise stimulus that I have developed to measure orientation perception. The principles motivating the development of this stimulus are similar to those used to develop the signal-in-noise stimulus that has been used so successfully to study motion perception. The new orientation-in-noise stimulus achieves the goals of being high contrast and broadband in spatial frequency, and yet perceptually challenging (Fig. 3). Probing perceptual discriminations with this stimulus has elucidated some novel aspects of orientation processing in the human visual system. In particular, the characteristics of the orientation-in-noise thresholds suggest that oriented signals are locally pooled in early visual areas to support performance, both in the spatial domain (Chapter 2) and in the temporal domain (Chapter 3). Moreover, oriented signals are pooled in an orientation-specific manner, where orientation signals presented in the context of a parallel surround are less discriminable than signals presented in an orthogonal surround (Chapter 4). This orientation-specific pooling occurs early in visual processing, and most likely depends on orientation-selective mechanisms in early cortical areas (Chapter 5). A computational model based on features of orientation-selective mechanisms in V1 captures these human thresholds, and provides insights into the nature of orientation discrimination. These behavioural results and computational modelling provide a foundation for future research probing the neural mechanisms of orientation processing using the novel orientation-in-noise stimulus.

Chapter 2

Orientation Discrimination in Visual Noise Using Global and Local Stimuli

Introduction

Neurons in primary visual cortex respond selectively to stimulus attributes such as orientation, contrast, spatial frequency, and direction of motion (Hubel & Wiesel, 1959; 1962; 1968). A fundamental goal for vision science is to establish how these underlying neural mechanisms support visual perception and how they are related to psychophysical thresholds. In studies of orientation discrimination, psychophysical thresholds have typically been measured using line or grating stimuli, similar to those used to measure neural responses electrophysiologically. With lines and gratings, the perceptual discrimination is made challenging by reducing the difference in tilt angle (e.g., Andrews, 1967a,b; Vogels & Orban, 1985, 1986; Makela, Whitaker & Rovamo, 1993; Westheimer & Ley, 1997) or by reducing the contrast (Blakemore & Campbell, 1969; Movshon & Blakemore, 1973). These same stimulus attributes have been varied to measure orientation bandwidth and contrast sensitivity of orientation-selective neurons in visual cortex and those tuning properties have formed the basis of computational models developed to account for orientation discrimination (e.g., Barlow, 1972; Bradley, Skottun, Ohzawa, Sclar & Freeman, 1987; Hawken & Parker, 1990).

There remains some uncertainty, however, about the relationship between the neural basis of orientation discrimination and perceptual thresholds for orientation tasks. On the one hand, broad orientation tuning functions of cortical neurons can support fine discriminations (Parker & Hawken, 1985; Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987). On the other hand, it has been shown that while the orientation tuning of some neurons matches perceptual performance, most do not (Vogels & Orban, 1990). Furthermore, varying contrast

and spatial frequency has less of an effect on perceptual performance (Burbeck & Regan 1983; Paradiso, Carney & Freeman, 1989) than it has on the response of V1 neurons (Movshon, Thompson, & Tolhurst, 1978). Taken together, these differences have posed a problem of designing appropriate visual stimuli and experimental paradigms because it has been difficult to separate orientation processing from the effects of contrast and spatial frequency.

One approach to address this kind of problem when studying visual discriminations has been to make the task more challenging by adding noise to the stimulus, rather than reducing contrast or reducing the stimulus difference being compared. This noise technique has been used effectively in the motion domain (e.g., Newsome & Paré, 1988; Britten, Shadlen, Newsome & Movshon, 1992) where normal observers and neurons in MT can accurately determine the dominant direction of motion in displays in which most of the dots move randomly and only a small percentage move coherently. These stimuli have also been used in animal and human studies following lesions to the motion pathway. With coherent motion stimuli, only mild to moderate deficits in motion discrimination were found, but with even a small amount of random visual noise added to the stimulus, performance was severely disrupted (Pasternak, Albano & Harnitt, 1990; Schiller, 1990; Schiller & Lee, 1994; Rudolph & Pasternak, 1999, Hess et al, 1989; Vaina et al, 1990; Baker et al, 1991). Since these “noisy” stimuli are composed of high contrast elements, the visibility of the stimulus is not a limiting factor and the perceptual deficits are confined to the motion domain. These results reflect a difference in the ability of relevant neural circuits to successfully distinguish the visual motion signal from noise and illustrate the effectiveness of noise stimuli for studying visual discrimination.

We have developed a similar signal-in-noise paradigm in the orientation domain using two types of oriented texture that provide greater selectivity for studying orientation discrimination independent from contrast and spatial frequency. The stimuli are designed to be highly visible, the discrimination involves comparing large orientation differences, and yet the task is perceptually challenging. This is achieved by using stimuli that are high contrast, broadband in spatial frequency, and contain an orientation signal embedded in unoriented noise. The strength of the orientation signal can be varied from 0% to 100%, and the threshold is the smallest amount of orientation signal necessary to discriminate between horizontal and vertical. One type of orientation noise stimulus is Global in nature, because the underlying orientation signal extends across the entire display. The other type is Local, because the orientation signal is spatially limited. Comparison of the thresholds for Local and Global stimuli provides insights into orientation processing mechanisms. In addition, the nature of spatial integration of orientation information can be addressed by comparing thresholds for various stimulus sizes. Finally, using noise stimuli allows for quantitative estimates of internal neural noise at both the early stages of orientation-selective neurons and at later stages of perceptual decision-making.

We have studied orientation discrimination by comparing psychophysical thresholds and the results from a computational model for a variety of sizes of the Local and Global orientation noise stimuli. Thresholds for both stimuli improved with larger stimulus area, reaching an optimal threshold of only 11% orientation signal. At smaller stimulus sizes, thresholds for the Local stimulus were significantly better than for the Global stimulus. The experimental and model results suggest that performance may be mediated by pooling the responses of

low-level neural mechanisms and limited by two stages of intrinsic neural noise. A preliminary report included some of these data (Anderson, Radisic, Murphy & Jones, 2000).

Methods

Subjects

Four subjects participated in the experiments. One observer (ZR) was highly practiced on the task, two observers (JA, KD) had some practice before collecting data, and one observer (MV) had no practice before testing, in order to examine the role of experience. All four subjects had normal or corrected-to-normal vision.

Visual Stimuli

We have developed two types of visual stimuli to measure orientation discrimination. The stimuli were high contrast grey-level patterns, containing a broad range of spatial frequencies, with an independently variable amount of horizontal or vertical orientation signal in the presence of unoriented noise. Pixel values were selected from a uniform random distribution of 256 grey-levels. For both kinds of stimuli, the parameter P represents the strength of the orientation signal, namely, the percentage of pixels carrying the orientation signal versus noise pixels. When $P=100\%$ the stimulus was a one-dimensional white noise grating at either a horizontal or vertical orientation; when $P=0\%$ the stimulus was uniform random noise, with no dominant orientation. The Global and Local stimuli were the same when $P=100\%$ or $P=0\%$, however, for intermediate values of P they were dissimilar (Fig. 3).

The "Global signal" stimulus was generated by starting with a one-

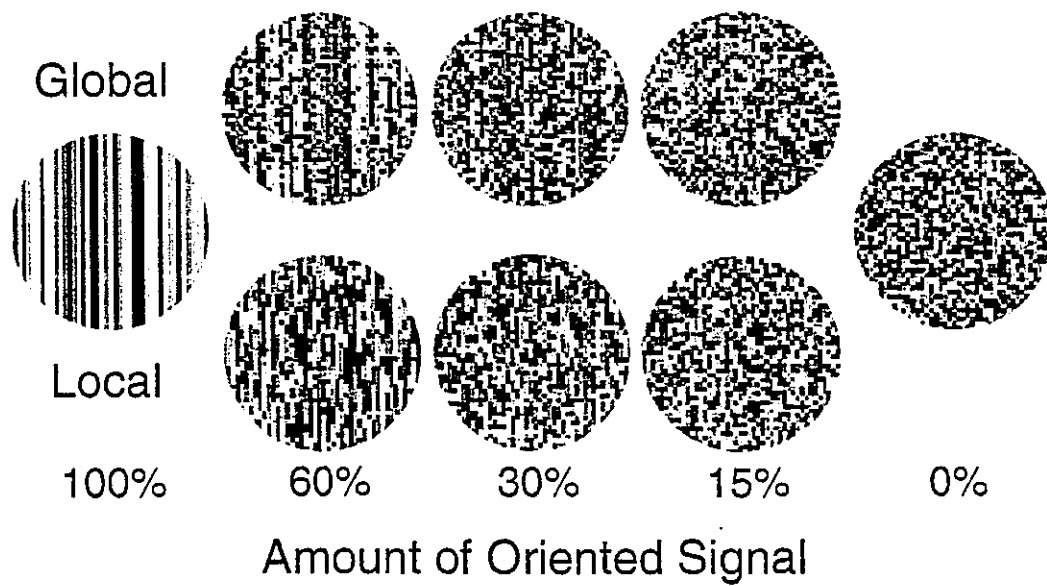


Figure 3. Examples of the two kinds of orientation stimuli used in experiments at various orientation signal strengths. The stimuli are composed of an oriented signal component, and an unoriented noise component. Examples of the Global orientation stimulus are presented on the top, and examples of the Local orientation stimulus are presented on the bottom. When the orientation signal strength is either 100% or 0%, the two kinds of stimuli are identical. For intermediate levels of orientation signal, they are dissimilar. Global stimuli contain oriented contours that extend across the entire stimulus, whereas Local stimuli contain local oriented contours. All of the stimuli in these examples are vertical.

dimensional horizontal or vertical white noise grating, randomly selecting ($100-P$)% of the pixels, and replacing them with new random grey-levels. The resulting stimulus resembles an oriented pattern covered by a variable amount of salt and pepper noise (Fig. 3). The term “Global” was used to describe this stimulus because it contained partially obscured oriented contours of a particular grey-level that extended across the entire stimulus.

The “Local signal” stimulus was generated by sequentially assigning grey-levels to pixels along each orientation stripe. With probability $P/100$, the next pixel continued with the same grey-level, otherwise a new randomly chosen grey-level was assigned. Each orientation stripe was drawn independently. The resulting image resembles an oriented pattern of grey streaks with variable average length (Fig. 3). The term “Local” was used to describe this stimulus because it contained local oriented contour segments with independent grey-levels and no inherent continuity that extended across the entire stimulus.

The visual stimuli were generated on a computer workstation (Sun Microsystems, Ultra-10/Creator3D) using custom software written in Matlab (Mathworks). The stimuli were displayed on a 19" colour monitor (Hitachi CM751U) with 0.26 mm dot pitch, a spatial resolution of 1280x1024 pixels, an 8-bit gamma correction lookup table, and 76 Hz frame rate. Stimuli were presented within a circular aperture formed by a matte black paper mask placed in front of the display. Seven aperture diameters were used: 0.7° , 2.1° , 3.5° , 4.9° , 7° , 10.5° , and 14° . The stimuli were viewed binocularly from a distance of 57 cm and had a mean luminance of 20 cd/m^2 .

Procedure

A two-alternative forced-choice paradigm was used to determine

orientation discrimination thresholds. Within one trial, a horizontally or vertically oriented stimulus was displayed for 1 second. Subjects were instructed to judge whether the stimulus was oriented horizontally or vertically and to respond by pressing one of two keys on the keyboard. Subjects were not given feedback.

Unless otherwise noted, threshold estimates were obtained using a method of constant stimuli, where each threshold estimate was based on 120 trials (10 presentations for each of the 12 different signal levels). Response data were fit with a Weibull function (Quick, 1974) using the method of least squares. Thresholds were calculated at the 82% correct level, which corresponds to the point of maximum slope on the psychometric function (Harvey, 1986). A 3-down 1-up staircase procedure was used in some conditions, where threshold estimates were based on 100 trials. In this case, thresholds were calculated at the 79.4% correct level, which is the level of correct response to which this staircase procedure converges (Levitt, 1971). At the beginning of each experimental run, the initial level of orientation signal was set to be highly visible (60% signal). The amount of signal was reduced in decrements of 5% after 3 correct responses for the first 33 trials. Step sizes were reduced to 4% and 3% after trials 33 and 66 respectively.

Mean thresholds for the seven aperture sizes and two stimulus classes are based on 5 runs of 120 trials for each subject. Testing occurred over a 7 day period, where each daily session consisted of threshold estimates for both the Global and Local stimuli using one aperture size. Subject MV was tested over a period of 8 days using the Local stimulus and 4 aperture sizes (14° , 4.9° , 2.1° , and 0.7°) each day.

Model Simulation and Analysis

We formulated a model of local orientation processing based on pooling simple cell responses and compared it with the human psychophysical thresholds. The model was implemented in two stages. First we implemented a computer simulation to determine the thresholds of a noise-free ideal observer, assuming the stimulus images were convolved with oriented linear spatial filters. Second we analyzed the differences between the simulated ideal observer responses and the measured human responses to characterize these differences in terms of early and late stages of noise.

The ideal observer was implemented as a MATLAB function. Given an input stimulus image for a single trial, it computed an output response of either "horizontal" or "vertical". The stimulus image was convolved with oriented filters designed to resemble horizontal and vertical simple cell receptive fields. Three sizes of filter were used, with the smallest being 3x3 pixels ($\begin{bmatrix} -1 & 2 & -1 \\ -1 & 2 & -1 \\ 1 & 2 & -1 \end{bmatrix}$) and the others being 6x6 and 9x9 versions of the same even-symmetric kernel. This simple linear filter has an orientation bandwidth of $\pm 27^\circ$ and a spatial frequency bandwidth of 1.6 octaves. These filter sizes correspond to approximately 0.25° , 0.5° , and 0.75° . Within each orientation channel, the oriented filter responses were full-wave rectified ($|x|$) and pooled by summing over the full area of the stimulus. This yielded two overall responses, one for vertical and one for horizontal. These were compared and the ideal observer response corresponded to the orientation of the filters that produced the larger response. Thresholds for the ideal observer were obtained by running the same MATLAB software used with human observers, but substituting the ideal observer function in place of a function that received a human subject's key press. Simulations were

carried out in this manner for all seven aperture sizes using both the Global and Local stimuli. Mean thresholds were based on 5 runs of 120 trials per condition.

The second stage in modelling local orientation processing was to analyze the contribution of intrinsic neural noise to human performance. Instead of adding noise to the simulation, we chose a more direct analytical approach. Theoretical equations (described later) were fit to the human threshold data using a method of least-squares to obtain best-fitting parameters for “early-noise” which corresponds within the model to the first stage of orientation processing, at the level of individual simple cells, and “late-noise”, which corresponds to noise or uncertainty in the psychophysical decision stage after the orientation signals have already been pooled.

Results

Human Results

Orientation discrimination thresholds were measured for 3 subjects using the Global and Local orientation noise stimuli for a range of aperture sizes (0.7° to 14°). The percent orientation signal required to discriminate between vertical and horizontal was found to vary as a function of aperture size and to depend on the type of orientation signal used (Fig. 4).

Orientation discrimination thresholds were consistent within subjects (Fig. 4), as well as between subjects (Fig. 5), as indicated by the small error bars. For both Global and Local stimuli, optimum thresholds of approximately 11% orientation signal were obtained with the largest aperture size (14°). Discrimination thresholds were much poorer at the smallest aperture size (0.7°), where the range of thresholds was 36.3-43.4% signal for the Global stimulus and

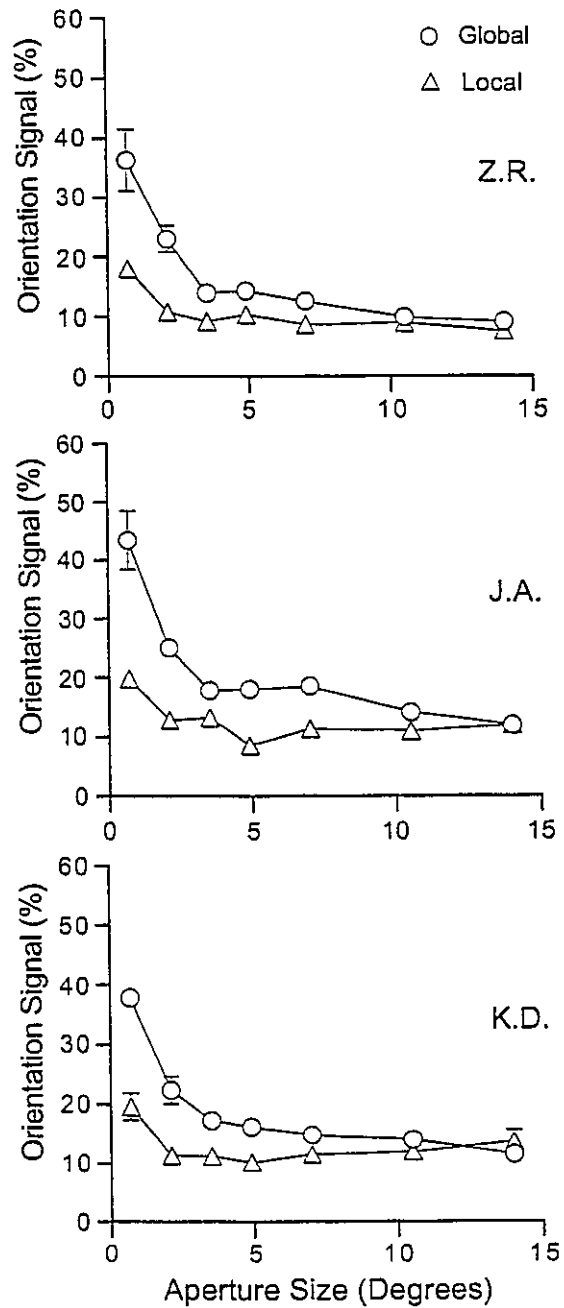


Figure 4. Effect of aperture size on orientation discrimination thresholds for three observers. Open circles represent thresholds for Global stimuli; open triangles represent thresholds for Local stimuli. Error bars represent ± 1 SEM.

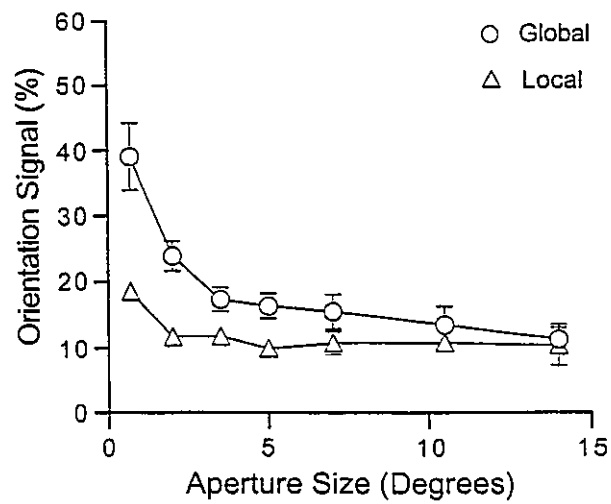


Figure 5. Effect of aperture size on orientation discrimination thresholds. Mean thresholds for observers in Figure 4. Axes and plot symbols are the same as in Fig. 4.

18.0-19.8% signal for the Local stimulus. At the smallest aperture sizes (0.7° and 2.1°), discrimination with the Global stimulus required about twice as much orientation signal compared to the Local stimulus. This indicates that perception of the Global orientation signal was more susceptible to noise, whereas the Local orientation signal was more robust.

For both kinds of orientation noise stimuli, performance improved with increasing aperture size. For the Local stimulus performance improved very quickly, reaching the optimum threshold of approximately 11% at an aperture size of 2.1° , with no further improvement even as aperture size was increased up to 14° . For the Global stimulus, there was an initially rapid improvement as aperture size was increased from 0.7° to 3° , followed by a more gradual improvement. Thresholds for the Global stimulus remained elevated above thresholds for the Local stimulus up until an aperture size of about 7° - 10° .

To investigate whether thresholds were influenced by stimulus duration, the presentation time was reduced from 1 s to 100 ms. Reducing the presentation time did not affect thresholds (Fig. 6). There was no difference in the thresholds for the Local orientation stimuli and only a slight increase in thresholds with brief presentations of the larger aperture sizes for the Global signal stimulus. These results demonstrate that subjects were able to extract the oriented signal from the stimulus display quite rapidly, and suggest that performance on this task relies upon simple neural mechanisms that do not require long exposure times.

Previous studies have shown that the ability to discriminate very small differences in tilt angle using line or grating stimuli can improve with practice (e.g., Vogels & Orban, 1985; Shiu & Pashler, 1992; Matthews, Liu & Qian, 2001; Schoups, Vogels, Qian & Orban, 2001). We investigated whether thresholds for the

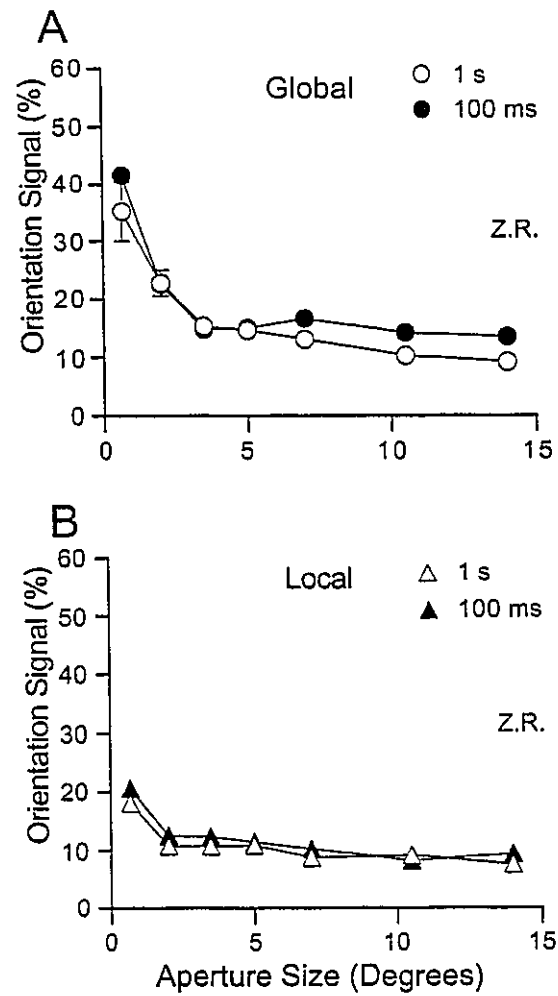


Figure 6. Effect of stimulus presentation time on orientation discrimination thresholds. Open symbols are thresholds for 1 second presentation time; closed symbols are thresholds for 100 millisecond presentation time. Thresholds were not different with the shorter presentation time, for both (A) Global stimuli, and (B) Local stimuli.

oriented noise stimuli improved with practice by plotting thresholds for the first 8 days of testing for a naive subject (MV). These thresholds were obtained using a staircase method for the Local stimulus, with 100 ms presentation time and 4 aperture sizes. No systematic improvement in thresholds was found over the 8 days (Fig. 7). Furthermore, thresholds measured on the very first day of testing were comparable to those of highly practiced subjects (cf. Fig. 4).

We examined the nature of the orientation information in the stimuli to determine whether a difference in information content could explain the differences in discrimination thresholds between the Local and Global stimuli. Both types of stimulus were evaluated using a two-dimensional Fourier transform (FFT), and the results are shown in Figure 8, along with the power spectrum corresponding to a 100% orientation signal for comparison. All the signals in this example were oriented vertically, and the amount of signal in the Global and Local stimulus examples was 58%. The unoriented noise in the stimuli results in energy in the power spectra distributed over a variety of orientations and spatial frequencies. In the Global stimulus, the majority of the energy in the power spectrum was concentrated at a single orientation corresponding to vertical. In contrast, the oriented energy in the Local stimulus was more dispersed away from the vertical orientation. According to the Fourier transform, which provides an analysis of the overall structure of the stimulus, the Global stimulus contained more information at vertical than was the case for the Local stimulus. Subjects, however, performed better with the Local stimulus. These results show that the difference in performance cannot simply be explained by a difference in the amount of oriented energy in the two types of stimuli. Instead, the results suggest that subjects depend more on a local analysis of the orientation structure

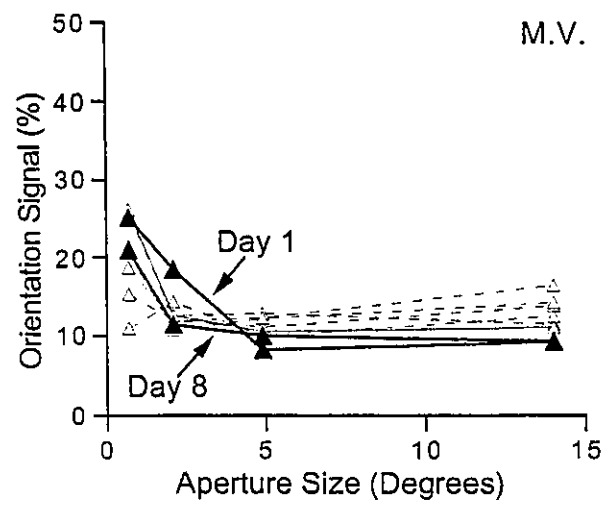


Figure 7. Effect of practice on discrimination thresholds. Thresholds for a naive subject (MV) were tracked over 8 days, using Local stimuli. Thresholds did not improve significantly. Thresholds measured on Day 1 and Day 8 are highlighted for comparison.

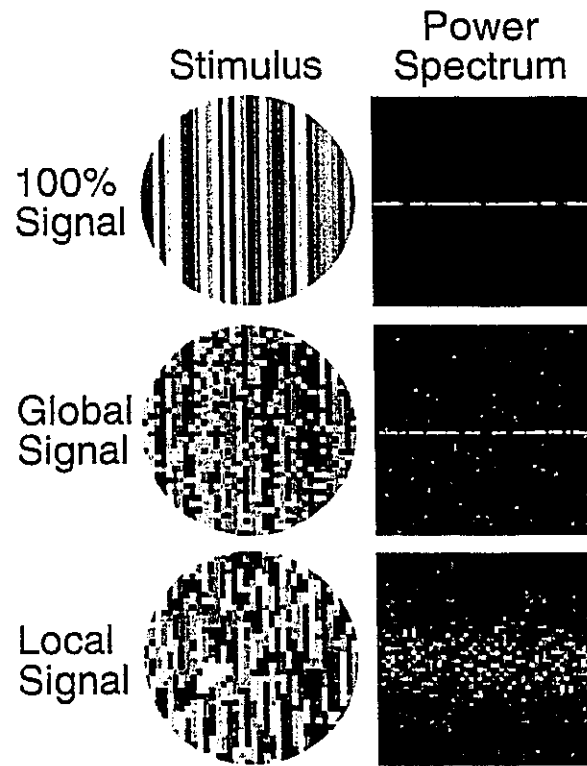


Figure 8. Fourier power spectra of stimuli used in experiments. Three example stimuli are presented on the left and corresponding Fourier power spectra are presented on the right. The top stimulus containing 100% orientation signal has a corresponding power spectrum with energy at a single orientation, distributed across all spatial frequencies. Both Global and Local stimulus examples contain 58% vertical orientation signal. In the Global stimulus, a small amount of orientation energy is evident at a variety of orientations and spatial frequencies, but the majority is still concentrated at a single orientation. In the Local stimulus, orientation energy is significantly more dispersed around the dominant orientation. This reveals that there is more orientation energy present at vertical, as opposed to neighbouring orientations, in the Global stimulus.

of the stimulus.

Model Simulation Results

The purpose of implementing an orientation summation model was to simulate potential neural mechanisms for orientation discrimination. A schematic diagram illustrates the computational steps involved in the simulated noise-free ideal observer (Fig. 9). Stimuli were convolved with both vertical and horizontal spatial filters, the filtered responses were rectified and spatially pooled within each orientation channel, and the response corresponded to the orientation of the filter that produced the larger response.

Thresholds were obtained for the ideal observer using 3 filter sizes (0.25° , 0.5° , 0.75°) (Fig. 10). These sizes were selected to be comparable to the range of receptive field sizes found in the central visual field of macaque V1 (Hubel & Wiesel, 1968). Two major similarities are apparent between the ideal observer thresholds and the human thresholds. First, for all filter sizes and all aperture sizes, thresholds were poorer for the Global stimulus than for the Local stimulus. Second, increasing the aperture size improved performance rapidly at smaller aperture sizes, and more gradually at larger aperture sizes. The ability to pool additional orientation information across space has a profound influence on thresholds for smaller aperture sizes and gradually provides diminishing returns at larger aperture sizes. Because the ideal observer pooled oriented filter responses without any loss of information, thresholds continued to improve indefinitely as the stimulus aperture was increased for both Global and Local stimuli. In the limit, thresholds approach arbitrarily small signal levels for very large apertures.

Ideal observer thresholds using the smallest filter size (0.25°) yielded

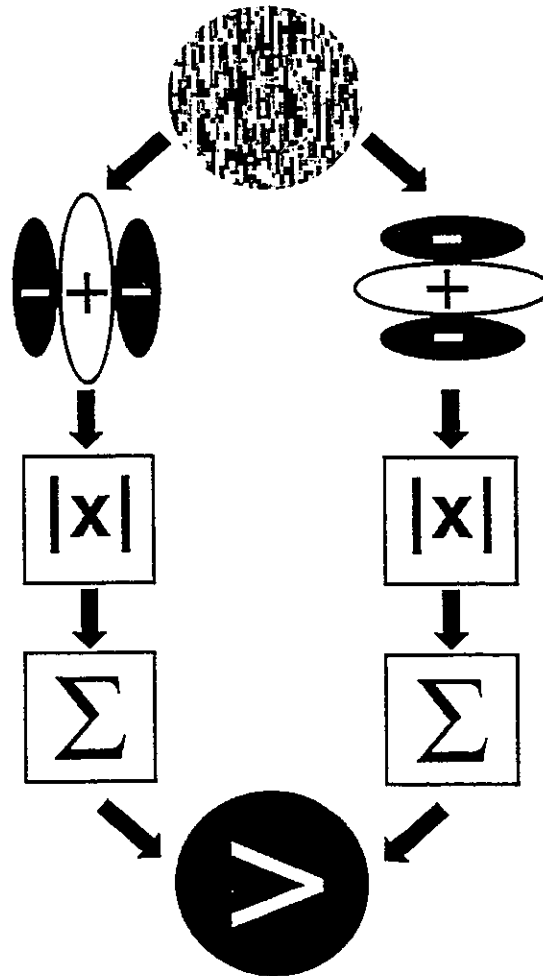


Figure 9. Schematic diagram of local orientation summation model. The stimulus, depicted at the top, was convolved with vertically and horizontally oriented filters. Within each orientation channel, filter responses were full wave rectified ($|x|$) and summed together. The model response corresponded to the orientation of the filter that produced the larger response.

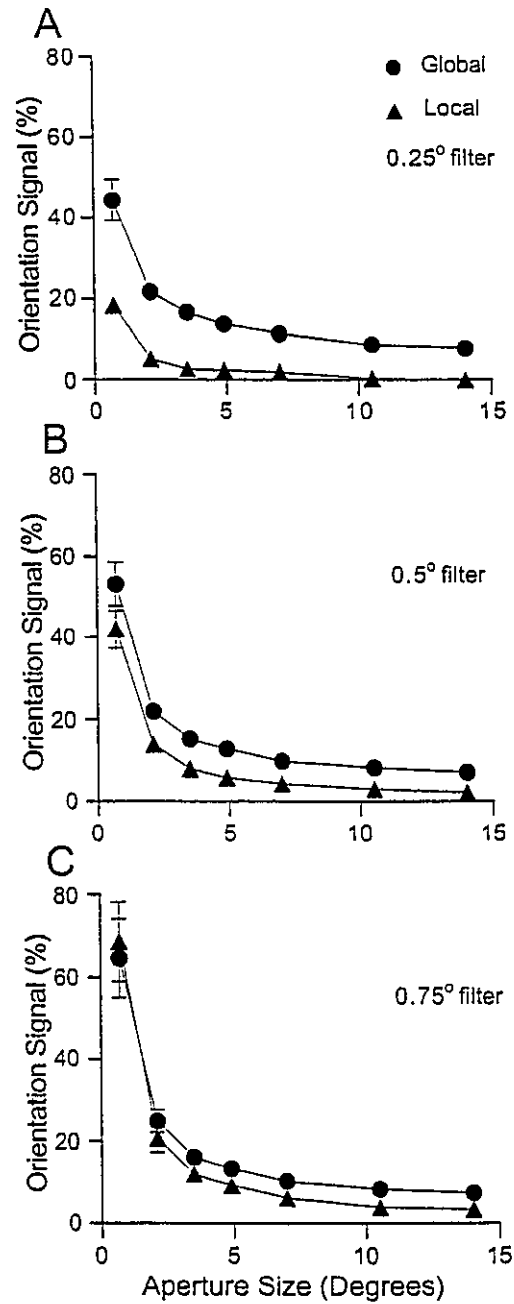


Figure 10. Orientation summation model thresholds for various filter sizes. The model thresholds were computed and plotted as a function of aperture size for filters of size (A) 0.25° , (B) 0.5° , and (C) 0.75° filters. Solid circles represent thresholds for Global stimuli; solid triangles represent thresholds for Local stimuli. The 0.25° filters are most similar to the human results.

results most similar to human thresholds (Fig. 11). This filter size closely matches the size of the smallest simple cell receptive fields in macaque V1 (Hubel & Wiesel, 1968). Human and ideal observer results for the Global stimuli were very similar in both absolute threshold levels and the overall shape of the functions (Fig. 11A). Ideal observer performance at large aperture sizes was slightly better than human performance, however reducing the aperture size resulted in the same gradual increase in thresholds that was observed with human thresholds. For the Local stimuli, the ideal observer threshold functions followed the same shape (Fig. 11B), and at the smallest aperture size, approximately 19% signal was required for accurate discrimination, which was remarkably similar to human thresholds. For the largest aperture sizes and Local stimuli, the ideal observer discrimination threshold approached 0% signal, while the human threshold never improved beyond about 11%. This suggests that human performance was limited by an intrinsic factor not present in the ideal observer, most likely neural noise.

Model Analysis Results

Orientation discrimination thresholds in this experiment are well described by two parameters: the rate of improvement over small aperture sizes, and a performance limit for large aperture sizes. This is summarized in the equation:

$$threshold = \max (K N^{-1/2}, T_L)$$

where K is related to the effectiveness of the type of orientation signal, N is the aperture size, and T_L is the optimum threshold limit for larger aperture sizes. This equation was fit to the threshold data using a method of least squares (Fig. 12). Best fitting parameters were: $K = 15.5$ (Local), $K = 33.7$ (Global), $T_L = 11.2$.

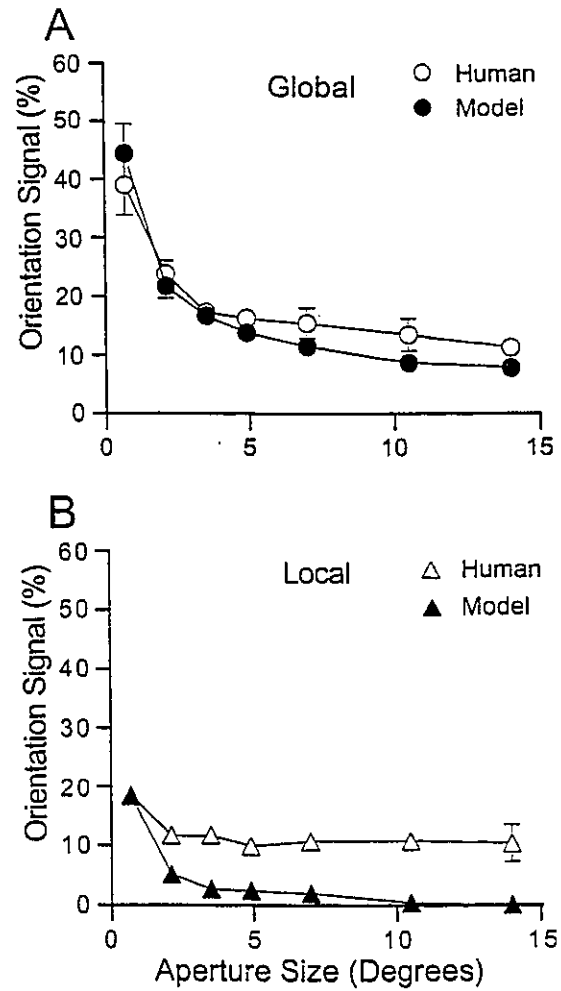


Figure 11. Comparison of thresholds from model and human subjects. Open symbols represent human thresholds; closed symbols represent model thresholds for 0.25° filter. Circles represent (A) Global stimuli; triangles represent (B) Local stimuli.

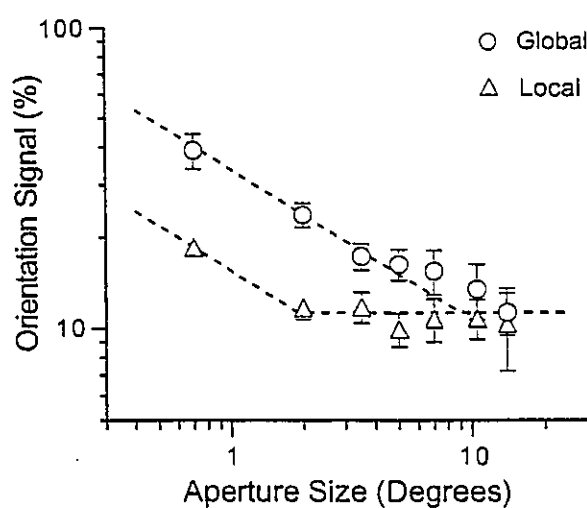


Figure 12. Relationship between orientation discrimination threshold and aperture size. Thresholds for Local and Global stimuli plotted on log-log axes are well described by an equation of the form: $threshold = \max(K N^{-1/2}, T_L)$, where K represents the effectiveness of the type of orientation signal, N represents aperture size, and T_L represents the optimum threshold for larger aperture sizes. The dashed line represents the best least-squares fit of this equation, with $T_L = 11.2\%$ orientation signal, $K = 15.5$ (Local, $r^2 = 0.93$), and $K = 33.7$ (Global, $r^2 = 0.97$).

Performance on this task is well described by this equation ($r^2 = 0.93$ for Local, $r^2 = 0.97$ for Global).

Signal detection theory provides a way to predict performance of an ideal neural mechanism that has both early and late noise components. Within this framework, the threshold is predicted by the following equation:

$$threshold = Z (\sigma_L^2 + k^2 \sigma_E^2 / N)^{1/2}$$

where k is a parameter related to the effectiveness of the type of orientation stimulus in evoking a neural response, σ_E is the standard deviation of the early noise, σ_L is the standard deviation of the late-noise, N is the number of independent stimulus samples, which is taken to be proportional to the aperture size, and Z is the z-score corresponding to the threshold measurement criterion. In the present experiments, thresholds were obtained at 82% correct, corresponding to a z-score of 0.915. Best fitting parameters were: $\sigma_L = 9.8$, $k\sigma_E = 14.4$ (Local), $k\sigma_E = 34.2$ (Global), all in units equivalent to percent orientation signal ($r^2 = 0.93$ for Local, $r^2 = 0.99$ for Global). It is not possible from our experimental data to tease apart the parameters k and σ_E .

Discussion

The orientation discrimination thresholds can be described in terms of three main effects. First, the Local orientation signal was a more effective stimulus than the Global orientation signal, particularly at the smaller aperture sizes. Second, increasing the size of the stimulus, which increases the total amount of orientation signal available in the stimulus, led to a significant improvement in thresholds. Finally, at the largest aperture sizes, discrimination thresholds reached an asymptotic level of about 11% signal. These optimum thresholds were independent of both the type of orientation signal and further increases in

stimulus size, suggesting that they are a consequence of a limiting factor intrinsic to the observer.

The orientation summation model captures the main features of human performance with the two types of orientation noise stimuli. Model performance, like human performance, is better for Local stimuli than for Global stimuli. Even this simple model captures the difference between the stimulus types yielding lower thresholds when the orientation signal is spatially localized. The model thresholds also improve with increasing aperture sizes at a rate that is similar to human performance. Finally, model thresholds asymptotically approach an optimum level of performance for larger apertures.

Orientation Pooling

An important feature of the orientation model is that information is pooled across space and discrimination decisions are based on this pooled signal. Evidence for orientation pooling has also arisen in studies concerned with tilt discrimination, where increasing the length of a tilted line improves tilt discrimination thresholds, even though these lines are longer than the length of foveal receptive fields (e.g., Andrews, 1967b; Makela et al, 1993; Westheimer & Ley, 1997; Henrie & Shapley, 2001). To account for this improvement, signals from adjacent neurons must be combined for better response. Similarly, orientation pooling has been implied in studies concerning “textural analysis”, where the overall orientation perceived in a 2-dimensional array of tilted Gabor patches is the average of the orientations of the local elements (e.g., Dakin & Watt, 1997; Parkes, Lund, Angelucci, Soloman, & Morgan, 2001).

In the present experiment, the initial rate of improvement with increasing aperture size is the same for both types of stimulus. Despite a factor of two

difference in the thresholds for the Local and Global stimuli, when plotted on a log-log scale, the initial thresholds for both types of stimulus are well fit by a power function with slope of $-1/2$, suggesting a common underlying mechanism for the pooling of orientation signals (Fig. 12). This mechanism can be understood by considering principles of signal processing. For example, in the presence of additive noise, performance of an ideal observer improves proportional to the square-root of "N", where N represents the number of independent samples of the stimulus. With the present stimuli, it might at first seem appropriate to define N in terms of the stimulus area, however, when thresholds are plotted as a function of area, the rate of improvement is substantially shallower than predicted by the square-root rule. Instead, performance with the orientation noise stimuli is better accounted for when N is defined in terms of stimulus diameter. This is likely due in part to non-uniform sampling across the visual field: oriented signals that fall on more peripheral receptive fields are not sampled as densely and therefore make less of a contribution than orientation signals that fall on more central receptive fields. As a result, it may be more appropriate to define N in terms of cortical area, such that improvements in signal-to-noise result from the increased amount of cortical territory being activated. Based on current estimates of the visual field representation in human V1, the area of the cortical image of a circular stimulus centered on the fovea grows roughly linearly with the stimulus diameter, for the range of stimulus sizes used in this experiment (Wong & Sharpe, 1999). In our experiments, orientation discrimination thresholds improved in proportion to the square-root of the stimulus diameter, or equivalently, in proportion to the square-root of the cortical area activated by the stimulus. This improvement with increasing aperture size can therefore be described as optimal, since it matches the prediction of an ideal observer. Thresholds continued to

improve for sizes up to 10° for the Global stimulus, making it unlikely that the pooling of orientation signals is mediated only by horizontal connections in V1. Instead, these results raise the possibility that extrastriate areas, with larger receptive fields, also contribute to performance on this task.

Intrinsic Noise

For larger aperture sizes, orientation discrimination thresholds reached a limit of about 11% signal. This limit likely reflects noise in the neural mechanisms underlying performance on this task. Many studies have found that detection and discrimination tasks near threshold are limited by intrinsic neural noise (e.g., Pelli, 1990). Recent experimental and computational evidence suggests that neural noise can be considered as arising at two stages of orientation processing (Parkes et al., 2001). On the one hand, “early-noise” arises at the level of orientation-selective filters at early stages of visual processing and reflects uncertainty in the coding of local orientation signals. The effects of early-noise can be reduced by increasing the amount of signal being pooled, thereby decreasing the variance of the noise in the sum of the filter responses. Thus, the initial improvement in thresholds with increasing aperture size is consistent with early-noise. On the other hand, “late-noise” is independent of the total amount of stimulus signal, and likely arises after orientation signals are pooled. The performance limit of 11% observed in the present experiment for larger apertures is independent of stimulus area, and is therefore consistent with late-noise.

The optimum thresholds reported here may seem relatively high when compared to values that have been reported using other signal-in-noise paradigms. In motion discrimination tasks, for example, as little as 2-5% coherent motion signal is sufficient under ideal conditions for discriminating direction of

motion in normal observers (e.g., Newsome & Paré, 1988; Baker et al., 1991). It is important to keep in mind that the noise is expressed in units related to the particular motion or orientation stimulus used in the experiment and so cannot be compared directly. It is possible that late-noise equivalent to 11% orientation signal may correspond to a different value in terms of coherent motion signal but reflect the same underlying magnitude of intrinsic neural noise.

Lack of Practice Effects

Although perceptual learning has been documented in studies using tilt discrimination with a small difference in angle (e.g., Vogels & Orban, 1985; Shiu & Pashler, 1992; Matthews et al., 2001; Schoups et al., 2001), we found no evidence of perceptual learning using orientation-in-noise discrimination with a large difference in angle. Recent physiological evidence suggests that the amount of neural noise in orientation-selective neurons underlying performance in an orientation discrimination task remains unchanged with practice. Instead, perceptual learning increases the sensitivity of orientation-selective neurons, which is reflected by a change in slope of orientation tuning curves at the learned orientation of trained neurons in V1 (Schoups et al., 2001). Although these might be beneficial in tilt discrimination tasks, small adjustments in orientation tuning curves of underlying neural mechanisms would not be expected to lead to improvements in behavioural performance when discriminating large orientation differences in noise, especially when the level of intrinsic neural noise remains unchanged. The absence of practice effects in our results is therefore consistent with current theories of perceptual learning.

Relationship between Motion and Orientation Discrimination in Noise

The signal-in-noise paradigm has been used effectively in the motion domain for studying the mechanisms underlying normal and abnormal motion perception. For example, the human motion-blind patient L.M. can perform surprisingly well on motion discrimination tasks where all dots move coherently, but when even a small percentage of noise dots are added to the stimulus, performance quickly falls to chance levels (Hess et al., 1989; Baker et al., 1991). Using a similar signal-in-noise paradigm to investigate orientation discrimination in subjects with visual deficits such as amblyopia may help elucidate some of the underlying neural mechanisms, since under some conditions amblyopes can discriminate orientation at near-normal levels (Vogels, Orban, & Vandebussche, 1984; Skottun, Bradley, & Freeman, 1986; Levi & Sharma, 1998; Demanins, Hess, Williams & Keeble, 1999). The stimuli used in those tasks, however, were highly visible elements in a noise-free setting. Perhaps orientation processing deficits in amblyopes would be more readily apparent in a task requiring the extraction of an oriented signal from visual noise.

Summary

We have developed and used a new orientation-in-noise paradigm for studying orientation perception separate from effects of contrast and spatial frequency. A computational model based on ideal observer simulation and analysis of the relationship between external stimulus noise and psychophysical thresholds support several conclusions about the neural mechanisms underlying orientation discrimination. These mechanisms are most sensitive to orientation signals that are spatially localized. Improvements in discrimination thresholds resulting from pooling of orientation information match the optimal performance

of an ideal observer. The extent of orientation pooling suggests a significant contribution from extrastriate cortical areas. The perceptual limits of orientation discrimination with these stimuli can be understood in terms of two stages of intrinsic neural noise: one at an early stage of orientation-selective neurons, and the other at a later stage of orientation pooling and perceptual decision-making. These experiments provide a framework for future studies of orientation processing, including electrophysiology and brain imaging, and studying deficits in orientation processing in developing and abnormal visual systems.

Chapter 3

Temporal Aspects of Orientation Pooling Using Visual Noise Stimuli

Introduction

Early stages of visual processing depend on orientation-selective responses of neurons in primary visual cortex. In computational models of visual processing, these receptive fields are most often modelled as a set of oriented bandpass filters (Wilson & Bergen, 1979) that must be integrated across space to yield a reliable response for perceptual decision-making. The quality of the pooled response depends upon the number of samples: as more independent signals are combined, the signal-to-noise of the pooled response improves. Many psychophysical studies of orientation discrimination have shown that there is spatial pooling of oriented filters because thresholds improve as the size of the stimulus increases. For example, orientation discrimination thresholds improve as a result of increasing the length of an oriented line or grating (Andrews, 1967b; Howell & Hess, 1978; Westheimer & Ley, 1997) or increasing the area of an oriented noise stimulus (Jones, Anderson, & Murphy, 2003). Spatial integration of orientation information seems to be an obligatory function that operates even when pooling local orientation signals from a central target and surrounding distractors impairs performance (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Anderson, Murphy, & Jones, 2001). Taken together, these examples suggest that spatial pooling of orientation-selective filters is a fundamental component of the processing that underlies orientation discrimination.

Temporal pooling of neural responses can also contribute to better visual performance. Longer presentation times facilitate detection and discrimination of brightness and low contrast stimuli (Nachmias, 1967; Breitmeyer & Ganz, 1977; Legge, 1978) and lead to better discrimination of fine changes in orientation tilt

(Andrews, 1967a; Watt, 1987; Zlatkova, Vassilev, & Mitov, 2000). In contrast, we have found that discrimination of a large orientation-in-noise difference does not improve with longer stimulus presentations (Jones et al., 2003). This difference between large and small orientation discriminations may arise because thresholds for larger orientation differences operate on a shorter time-course than thresholds for smaller orientation differences (Zlatkova et al., 2000). These findings raise the possibility that the information required for optimal discrimination of large orientation differences is available within 100 ms, so that increasing the stimulus presentation time beyond that does not provide additional information. These studies, however, used static stimuli and only increased the stimulus presentation time rather than presenting more independent samples of the orientation signal. Perhaps presenting more samples over time could provide additional information necessary to achieve better orientation discrimination thresholds. Testing the contribution of temporal pooling requires the use of stimuli that are more analogous to those used to investigate spatial pooling, specifically, a dynamic stimulus with more temporal samples of the orientation signal. If temporal pooling of orientation information operates in a manner similar to spatial pooling, then providing independent samples over time should promote better discrimination thresholds.

We have taken advantage of the orientation-in-noise paradigm that we recently developed (Jones et al., 2003) to study temporal pooling for discrimination of large orientation differences. The visual stimuli are high contrast, broadband in spatial frequency, and contain an oriented signal embedded in unoriented noise. The strength of the orientation signal can be varied from 0% to 100%, and the threshold is the smallest amount of orientation

signal necessary to discriminate an oriented signal from unoriented noise. Temporal pooling was assessed by making this stimulus dynamic with multiple, independently generated frames of the orientation noise stimulus. This dynamic stimulus effectively increases the number of samples and provides an ideal stimulus to test whether temporal pooling contributes to the discrimination of large orientation differences.

In the present study we compared discrimination thresholds for static and dynamic oriented noise stimuli. Thresholds were better with dynamic stimuli and continued to improve as the length of the presentation time was increased to 1 second. The results demonstrate that temporal pooling can support better discrimination of large orientation differences. We describe these results in terms of a model for orientation discrimination based on signal detection theory, where performance is limited by early and late stages of intrinsic noise. Overall, these findings demonstrate that orientation signals are integrated over time, as well as space, to overcome noise in the stimulus and uncertainty in low-level neural mechanisms.

Methods

Subjects

Three subjects participated in the experiments. One observer (NA) was highly practiced on the task, two observers (JC, PB) had no practice before testing and were naïve to the purpose of the experiment. All three subjects had normal or corrected-to-normal visual acuity.

Visual Stimuli

We used two types of orientation-in-noise stimuli (Global and Local) that

we have recently developed to measure orientation discrimination (Jones et al., 2003). Both stimuli were high contrast grey-level patterns, containing a broad range of spatial frequencies, with a variable amount of orientation signal in the presence of unoriented noise. To generate the stimuli, pixel values were selected from a uniform random distribution of 256 grey-levels. For both kinds of stimuli, the parameter P represents the strength of the orientation signal, namely, the percentage of pixels carrying the orientation signal versus noise pixels. When $P=100\%$ both stimulus types were a one-dimensional white noise grating at either a horizontal or vertical orientation; when $P=0\%$ both types were uniform random noise, with no dominant orientation.

The Global orientation stimulus was generated by starting with a one-dimensional horizontal or vertical white noise grating, randomly selecting $(100-P)\%$ of the pixels, and replacing them with new random grey-levels (Fig. 13). The term "Global" was used because the stimulus contained partially occluded oriented contours that extended across the entire stimulus. The Local orientation stimulus was generated by sequentially assigning grey-levels to pixels along each orientation stripe. With probability $P/100$, the next pixel continued with the same grey-level, otherwise a new randomly chosen grey-level was assigned. Each orientation stripe was drawn independently (Fig. 13). The term "Local" was used because the stimulus contained oriented contour segments with independent grey-levels and no inherent continuity extending across the entire stimulus.

The visual stimuli were generated on an Apple Macintosh G4 computer in the MATLAB (Mathworks) programming environment using Psychtoolbox routines (Brainard,1997). Stimuli were displayed on a 17" Apple Studio Display colour monitor at a resolution of 800 x 600 pixels, a frame rate of 85 Hz, and a

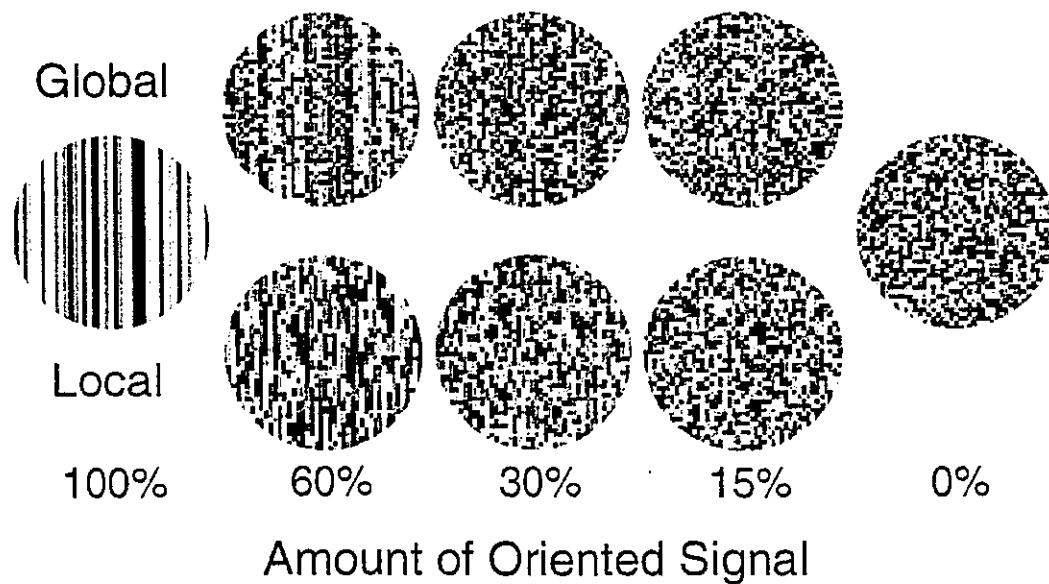


Figure 13. Orientation-in-noise stimuli used in experiments. Stimuli are composed of an oriented signal component and an unoriented noise component. Examples are presented for the Global orientation stimulus (top) and the Local orientation stimulus (bottom). When the orientation signal strength is either 100% or 0%, the two kinds of stimuli are identical; for intermediate levels of orientation signal, they are dissimilar. Global stimuli contain oriented contours that extend across the entire stimulus, whereas Local stimuli contain local oriented contours. All of these examples contain a vertical orientation signal.

mean luminance of 40 cd/m^2 . Stimuli were presented within a circular aperture. Seven aperture diameters were used: 0.7° , 2° , 3.5° , 5° , 7° , 10.5° , and 14° . All viewing was binocular from a distance of 57 cm.

Each stimulus was generated at the beginning of a trial, and presented for 100 ms (9 frames) or 1 s (85 frames). The temporal aspects of the stimulus were controlled by manipulating the 8-bit lookup table. For static stimuli, the lookup table values were unchanged. For dynamic stimuli new random grey-levels were assigned to the lookup table on each frame. This resulted in a dynamic stimulus that was broadband in temporal frequency content.

Procedure

A two-interval forced-choice paradigm was used to determine orientation discrimination thresholds. Subjects were instructed to judge which interval contained the oriented stimulus and to respond by pressing one of two keys on the keyboard. Within a trial, one interval contained either a horizontally or vertically oriented stimulus, and the other interval contained an unoriented noise stimulus (0% orientation signal). A trial started with a central fixation point (500 ms) followed by the first interval (100 ms or 1 s), a uniform black screen (500 ms) and the second interval (100 ms or 1 s).

Threshold estimates for each experimental run were based on 60 trials and were made using the QUEST method of threshold estimation (Watson & Pelli, 1983). Thresholds were calculated at the 82% correct level, corresponding to the point of maximum slope on the underlying Weibull psychometric function (Harvey, 1986). Each experimental run consisted of 2 interleaved staircases to measure thresholds separately for the vertical and horizontal stimuli. No orientation biases were observed, and so mean thresholds were collapsed across

orientation. Mean thresholds for each subject were based on 6 experimental runs. Testing occurred over a 6 day period, and each session consisted of threshold estimates for all seven stimulus sizes and both Global and Local stimuli. Thresholds for static and dynamic stimuli were measured on alternate days.

Model Analysis

Psychophysical thresholds were fit with a theoretical equation (described later) that describes performance in terms of two stages of intrinsic noise. The “early noise” stage corresponds to the first stage of orientation processing and reflects uncertainty at the level of signal filtering. The “late noise” stage corresponds to uncertainty in the decision stage after the orientation signals have been pooled. Best fitting parameters were determined for the full set of psychophysical thresholds using a method of least squares.

Results

Orientation discrimination thresholds were first measured for 3 subjects using both static and dynamic versions of the Global and Local orientation noise stimuli with a 100 ms presentation time. In general, the thresholds were better for dynamic than for static stimuli (Fig. 14). Thresholds were consistent within subjects, as indicated by the small error bars, and similar between subjects. Thresholds were poorer at the smallest aperture size (0.7°) and improved with larger stimuli. Optimal thresholds for the Local stimuli (8.0% dynamic, 9.8% static) were achieved at an aperture size of 3.5° or larger. For the Global stimulus, thresholds improved rapidly when the aperture size was increased from 0.7° to 3.5° , followed by a slower improvement rate for larger aperture sizes. This general pattern of threshold improvement with increasing aperture size is the same as we have previously reported and demonstrates spatial pooling of

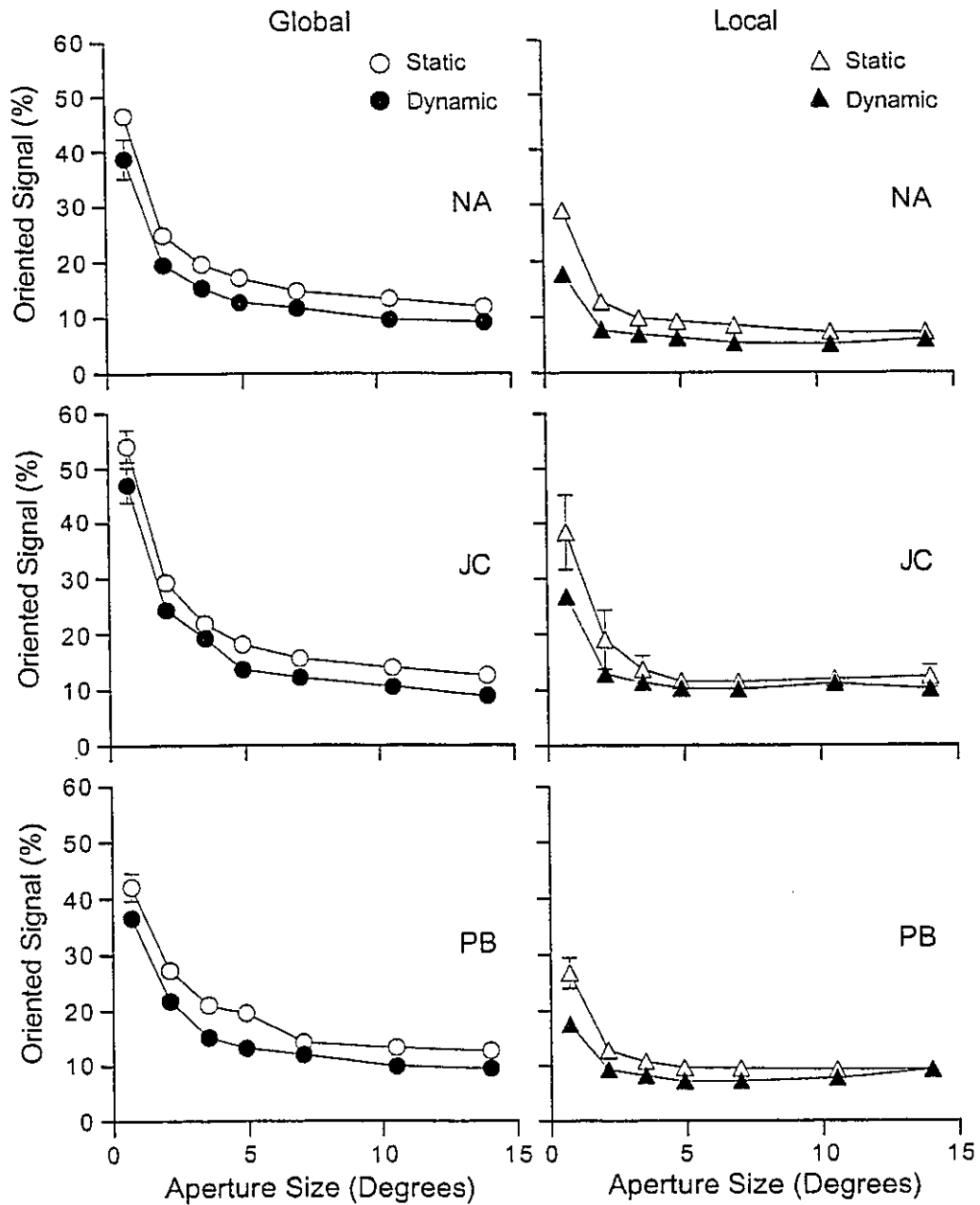


Figure 14. Orientation discrimination thresholds for three observers using static and dynamic stimuli. Thresholds for Global (left, circles) and Local (right, triangles) stimuli improved with increasing aperture size, indicating spatial integration. Thresholds also improved with dynamic stimuli (closed symbols) compared to static stimuli (open symbols), indicating temporal integration. Both static and dynamic stimuli were presented for 100 ms. Error bars represent ± 1 SEM.

oriented signals (Jones et al., 2003).

Discrimination thresholds for the Local stimuli were considerably better than thresholds for the Global stimuli as we have previously reported (Jones et al., 2003). For example at a 2° aperture size, with a static Local stimulus, subjects require 14.8% orientation signal at threshold, whereas with a static Global stimulus subjects required almost twice as much signal (27.1%) to discriminate the orientation from unoriented noise. Despite this difference, switching from a static to dynamic 100 ms stimulus led to a similar degree of improvement for both (Fig. 14). On average, at a given aperture size, subjects viewing the dynamic Global stimulus required $4.4 \pm 0.6\%$ less orientation signal at threshold, and for the dynamic Local stimulus they required $3.7 \pm 1.3\%$ less orientation signal compared to their thresholds for static stimuli.

In the first experiment, the dynamic nature of the stimuli was achieved by randomly changing the lookup table values for each frame. This yields a stimulus where the grey-levels in the display flicker at 85 hz, however the spatial structure of the oriented stimulus does not change over frames. We considered whether the improvement observed with the dynamic stimuli could be due to an increased salience for the location of the oriented contours in the display, and not a temporal pooling of signals per se. We addressed this issue by using animated stimuli where each frame was generated with a new random seed for the spatial structure of the stimulus. Thresholds for this frame animated stimulus were not different from thresholds where the lookup table was changed (Fig. 15). These results demonstrate that oriented signals are pooled temporally, even when the spatial structure of the signal changes across time.

Since providing more samples within the 100 ms dynamic stimuli led to

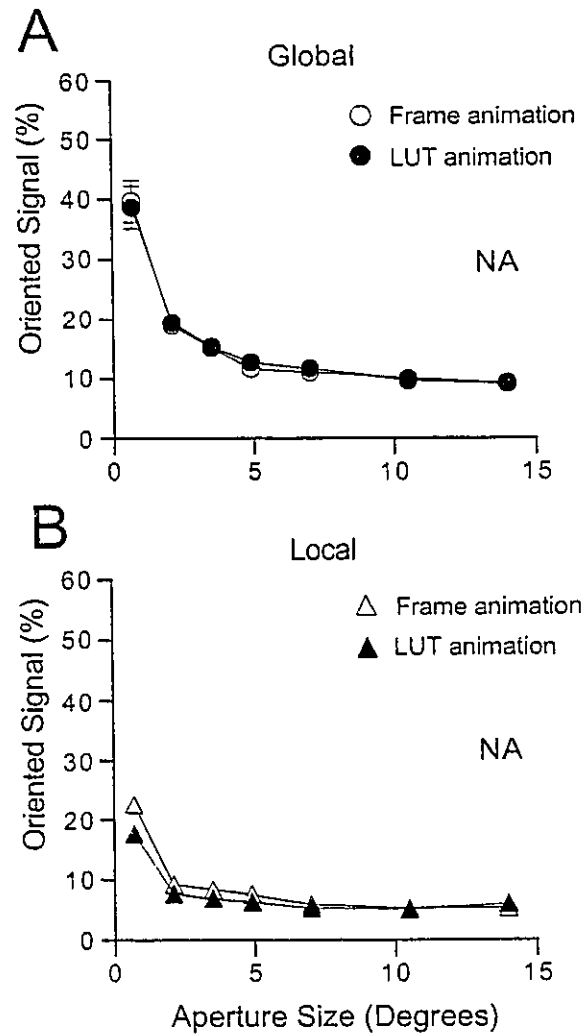


Figure 15. Equivalence of orientation discrimination thresholds using different animation methods. For dynamic stimuli presented using frame animation (grey symbols), each video frame was independently generated using a different random seed. For lookup table animation (black symbols), new random entries were assigned to the lookup table for each frame. Thresholds were not different with the two animation methods for both Global (A) and Local (B) stimuli.

improved orientation discrimination thresholds, we tested whether providing additional samples within 1 s would lead to an even greater improvement. We have shown previously that thresholds for 100 ms and 1 s presentation times are not different for static stimuli (Jones et al, 2003). In contrast, increasing the presentation time of the dynamic stimuli to 1 s led to better orientation discrimination thresholds (Fig. 16). At the smallest aperture size (0.7°), approximately 10% less orientation signal was needed at threshold for the 1 s dynamic Global stimulus, and approximately 7% less signal at threshold for the 1 s dynamic Local stimulus. It is interesting to note that the threshold for the smallest aperture size of the 1 s dynamic Local stimulus was comparable to that for the largest aperture size of the static Local stimulus, illustrating that very low orientation discrimination thresholds can result from either a large number of spatial samples or a large number of temporal samples.

Signal detection theory (Green & Swets, 1966) provides a method for determining orientation discrimination thresholds for the Global and Local orientation-in-noise stimuli in terms of early and late components of intrinsic noise (Jones et al., 2003). In this framework, performance is predicted by the following equation:

$$threshold = Z (\sigma_L^2 + k^2 \sigma_E^2 / N)^{1/2}$$

where k is a parameter related to the effectiveness of the type of orientation stimulus in evoking a neural response, σ_E is the standard deviation of the early noise, σ_L is the standard deviation of the late-noise, N is the number of independent spatial samples and is proportional to the aperture size, and Z is the z-score corresponding to the threshold measurement criterion. In the present experiments, thresholds were obtained at 82% correct, corresponding to a z-score

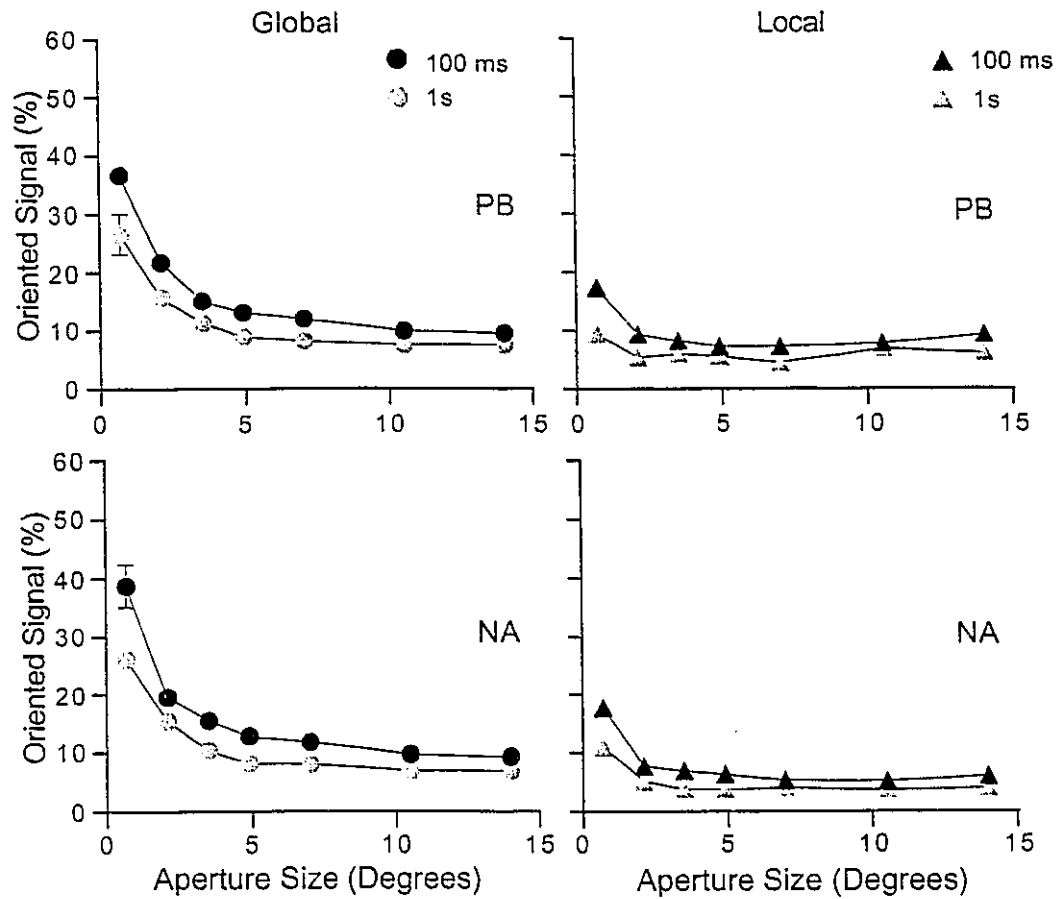


Figure 16. Effect of increasing presentation time of dynamic stimuli. Orientation discrimination thresholds for two observers were measured using Global (left, circles) and Local (right, triangles) stimuli with a presentation time of 100 ms (black) and 1 s (grey). Thresholds improved with longer presentation times.

of 0.915. This model was fit to the entire set of threshold data using the method of least squares (Fig. 17). Performance was well captured with a common source of late noise assumed for all conditions ($\sigma_L = 4.3$). For both Global and Local stimuli, best fitting early noise parameters were lower for the dynamic than for the static stimuli, and were lower for the 1 s dynamic stimuli than the 100 ms dynamic stimuli ($k\sigma_E = 43.2$ (Global static), 35.3 (Global dynamic 100ms), 22.9 (Global dynamic 1 s); $k\sigma_E = 26.5$ (Local static), 17.9 (Local dynamic 100ms), 7.8 (Local dynamic 1s). Performance was well described by this equation ($r^2 = 0.98$). It is not possible with our experimental data to tease apart the parameters k and σ_E . These results suggest that at both early and late stages of intrinsic noise, the overall amount of variability of the neural signal is lower with the dynamic than the static stimuli.

Discussion

The results can be summarized in terms of two main findings. First, orientation discrimination thresholds were better with the dynamic than the static orientation-in-noise stimuli and continued to improve when the presentation time of the dynamic stimuli was extended from 100 ms to 1 s. Second, the improvement in thresholds is similar for both the Global and Local dynamic stimuli and for all aperture sizes despite their different spatial characteristics. Taken together, these results show that increasing the number of independent samples over time leads to better orientation discrimination thresholds. This is consistent with the notion that the signal-to-noise of the underlying neural mechanisms improves when oriented signals are pooled across time as well as space.

The orientation discrimination thresholds are well described using a model

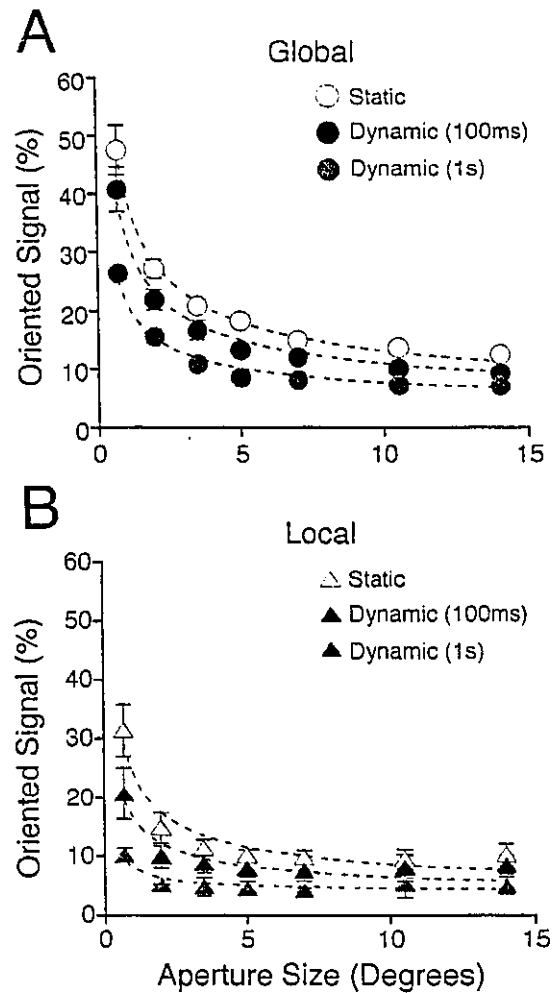


Figure 17. Comparison of orientation discrimination thresholds from human subjects and model. Mean thresholds from human subjects are well described by an equation of the form: $threshold = Z (\sigma_L^2 + k^2 \sigma_E^2 / N)^{1/2}$, where N is aperture size, Z is the z-score for threshold measurement criterion, σ_L represents standard deviation of a late noise component and $k\sigma_E$ is the standard deviation of an early noise component. One value of σ_L was assumed for all conditions. The dashed line represents the best least squares fit ($r^2 = 0.98$).

designed to account for early and late stages of intrinsic neural noise. Thresholds for smaller aperture sizes are most influenced by the parameter describing performance in terms of early noise, which reflects uncertainty at the earliest stage of filtering. Early-noise values were lower for dynamic stimuli, suggesting that the uncertainty at the level of orientation filtering was reduced when more temporal samples were added. Uncertainty could be reduced either because the dynamic component of the stimuli provided a better match for the spatiotemporal receptive fields of the underlying neural mechanisms, or because the effective number of samples for making a perceptual decision was increased. In the present study, it was not possible to distinguish between these two possible sources of uncertainty reduction. The threshold limit for larger aperture sizes is captured by the late-noise parameter, which reflects uncertainty at the decision stage after oriented signals are pooled, and is independent of the number of spatial and temporal samples. The threshold data are well fit when a common source of late-noise was used for all of the experimental conditions.

The improvement in orientation discrimination found with dynamic stimuli may seem surprising in light of previous studies showing that dynamic noise impairs contrast discrimination (Legge, Kersten, & Burgess, 1987) and letter identification (Gold, Bennett, & Sekuler, 1999) to a greater extent than static noise. This apparent difference, however, can be understood by considering that dynamic masking noise may effectively increase the strength of the masking, and as a result more effectively mask the underlying static signal. In these previous studies, the target orientation signal remained static, whereas the orientation signal in our experiments was dynamic. If dynamic stimuli reduce uncertainty within underlying neural mechanisms, then the dynamic properties in the stimuli

should be more salient. Taken together, these results suggest that dynamic aspects of a stimulus, whether signal or noise, are more effective components for perception.

The remarkably low orientation discrimination thresholds obtained under ideal spatiotemporal conditions reveal an exquisite sensitivity to orientation. Orientation can be discriminated when as few as 5% of the stimulus pixels carry the oriented signal. These thresholds are similar to optimal thresholds measured for motion signal-in-noise tasks, where normal observers require 2-5% coherent motion signal to discriminate the direction of motion (Newsome & Pare, 1988; Baker, Hess, & Zihl, 1991). These performance limits found using signal-in-noise stimuli for both orientation and motion may therefore reflect a common property of the neural circuits that underlie each of these perceptual tasks. Perhaps it is intrinsic neural noise that occurs in the later stages of perceptual decision-making.

Analysis of the contribution of early-noise to orientation discrimination suggests that thresholds improved to approximately the same extent for Global and Local stimuli. Threshold improvement is captured by the joint parameters $k\sigma_E$ in the analysis model, which provide a description of the “effectiveness” of the oriented signal. Larger $k\sigma_E$ values correspond to greater uncertainty about the orientation of the stimulus. For the Global stimulus, $k\sigma_E$ improved by 7.9 % orientation signal (from 43.2 to 35.3) with the 100 ms dynamic stimulus, while $k\sigma_E$ improved by 8.6 % orientation signal (from 26.5 to 17.9) with the Local 100 ms dynamic stimulus. Moreover, the degree of improvement was surprisingly consistent across aperture sizes. Thresholds were on average 1.28 times better (range = 1.17-1.38) for all sizes of the 100 ms dynamic Global stimulus and on

average 1.31 times better (range = 1.21-1.51) for all sizes of the 100 ms dynamic Local stimulus. The similar improvements observed for all spatial conditions may reflect a fundamental mechanism that underlies performance with dynamic stimuli and operates independently of spatial pooling mechanisms.

Within the framework of signal detection theory, the improvement in threshold with dynamic stimuli suggests there is effectively more than one temporal sample available within the 100 ms stimulus presentation, and samples can be combined over time to reduce uncertainty. Thresholds were approximately 1.2-1.5 times lower with 100 ms dynamic stimuli compared to static stimuli. If threshold improvement is due to an improvement in signal-to-noise, then signal detection theory predicts that there are approximately 1.5-2 samples pooled within a 100 ms presentation window (assuming a simple square-root of "N" rule). Sample times for the present study are therefore estimated to be about 50-75 ms. This is generally consistent with the finding that the stimulus energy required to identify large orientation differences is available within 20-50 ms of stimulus onset (Zlatkova et al., 2000). Moreover, these numbers are in good agreement with the estimated integration times of 40-80 ms of V1 simple cells (Hawken, Shapley, & Grosf, 1996).

The orientation discrimination thresholds for dynamic stimuli continued to improve when the presentation time of the dynamic stimuli was increased from 100 ms to 1 s. This improvement is in contrast with previous results using static orientation-in-noise stimuli where thresholds did not change when presentation time was increased to 1 s (Jones et al., 2003). One could argue that increasing the presentation time of the static stimuli allows for more eye movements that may increase the number of independent samples available. The latency of saccadic

eye movements, however, is on average 200 ms (Saslow, 1967), which is much longer than the sample times estimated from the present and previous studies. Moreover, the oriented samples obtained by eye movements are not independent over the population of filters, since they are from the same static stimulus.

Ideal temporal integration predicts a square-root of "N" improvement when presentation time is increased from 100 ms to 1 s. If N is defined as the number of temporal samples then N should be ten times greater in the 1 s compared to the 100 ms condition and there should be an approximately three-fold improvement in thresholds. The present results, however, showed an improvement of at best a factor of two, which is substantially shallower than the square-root of N rule predicts. Thus, in contrast to performance in the spatial domain, human observers do not act as ideal observers when pooling across a 1 s temporal window. This limitation could arise either because the duration of the temporal integration window is shorter than 1 s, or because the integration of oriented signals is lossy over 1 s.

In the same way that spatial pooling of orientation information has been demonstrated by presenting independent samples over space, temporal pooling was revealed by presenting independent temporal samples over time. The remarkably good orientation discrimination thresholds achieved with the dynamic orientation-in-noise stimulus likely arise because presenting more temporal samples provides a more effective stimulus by reducing uncertainty in the early stages of orientation processing, while the threshold limit likely reflects intrinsic noise present in later stages following temporal pooling.

Chapter 4

Orientation Discrimination in Visual Noise is Affected by Context

Introduction

Early stages of visual processing and perception involve an interplay between local processing and contextual interactions. Much of the framework for our current understanding of early visual processing is built on the finding that neuronal receptive fields operate as local processing filters that are tuned for the orientation of the stimulus. When stimuli are restricted to the receptive field the neural response is local in nature and has been most frequently modeled as the output of oriented spatial filters (Wilson & Bergen, 1979). This local processing, however, can be modulated by contextual interactions. Although stimuli presented outside of a neuron's classical receptive field do not elicit a response, they can sometimes influence responses when presented in conjunction with the neuron's preferred stimulus. These context effects have been proposed to depend on the dense array of horizontal connections found in visual cortical areas, where interactions are often orientation specific (Gilbert & Wiesel, 1979; 1989). Typically, a neuron's response to a stimulus presented within the classical receptive field is suppressed by the addition of parallel stimuli presented outside the classical receptive field, while the addition of orthogonal stimuli have either no effect, less suppression, or some facilitation of the response to the central target (Blakemore & Tobin, 1972; Nelson & Frost, 1978; Knierim & Van Essen, 1992; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Sengpiel, Sen, & Blakemore, 1996; Levitt & Lund, 1997; Walker, Ohzawa, & Freeman, 1999; Li, Thier, & Wehrhahn, 2000).

Perceptual discriminations can also be affected when the target is surrounded by specific features. Tilt discrimination thresholds can be elevated by a factor of two when surrounded by parallel elements, but are less affected or not

affected by orthogonal stimuli (Li et al., 2000; Mareschal, Sceniak, & Shapley, 2001). In perceived tilt tasks, target stimuli appear to be tilted away (repulsed) from the elements in the surround (Blakemore, Carpenter & Georgeson, 1970; Tolhurst & Thompson, 1975; Westheimer, 1990). A number of experiments have examined the effects of surround orientation on either perceived contrast or contrast detection. The perceived contrast of a center grating is reduced approximately two-fold when surrounded by parallel elements and is less affected by orthogonal surround elements (Cannon & Fullenkamp, 1991). When the contrast of the central target is near threshold levels, the general pattern of surround modulation is different. Contrast detection thresholds for the center are better when the surround contains either higher contrast parallel elements (Polat & Sagi, 1993, 1994) or low contrast orthogonal elements (Yu, Klein, & Levi, 2002).

The link between behaviour and underlying neural mechanisms is strengthened when considering contrast dependant surround modulation because of the similarity between psychophysical and neurophysiological results. It has been more difficult, however, to make the link between psychophysical and neurophysiological orientation-specific context effects. For example, when a high contrast center is surrounded by parallel high contrast elements, the firing rate is suppressed, yet the presence of the oriented center is easily discriminated in a psychophysical task. Tilt discrimination thresholds are affected by parallel surrounds, but results from single unit physiology would predict that the overall visibility of the oriented signal should also be compromised. The challenge is to create a stimulus containing an oriented signal that is high contrast, but perceptually difficult enough for orientation-specific thresholds to be measured. We have developed a signal-in-noise paradigm in the orientation domain using

an oriented texture that provides selectivity for studying orientation discrimination independent from contrast (Jones, Anderson & Murphy, 2003). This is achieved by using stimuli that are high contrast, broadband in spatial frequency, and contain an oriented signal embedded in unoriented noise. The strength of the orientation signal can be varied from 0% to 100%, and thresholds are measured as the smallest amount of orientation signal necessary to discriminate the underlying orientation. We have shown previously that discrimination thresholds improve with larger stimulus area, reaching a performance limit at 11% orientation signal.

We have used this signal-in-noise orientation stimulus to investigate orientation-specific context effects on the ability to discriminate an oriented signal from unoriented noise. We found a two-fold increase in threshold when the surround contained a strong orientation signal parallel to the center. Thresholds were slightly elevated when the center was surrounded by unoriented noise, but not affected by an orthogonal surround. To estimate the spatial extent and strength of surround interaction, we varied the size of the center, the size of a gap between the center and surround, and the orientation signal in the surround. These results are well captured by a computational model based on responses from filters resembling V1 simple cells that are pooled and inhibited in an orientation-specific manner. The psychophysics and model results demonstrate obligatory pooling of orientation-specific information over a large spatial region, and may involve mechanisms beyond V1. Some of these results have been presented previously (Anderson, Murphy, & Jones, 2001,2002).

Methods

Subjects

Six subjects, four of whom were naive to the purpose of the experiment, participated in these experiments. NA was highly practiced at the time of testing. All observers had normal or corrected to normal vision.

Visual Stimuli

We investigated the effects of context on orientation discrimination using a center-surround configuration. The center and surround components contained a local oriented signal that we have previously used to investigate orientation processing (Jones et al., 2003). This local orientation pattern was a high contrast grey-level pattern, containing a broad range of spatial frequencies, with an independently variable amount of horizontal or vertical orientation signal. Pixel values were selected from a uniform random distribution of 256 grey levels. The parameter P represents the strength of the orientation signal, namely, the percentage of pixels carrying the orientation signal versus noise pixels. Grey levels were sequentially assigned along oriented stripes, and each oriented stripe was drawn independently. With probability $P/100$, the next pixel within the oriented stripe continued with the same grey-level, otherwise, a new random grey level was chosen. For example, when $P = 100\%$, the pattern was a one-dimensional noise grating oriented either vertically or horizontally; when $P = 0\%$ the stimulus was uniform random noise with no dominant orientation. For intermediate values of P , the resulting stimulus was a pattern of local oriented contour segments with independent grey-levels and variable average length (Fig. 18).

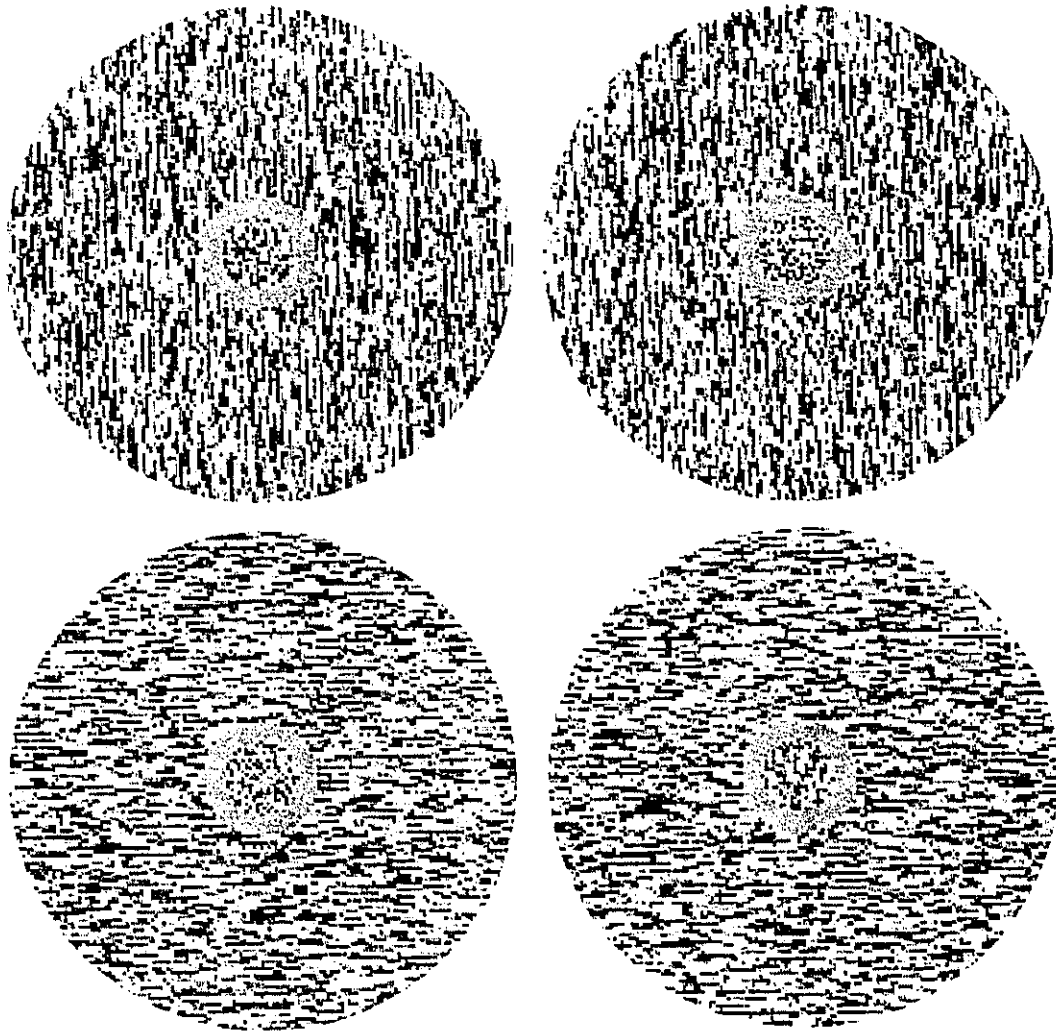


Figure 18. Examples of the center surround stimuli used in experiments with various center-surround configurations. The top left example contains a parallel center-surround configuration, and the bottom right example contains an orthogonal configuration. The top right and bottom left examples are corresponding stimuli with an unoriented noise center. The strength of the oriented center in these examples is 30%, and the strength of the oriented surround signal is 80%.

The center-surround configuration consisted of a circular center within an annular surround with a total diameter of 14° (Fig. 18). The center and surround components were independently generated using a new random number seed for each stimulus presentation. Stimuli were generated on a Sun Microsystems Ultra 10 3-D Creator in the MATLAB (Mathworks) programming environment. Stimuli were displayed on a 19" colour monitor (Hitachi CN751U) with a 0.26mm dot pitch, a spatial resolution of 1280×1024 pixels, an 8-bit gamma correction lookup table, and 76 Hz frame rate. Viewing was binocular from a distance of 57 cm.

The effect of context was studied in four experiments that varied surround type, center size, gap size, and the strength of the orientation signal in the surround. In the first experiment, thresholds were measured for a 2° oriented center with surrounds that contained either uniform black, unoriented noise, 80% orthogonal orientation, or 80% parallel orientation in the surround. We used a 2° center because this is the smallest aperture size where observers reach optimal performance levels (Jones et al., 2003). In the second experiment, the center size was varied (2° , 3.5° , or 5° diameter). In the third experiment, the center size was fixed at 2° and a uniform grey gap (0.07° - 1.6°) was introduced between the center and the surround. Thresholds were measured with parallel and orthogonal orientations in the surround. In the fourth experiment, the center size was fixed at 2° and the strength of the parallel or orthogonal orientation signal in the surround was varied. To make the strength of the orientation signal in the surround perceptually equivalent across subjects, the strength of the surround signal was set to be a multiple (1, 2, 4, or 6x) above each subjects' threshold in the no surround condition.

Procedure

A two-interval forced-choice paradigm was used to determine orientation discrimination thresholds. Within each trial, one interval contained a stimulus with oriented signal in the center, and the other interval contained a stimulus with unoriented noise in the center. A central fixation point appeared at the beginning of each trial for 500 ms, and the stimuli were presented for 100 ms, each separated by a 500 ms interval when a uniform black field was presented. Subjects were instructed to judge which interval contained the oriented signal in the center and to respond by pressing one of two keys on the keyboard.

Orientation discrimination thresholds were obtained using a 3-down 1-up staircase procedure, where threshold estimates were based on 100 trials. Thresholds were calculated at the 79.4% correct level, which is the level of correct response to which this procedure converges (Levitt, 1971). The initial level of signal in the center was set to be highly visible (i.e., 60% signal) at the beginning of each staircase. Each experimental run consisted of 4 interleaved staircases, where thresholds were estimated separately for parallel and orthogonal center-surround configurations for both horizontally and vertically oriented centers. Mean thresholds are based on 6 threshold estimates for each subject.

Model Simulation

We developed a computational model based on pooling simple cell responses to simulate the underlying neural processing that may contribute to the context effects on human performance. This model is an elaboration of a previous computational model that we developed to account for human psychophysical thresholds for orientation discrimination with orientation in noise stimuli (Jones et al., 2003). This model observer was implemented as a MATLAB function, and

thresholds were obtained by running the same software used to determine human psychophysical thresholds, but substituting the ideal observer function in place of a function that received a human subject's keypress. Within the model framework, stimulus images were convolved with filters designed to resemble horizontal or vertical simple cell receptive fields. For each orientation channel, the filtered responses were rectified and pooled by summing over the center component, and the model response was based on the orientation of the set of filters that produced the larger response. This summation model captures both absolute performance levels and the rate of improvement with increasing stimulus area observed in humans. To account for context effects in the present model, an additional computational step was added where signals from surrounding filters modulated responses to the central orientation.

A schematic diagram of the model with these center-surround interactions is provided in Figure 23. Stimuli were convolved with horizontally and vertically oriented kernels that were 3x3 pixels in size ($\begin{bmatrix} -1 & 2 & -1 \\ -1 & 2 & -1 \\ -1 & 2 & -1 \end{bmatrix}$). These simple linear filters had an orientation bandwidth of $\pm 27^\circ$ and a spatial frequency bandwidth of 1.6 octaves. For the human subject viewing conditions, this filter size corresponds to approximately 0.25° , which closely matches the size of the smallest foveal simple cell receptive fields in macaque V1 (Hubel & Wiesel, 1968). Filtered responses within each orientation channel were full-wave rectified and modulated by pooled activity from surrounding filters within the same orientation channel. Surround influence was modelled using divisive inhibition, where the response from each filter was divided by the sum of the responses from surrounding filters within the same orientation channel. This inhibition is formulated as:

$$R_{\theta,i} = R_{\theta,i} / (1 + \omega \sum R_{\theta,i})$$

where $R_{\theta,i}$ is the strength of the response from the i^{th} filter with orientation θ , ω is a constant, and $\sum R_{\theta,i}$ is the Gaussian weighted response from surrounding filters. Two variables controlled the nature of surround influence, ω which determined the strength of the inhibition from surrounding filters, and σ which determined the bandwidth of the Gaussian filter used to weight the responses from surrounding filters. Responses within each of the oriented channels were then pooled by summing over the area of the center stimulus. The model observer output for each input image was the difference between the response strength from the vertical and the horizontal orientation channels. When unoriented noise was presented, the strength of the response from each oriented channel was approximately equal, and thus the response difference was close to zero. Conversely, an oriented signal provided a stronger response for the appropriately oriented channel, thus the model response (i.e., interval one or interval two) was based on the interval that produced the greatest response difference between the oriented channels. This response was used in place of the keypress in a psychophysical paradigm similar to that used to determine human psychophysical thresholds. Model thresholds were estimated with an 82% correct threshold criterion using the QUEST method (Watson & Pelli, 1983) implemented from Psychtoolbox routines (Brainard, 1997) in the MATLAB programming environment. Each model threshold estimate is based in 200 trials.

Results

Human Results

Effect of Surround Type

Discrimination thresholds were measured for a 2° center with a black

surround, 100% noise surround, orthogonal surround, and parallel surround. The amount of signal required to discriminate the oriented center from unoriented noise varied as a function of the surround type (Fig. 19).

When an oriented signal was presented in the center, with no orientation or texture in the surround, $12.0 \pm 0.3\%$ signal was required to discriminate the orientation from noise. This threshold served as a reference for other surround conditions. When unoriented noise was placed in the surround, there was a moderate increase in threshold ($14.9 \pm 0.6\%$). Thus, the presence of a high contrast pattern in the surround with no dominant orientation results in increased thresholds for the orientation signal.

When the orientation in the surround was orthogonal to the orientation in the center, thresholds were the same ($11.2 \pm 0.8\%$) as the no-surround condition. This high contrast pattern in the surround had no effect on the discrimination threshold. When the surround orientation was parallel to the center orientation, thresholds rose dramatically to $21.1 \pm 1.7\%$. The properties of the surround signal, although irrelevant to the task from the subject's point of view, have a profound influence on performance. Moreover, this effect was orientation-specific, suggesting that higher thresholds are not simply due to uncertainty about the location of the center or the presence of a high contrast pattern in the surround, but instead due to a fundamental interaction between the orientation signals in the center and surround.

Effect of Center Size

The size of the center was varied (2° , 3.5° , and 5°) to investigate the effect of the surround when the amount of orientation signal available in the center was increased (Fig. 20). When no pattern was present in the surround, increasing the

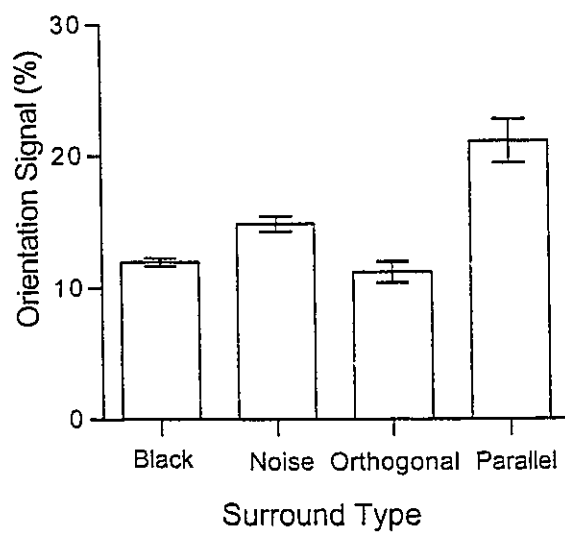


Figure 19. Effect of surround type on orientation discrimination thresholds. Mean thresholds for all observers. Error bars represent ± 1 SEM.

center size had no effect, since thresholds had already reached an optimal level of 12%. With an orthogonal surround, thresholds improved slightly with larger center sizes. In contrast, with a parallel surround there was a large improvement in orientation discrimination as the size of the center was increased. When the size of the center was increased to 3.5° , thresholds for a parallel surround improved substantially to 13.5%, and when the center size was further increased to 5° there was an additional improvement to 12.4%, approaching the no surround threshold of 12%.

Effect of Gap Size

Increasing the size of the center increased both the amount of oriented signal used for the task, while at the same time displacing the surround boundary further into the periphery. A variable sized gap was introduced between the center and surround to tease apart the effect of a more peripheral surround boundary from the effect of a greater amount of signal in the center. For all of the gap sizes the thresholds for stimuli with orthogonal orientation signals in the surround were not different from thresholds with black in the surround (Fig. 21). With parallel orientation signals in the surround, there was a gradual improvement as the size of the gap increased. Even with the largest gap (1.6°), however, orientation discrimination thresholds were still elevated with a parallel surround relative to no surround. These results illustrate that oriented information is pooled over a large spatial region. The rate of improvement with a larger gap size was not equivalent to the rate of improvement with a larger center size. With a 0.8° gap, thresholds were reduced to 17.9%, and with a 1.6° gap, thresholds were 15.5%. Under conditions with similar surround sizes and larger centers (i.e., 3.5° and 5° center sizes), thresholds were 13.5% and 12.4%

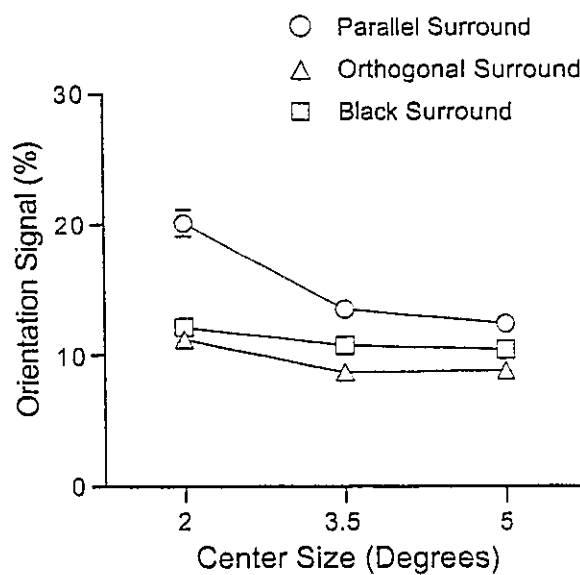


Figure 20. Mean effect of center size on surround influence. Open circles represent thresholds with a parallel surround; open triangles represent thresholds with an orthogonal surround; open squares represent thresholds with a black surround. Increasing center size reduces the effect of a parallel surround.

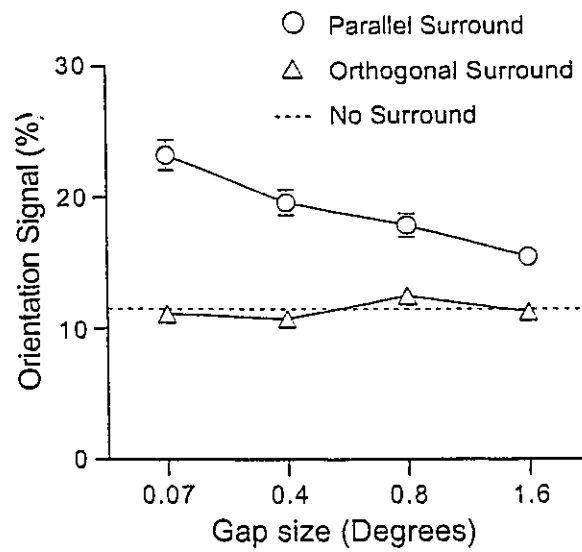


Figure 21. Effect of gap size between center and surround on surround influence. Open circles represent thresholds with a parallel surround; open triangles represent thresholds with an orthogonal surround; solid line represents thresholds with a 2° stimulus with a black surround. Increasing the size of the gap to 1.6° reduces the surround effect, but thresholds are still elevated.

respectively. This suggests that increasing the amount of oriented signal in the center and displacing the surround boundary further into the periphery both contribute to improvements in threshold.

Effect of Surround Signal Strength

The strength of the orientation signal in the surround was varied to determine how it affected the magnitude of the orientation context effect. Baseline discrimination thresholds for each subject were measured for a 2° center size with an unoriented noise surround. These thresholds were all close to 15%. Subjects were then tested with the orientation signal strength of the surround set to 1, 2, 4, or 6 times their baseline threshold. Orientation discrimination thresholds with a strong (6x) orthogonal orientation in the surround were lower relative to a noise surround, but not different from the no-surround configuration (Fig. 22). As the strength of the orthogonal orientation in the surround was reduced and its appearance moved towards unoriented noise (0x), discrimination thresholds gradually rose. As the strength of the parallel signal in the surround was increased from unoriented noise, thresholds were not different from thresholds with an unoriented noise surround until surround signal strength was more than twice (2x) the strength of a threshold stimulus. Increasing the strength of the parallel surround (>2x) led to poorer orientation discrimination thresholds. Thus, both weak orthogonal and weak parallel signals in the surround produced thresholds that were not different from surrounds containing unoriented noise, but elevated from thresholds with black in the surround.

Model Results

The model was designed to simulate potential neural mechanisms

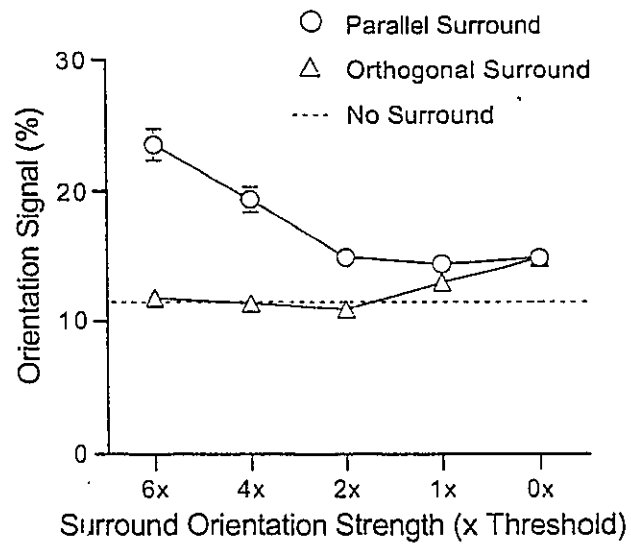


Figure 22. Effect of surround orientation strength on surround influence. Plot symbols are same as in Fig. 21. For strong parallel surround, reducing the strength of the surround reduces the effect of a parallel surround, whereas weak signals elevated thresholds compared to no surround.

responsible for orientation-specific pooling in human observers. A schematic diagram illustrates the computational steps involved in the model (Fig. 23). Stimuli were convolved with oriented filters, local responses were modulated by pooled activity from surrounding filters, and the model response was based on the difference between the response strengths from each oriented channel.

In the model, the surround influence was determined by two variables, ω that set the strength of the surround input, and σ that set the standard deviation of the Gaussian filter used to weight the surround response. Model thresholds were obtained using various combinations of values for ω (range: 0.05 to 0.15) and σ (range: 0.77° to 2.80°), and model performance was evaluated by determining the parameters that yielded the best least squares fit to the full set of human psychophysical thresholds. Optimal fits to the entire set of stimulus conditions were obtained using $\omega = 0.10$ and $\sigma = 1.75^\circ$, the parameters that yielded results most similar to human thresholds ($r^2 = 0.88$). In terms of visual angle, the size of this Gaussian filter is approximately 4.1° wide at half-height, suggesting oriented information is integrated over a large visual area.

Model thresholds were measured for the same set of stimuli used to measure human performance. First, model thresholds were measured for a range of center sizes with strong (80%) orientation signals in the surround (Fig. 24). For small center sizes (2°) close to twice as much signal was required with a parallel surround compared to a black surround. This was similar to the threshold elevation observed in humans with a parallel surround. As the size of the center increased model thresholds improved in a manner similar to human performance (cf. Fig. 20).

For orthogonal and black surrounds, model thresholds were slightly better

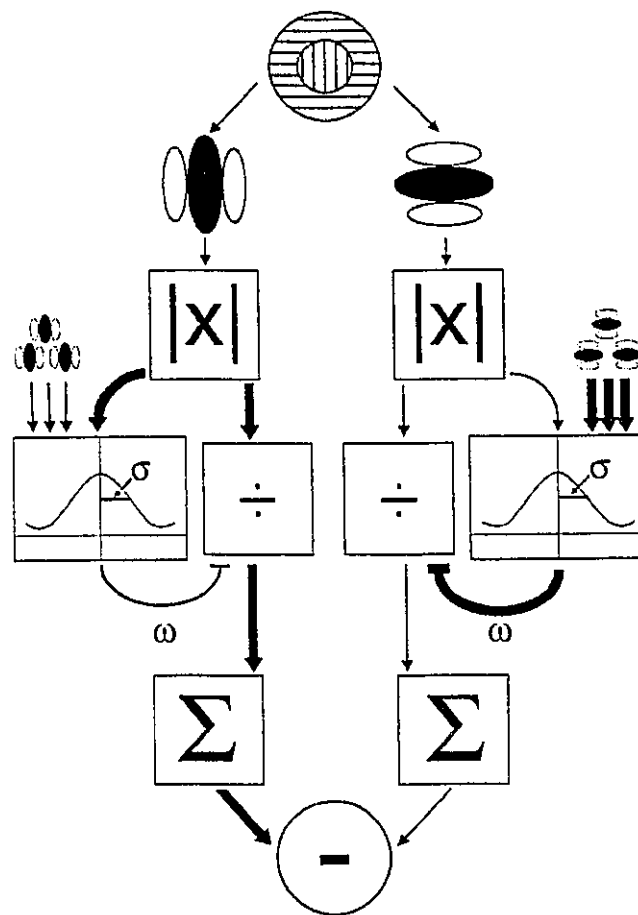


Figure 23. Schematic diagram of local orientation model. The stimulus, depicted at the top, was convolved with vertically and horizontally oriented filters. Within each orientation channel, filter responses were full wave rectified ($|x|$) and normalized by the gaussian-weighted activity of surrounding filters. Characteristics of the surround influence depended on the bandwidth of the gaussian (σ) and the strength of the surround contribution (ω). Normalized responses were summed together and the model response was the difference in response strengths from the orientation channels.

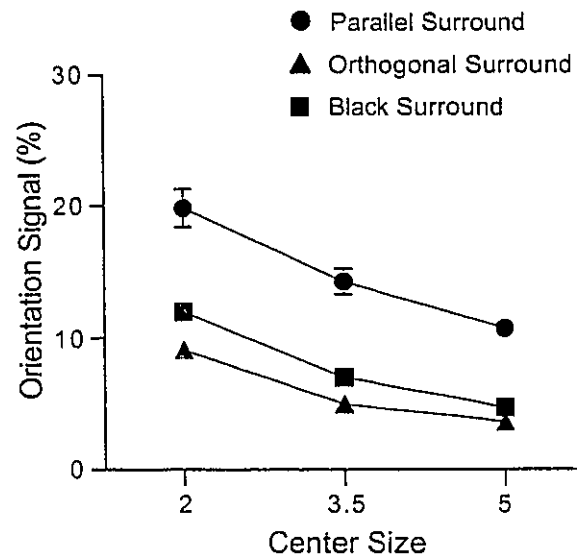


Figure 24. Model thresholds for different center sizes. Closed circles represent model thresholds with a parallel surround; closed triangles represent model thresholds with an orthogonal surround; closed squares represent model thresholds with a black surround. Increasing center size reduces the effect of a parallel surround. Error bars represent 95% confidence interval.

than the corresponding human thresholds (Fig. 24). This suggests that human performance may be limited by a factor not included in the model such as intrinsic noise. In addition, model thresholds with orthogonal surrounds were better than model thresholds with no surround. Taken together, these results show that the model provides a good fit to both the threshold levels and the overall shape of the functions.

The model also effectively captured the pattern of human performance with varying gap sizes (Fig. 25). With increasing gap size there was a gradual reduction in the surround effect. With parallel surrounds there was a steady improvement in thresholds as the gap increased. For orthogonal surrounds thresholds were better than no surround and there was no change in model performance until the gap was increased to 1.6° . Even at the largest gap size, however, model thresholds were still different from the thresholds with black surrounds.

Finally, model thresholds were measured for a variety of surround signal strengths (Fig. 26). With different surround signal strengths, threshold elevation with parallel surrounds was proportional to the surround signal strength, and thresholds for stimuli containing unoriented noise or weak oriented surrounds were elevated relative to thresholds with strong orthogonal signals. Model thresholds for stimuli with weak oriented signals or unoriented noise in the surround converged to the thresholds for black surrounds, whereas humans thresholds with these surrounds were elevated from black surround thresholds. The model results show that pooling of the surround signal in an orientation-specific manner effectively captures human performance.

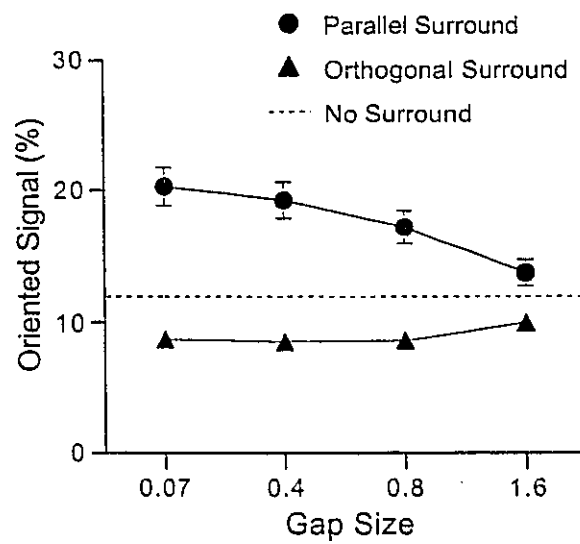


Figure 25. Model thresholds for different gap sizes. Closed circles represent model thresholds with a parallel surround; closed triangles represent thresholds with an orthogonal surround. Model thresholds with varying gap sizes are similar to human thresholds (cf. Fig 21).

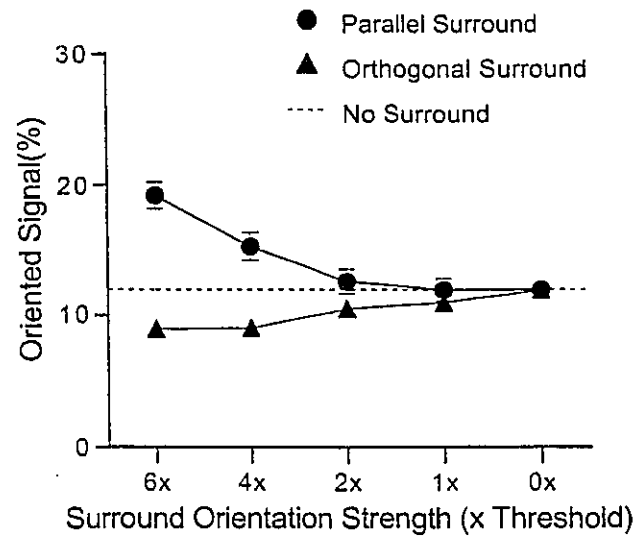


Figure 26. Model thresholds for different surround signal strengths. Plot symbols are same as in Fig. 25.

Discussion

The influence of an oriented surround on orientation discrimination can be described in terms of three main effects. First, approximately twice as much signal was required to accurately discriminate the orientation of the center when it was surrounded by a parallel pattern. Second, orientation discrimination thresholds with an orthogonal surround were not different from thresholds with no surround. Third, when the amount of oriented signal in the surround was reduced by either increasing the size of the center, increasing the distance between the center and the surround, or reducing the strength of the surround signal, the influence of the parallel surround was reduced. These results illustrate a clear orientation-specific effect of a surround on orientation discrimination thresholds.

The computational model allowed us to test whether human performance could be accounted for by orientation-specific pooling, and to quantify the strength and spatial extent of the parallel effect. This model captured the human results when signals were pooled over a Gaussian weighted region of 4.1° (full-width at half-height) and the strength of surround suppression was 10%. Model thresholds increased approximately two-fold when the center was surrounded by a parallel pattern. Thresholds were lower for stimuli in the context of an orthogonal surround than thresholds in the context of an unoriented noise surround or a uniform black surround. The influence of a parallel surround on model thresholds was reduced when center size was increased, gap size was increased, or surround signal strength was reduced and these changes were similar to human performance.

The strength of the parallel surround effect was reduced when the size of

the center was increased. Increasing the size of the center adds more spatial samples that can be integrated for a perceptual decision (Jones et al., 2003) and therefore effectively increases the strength of the orientation signal in the center. Reducing the amount of orientation signal in the surround, either by introducing a gap or decreasing the strength of the surround signal, also reduces influence of a parallel surround on orientation discrimination. Furthermore, the effect of a parallel surround is proportional to the strength of the surround signal. These results demonstrate that the effect of a parallel surround is related to both the strength and proximity of the parallel surround signal.

The orientation-specific effects of context that we observed are consistent with other psychophysical results investigating the role of context, where detection and discrimination thresholds are worse when the target is surrounded by similar elements. In the contrast domain, suprathreshold targets are judged to be lower contrast when surrounded by elements with similar spatial characteristics, indicating a suppressive effect of the surround (Chubb, Sperling & Solomon, 1989; Cannon & Fullenkamp, 1991; Elleberg, Wilkenson, Wilson, & Arsenault, 1998; Snowden & Hammett, 1998; Xing & Heeger, 2001). Tilt thresholds for high contrast lines or gratings are higher when the target has a parallel surround (Li et al 2000; Mareschal et al. 2001). Our results are consistent with these tasks, where discrimination thresholds for central, high contrast stimuli are reduced by parallel elements placed in the surround. For tasks using low contrast targets, the orientation-specific effect of surround elements is different. Given the appropriate spatial configuration, detection thresholds for low contrast targets can be *lower* when surrounded by high contrast parallel elements (Polat & Sagi, 1993,1994) or low contrast orthogonal elements (Yu, Klein, & Levi, 2002).

We developed a computational model based on orientation-specific pooling and inhibition that captured the human psychophysical results. To account for the effect of a parallel surround, the surround modulation needed to be orientation-specific. Orthogonal surrounds did not affect human thresholds and therefore the signals from the orthogonal orientation must not contribute during the surround modulation stage. However, the information from both orientations are required for the decision stage. When the model output is based on the difference in signal strength between orthogonal orientations, model performance was as good or better than human performance. In contrast, a model that simply compares which orientation channel has the larger response results in poorer orientation discrimination thresholds relative to human performance. These results suggest that information across orientation channels is not combined for these long-range modulatory effects, however information from both channels is used at a later stage. We also chose to model surround suppression using divisive inhibition from the surround filters. Similar results were obtained with a simulation where the modulatory effect of the surround was subtractive (data not shown), though the fit with the human data was not as good. Recent neurophysiological evidence also suggests that orientation-specific surround suppression on the responses of single neurons is best captured through a divisive type of interaction (Cavanaugh, Bair & Movshon, 2002).

Both human and model thresholds with an orthogonal surround were better than thresholds with an unoriented noise surround. Thus, if the unoriented noise condition is considered as the “baseline” reference, human and model thresholds were slightly facilitated in the presence of an orthogonal surround. Model thresholds with an unoriented noise surround and black surround were

equivalent. Human thresholds, on the other hand, were slightly elevated with an unoriented noise surround. A fundamental difference between an unoriented noise surround and a black surround is that unoriented noise is high contrast. This raises the possibility that human performance was affected by a local contrast gain mechanism that was not built into the model.

These differences between human and model performance suggest two kinds of pooling that operated on different spatial scales among oriented receptive fields. One form of interaction is not orientation-specific, and likely underlies effects that occur on a very local scale. Models designed to account for this form of interaction typically involve inhibition from neighbouring neurons that contain a wide range of orientation preferences. Examples of these local interactions include contrast gain effects (Heeger, 1992; Carandini & Heeger, 1994) and the sharpening of orientation selectivity (Bonds, 1989). Short-range connections between neighbouring orientation-selective domains are candidate mechanisms for this local pooling (Das & Gilbert, 1995). The other form of pooling, illustrated in the present experiment and in other more global center-surround effects, occurs in an orientation-specific manner and over a larger cortical distance. Long-range horizontal connections connecting iso-orientation regions (Gilbert & Wiesel, 1989) and/or orientation-specific feedback from higher cortical areas (Angelucci, Levitt, Walton, Hupe, Bullier & Lund, 2002) may underlie these long-range orientation-specific effects.

Results from the computational model suggest that orientation discrimination is modulated by just 10% of the pooled surround signal. In terms of cortical activity, this parameter may correspond to the strength of the intra-cortical inhibition that occurs between orientation-selective neurons.

Interestingly, approximately 18-20% of the synapses in V1 are GABAergic and therefore inhibitory in nature (Beaulieu, Kisvarday, Somogyi, Cynader, & Cowey, 1992). These numbers are compatible with the weighting parameter quantified by our model, and raises the possibility that the effect of the parallel surround is related to the number of inhibitory connections.

Both human and model results suggest that oriented signals are pooled over a large cortical distance. Human thresholds with a parallel surround were still elevated when the center and surround were separated by a 1.6° gap. According to estimates of the retinotopic map in human V1, a 1.6° gap corresponds to approximately 10 mm of cortical territory at an eccentricity of 1° (Horton & Hoyt, 1991). Current estimates of the average length of horizontal intrinsic connections in Macaque V1 are as short as 1 mm (Amir, Harel, & Malach, 1993), and as long as 4.5 mm (Angelucci et al., 2002). Our results suggest that oriented signals are pooled over a much longer distance than the length of horizontal connections. Thus it is difficult to account for the effect of the surround solely by the arrangement of long-range horizontal connections in V1. Moreover, the size of the Gaussian pooling window in our model was 4.1° at *half-height*. If the pooling region follows a Gaussian distribution, then there would still be a significant contribution from filters beyond 4.1° . Thus, the pooling region predicted by the model is a conservative estimate of the length of the center-surround interaction. The sheer extent of the modulatory region suggests that the effect of the surround depends on modulatory activity from beyond V1.

Recent evidence suggests that feedback from higher cortical areas may play a critical role in the orientation-specific modulation observed in V1 neural responses. While horizontal connections may account for short-range surround

effects on neural response gain, the length of horizontal connections is not sufficient to account for the spatial extent of orientation-specific surround suppression (Cavanaugh et. al, 2002; Angelucci et. al, 2002). Feedback projections, however, cover a larger extent of cortical territory in V1 than either feedforward or horizontal connections. Moreover, feedback projections are patchy, suggesting that these projections may be also orientation specific (Angelucci et al., 2002). The suppressive effects observed in the present experiment may also be mediated by activity in extrastriate regions, where orientation-selectivity and orientation-specific horizontal connections are maintained (Ghose & T'so, 1997; Amir et al., 1993)

Summary

Using an orientation-in-noise paradigm, we have illustrated that the effect of an oriented surround can have a dramatic effect on orientation discrimination thresholds. A computational model provides quantitative estimates of the area of orientation-specific pooling and the strength of the suppressive input. The behavioural and model results suggest that orientation information is pooled over a larger region than would be expected if performance in this task were mediated solely by mechanisms in V1. Instead, center-surround suppression that is observed in behavioural tasks may be mediated by feedback from extrastriate regions and/or mechanisms present in higher-level cortical areas that are thought to be responsible for form and object processing.

Chapter 5

Contextual Modulation of Orientation Discrimination under Dichoptic and Stereoscopic Viewing Conditions

Introduction

Orientation discrimination thresholds are modulated by surround elements in an orientation-specific manner. Tilt discrimination thresholds (Mareschal, Sceniak, & Shapley, 2001; Li, Their, and Wehrhahn, 2001) and orientation discrimination in noise thresholds (previous chapter) increase approximately two-fold for targets that are surrounded by parallel elements, but are unaffected for targets surrounded by orthogonal elements. These perceptual context effects likely depend on orientation-specific modulation that has been observed in the responses of single neurons in visual cortex. Typically, a neuron's response to a stimulus presented within the classical receptive field is suppressed when parallel stimuli are presented outside of the receptive field and is less affected by the addition of orthogonal surround stimuli (Blakemore & Tobin, 1972; Nelson & Frost, 1978; Krieger & Van Essen, 1992; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995; Sengpiel, Sen, & Blakemore, 1996; Levitt & Lund, 1997; Walker, Ohzawa, & Freeman, 1999; Li et al., 2000).

The results from the previous chapter illustrate that orientation discrimination thresholds are dramatically elevated in the presence of a parallel surround, and suggest that visual information is pooled in an orientation-specific manner. Discrimination thresholds with a parallel surround improved when there was a gap between the center and the surround. Even with a 1.6° gap between a parallel center and surround the thresholds remained elevated, illustrating that orientation-specific pooling occurs over a large spatial extent. Results from both the human observers and the computational model suggest that the pooling occurs across similarly oriented filters and that information from orthogonal

orientations is not combined. The parallel surround effect then arises from the suppression of filters that share the same orientation preference.

To further understand the orientation-specific pooling described in the previous chapters, I have explored the context effect under two additional viewing conditions. The goals of these experiments are to gain insights into what visual information is being pooled and to better understand the level at which orientation-specific pooling is occurring. In the first viewing condition, orientation discrimination thresholds were measured when the center and surround components were presented separately to each eye (dichoptic). A well-established property of information transmission along the visual pathway is that information from each eye is not combined until it reaches the visual cortex. Determining if orientation discrimination thresholds remain elevated with a parallel surround when the center and surround are presented dichoptically will indicate whether orientation pooling is occurring before or after binocular information is combined. In the second viewing condition, discrimination thresholds were measured when the center and surround were presented at different depth planes. Binocular neurons in V1 are disparity selective (Poggio & Fischer, 1977) and have well established tuning properties for different types of disparities. These neurons can be subdivided into three general classes: near cells, that respond to stimuli with a crossed (in front) disparity; far cells, that respond to stimuli with an uncrossed (behind) disparity; and tuned-excitatory cells, that are tuned to zero disparity. Establishing the nature of orientation pooling relative to disparity differences will reveal whether context effects are mediated by pooling specific to the orientation domain, or if pooling is also disparity-specific.

Orientation-specific context effects were measured using the center-

surround stimulus described in the previous chapter. Orientation discrimination thresholds remained elevated in the presence of a parallel surround when the center and surround were presented dichoptically, providing additional evidence that the parallel surround effect is mediated by cortical mechanisms. Moreover, the parallel surround effect was reduced, but not eliminated, when the center and surround were presented on different depth planes. This suggests that the pooling is not disparity-specific, and reflects a pooling process that is restricted to the orientation domain.

Methods

Subjects

Six subjects, five of whom were naive to the purpose of the experiment, participated in these experiments. NA was highly practiced at the time of testing. All observers had normal or corrected to normal vision.

Visual Stimuli

We investigated the nature of context effects under different viewing conditions using a center-surround configuration. The center and surround components contained a local oriented signal that we have previously used to investigate orientation processing and is described in detail elsewhere (Jones, Anderson, & Murphy, 2003). Briefly, this local orientation pattern was a high contrast grey-level pattern, containing a broad range of spatial frequencies, with an independently variable amount of horizontal or vertical orientation signal. To generate the local orientation pattern, grey levels were sequentially assigned along independently drawn oriented stripes. With probability $P/100$, where P represents the strength of the orientation signal, the next pixel within the oriented

stripe continued with the same grey-level, otherwise, a new random grey level was chosen. When $P = 100\%$, the pattern was a one-dimensional noise grating oriented either vertically or horizontally; when $P = 0\%$ the stimulus was uniform random noise with no dominant orientation. For intermediate values of P , the resulting stimulus was a pattern of local oriented contour segments with independent grey-levels and variable average length (Fig. 27).

The center-surround stimulus consisted of a 2° circular center and a 14° surround annulus (Fig. 27). The oriented patterns in the center and surround were generated from a new random number seed for each stimulus presentation. For all conditions, two stimuli were presented adjacent to one another on the monitor and were binocularly fused by viewing the display through front surface mirrors. Baseline thresholds for the center-surround effects were measured using stereoscopic stimuli where the center and surround were presented on the same depth plane. In the dichoptic condition, the center and the surround components were presented separately to the left and right eye (Fig. 27A). The eye to which the center and surround components were presented was randomized from trial to trial. In the stereoscopic condition, two stimuli containing both the center and the surround components were presented adjacent to one another on the display (Fig. 27B). Both stimuli were generated from the same random number seed. The oriented signal in each half of the display was shifted by 0.07° . Under the present viewing conditions, this shift resulted in a display where the center appeared to be approximately 2.6 cm in front or behind the surround. In front and behind conditions were randomized from trial to trial.

Stimuli were generated on a Macintosh Dual 1 GHz power-PC G4 in the MATLAB programming environment (version 5.2) using Psychtoolbox routines

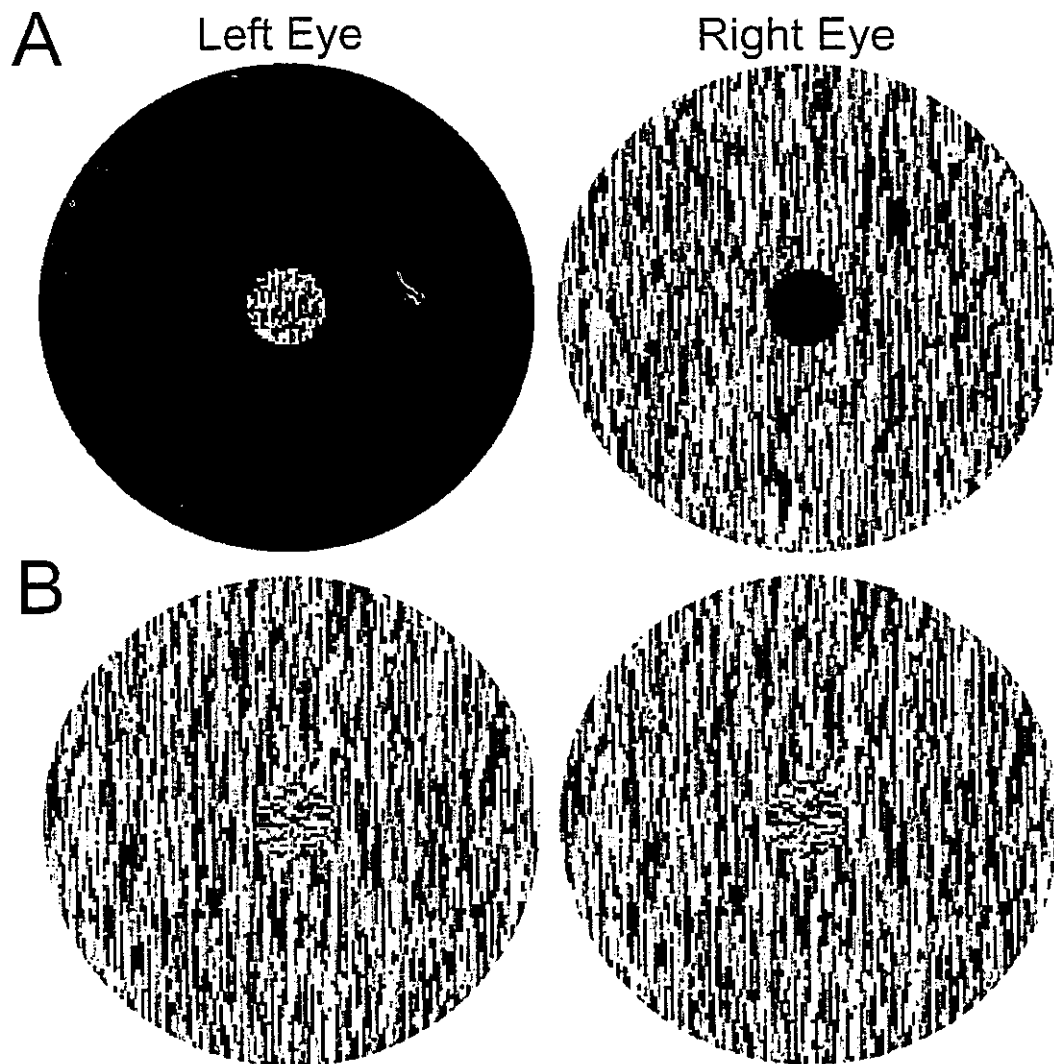


Figure 27. Examples of center surround (A) dichoptic and (B) stereoscopic stimuli used in the experiments. The fused dichoptic stimulus results in a parallel center surround stimulus, whereas the fused stereoscopic stimulus results in an orthogonal center surround stimulus where the center floats in front of the surround.

(Brainard, 1997) and displayed on a Sony 19" colour monitor with a resolution of 800 × 600 pixels and a frame rate of 85 Hz. Stimuli were viewed from an optical distance of 60 cm.

Procedure

A two-interval forced-choice paradigm was used to determine orientation discrimination thresholds. Within one trial, one interval contained a horizontally or vertically oriented center, and the other interval contained an unoriented noise center. A central fixation point appeared at the beginning of each trial (500 ms), followed by one stimulus presentation (100 ms), a black field (500 ms), and the other stimulus presentation (100 ms). Subjects were instructed to judge which interval contained the oriented center and to respond by pressing one of two keys on the keyboard. Subjects were not given feedback.

Thresholds were estimated using the QUEST method (Watson & Pelli, 1983), where each threshold estimate was based on 60 trials. Thresholds were calculated at the 82% correct level. Each experimental run consisted of 2 interleaved staircases, where thresholds were estimated separately for vertical and horizontal stimuli. Because no orientation biases were observed for the subjects, mean thresholds were collapsed across orientation. Mean thresholds are based on 12 threshold estimates for each subject under each condition.

Results

Orientation discrimination thresholds were measured for three subjects with parallel and orthogonal surrounds under binocular and dichoptic viewing conditions. For all conditions, the amount of oriented signal required to discriminate an oriented center from an unoriented noise center was greater when

the surround pattern was parallel to the center.

When the center and surround components were presented binocularly at zero disparity, orientation discrimination thresholds with an orthogonal surround were on average 13.3% (range: 11.7-14.9%) and with a parallel surround 24.6% (range: 20.1-27.8%; Fig. 28). These thresholds are similar to those observed with no orientation information in the surround (Jones et al, 2003), or an orthogonal surround under normal viewing conditions (previous chapter).

When the center was presented to one eye and the surround to the other eye (dichoptic), thresholds were on average 24.0% (range: 18.5%-29.6%), and are not different from the thresholds measured with binocular viewing (Fig. 28). For all subjects, the parallel surround effect was not reduced by presenting the center and surround components separately to both eyes. This suggests that the mechanisms mediating poor orientation discrimination in the presence of a parallel surround are located in the cortex where binocular information is first combined.

Discrimination thresholds were also measured for six subjects when the center and the surround were presented on different depth planes. For comparison, thresholds for stimuli with the center and the surround presented on the same depth plane are presented (Fig. 29, dark grey bars). When the center and surround were presented on different depth planes, discrimination thresholds with a parallel surround were still poor relative to thresholds with an orthogonal surround (Fig. 29, light grey bars). For some subjects (AH, RW, NA, and CT) orientation discrimination thresholds with a parallel surround were slightly better when the center and surround were on different depth planes. Those thresholds, however, were still higher than thresholds with an orthogonal

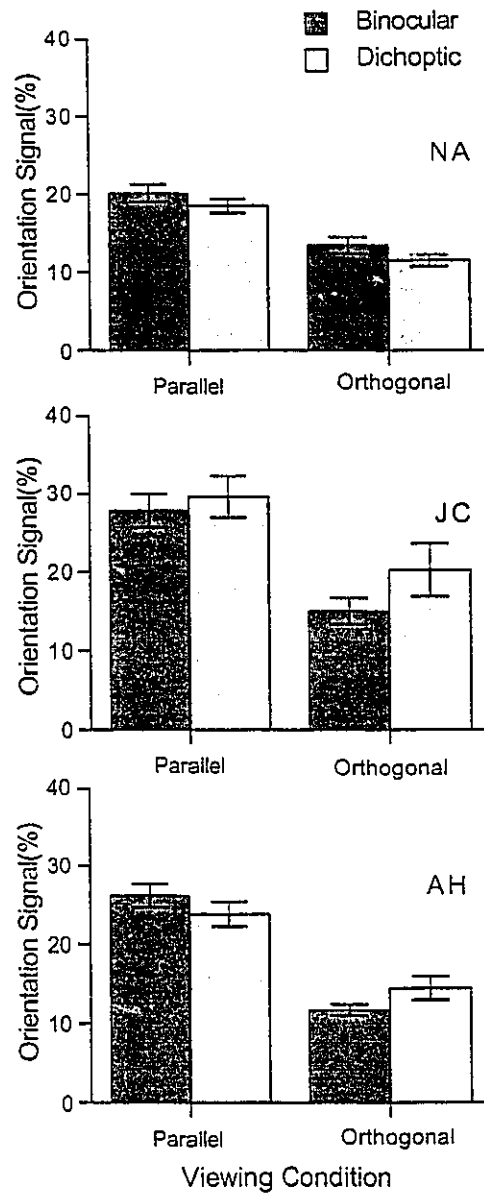


Figure 28. Effect of binocular vs dichoptic center-surround presentation on orientation discrimination thresholds for three observers. Dark grey bars represent binocular thresholds; light grey bars represent dichoptic thresholds. Presenting the center-surround stimulus dichoptically does not affect the parallel surround effect.

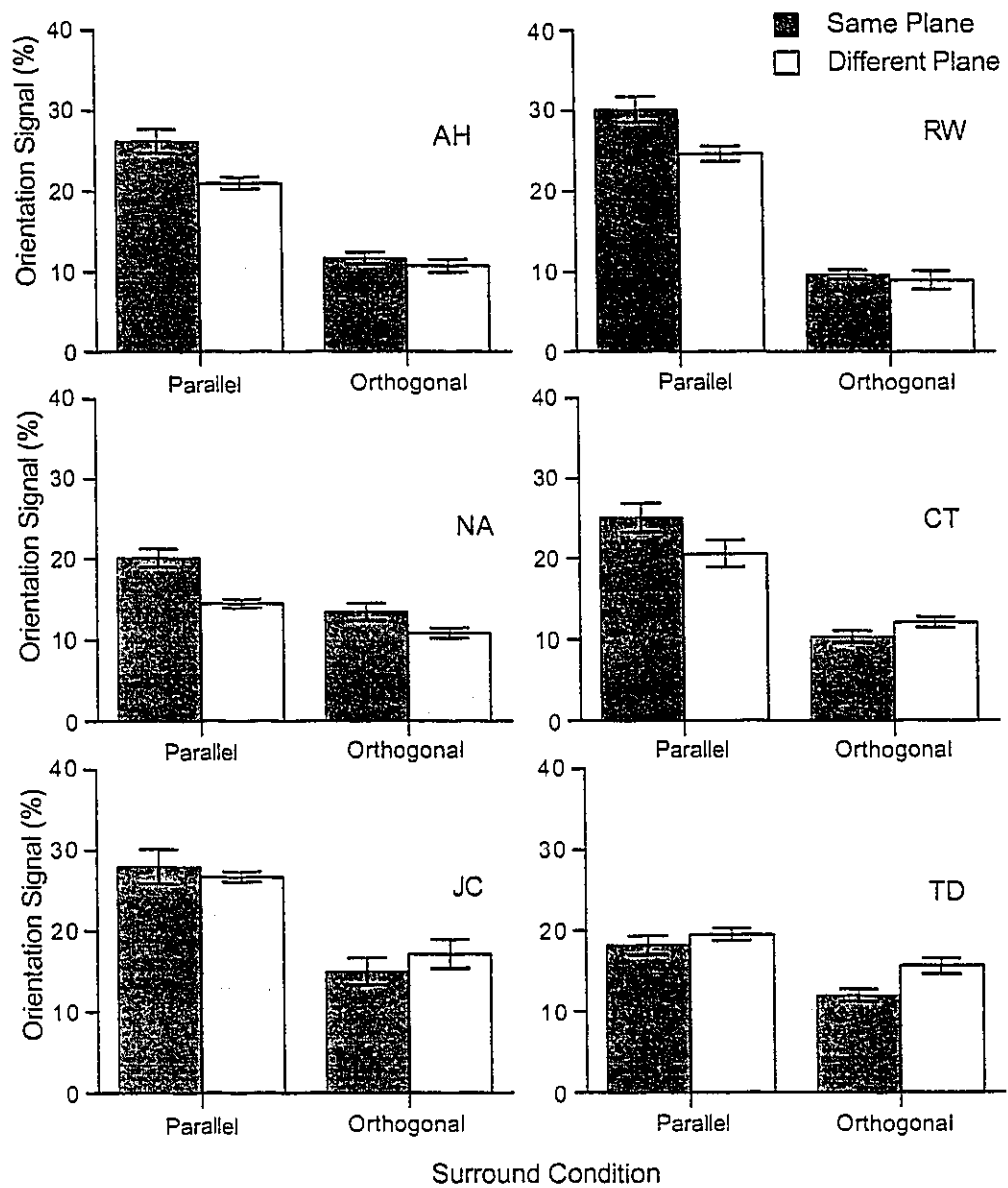


Figure 29. Effect of stereoscopic center-surround presentation on orientation discrimination thresholds for six observers. Dark grey bars represent thresholds for stimuli presented on the same plane, and light grey bars for thresholds stimuli on a different plane. Presenting the center on a different depth plane from the surround does not eliminate the parallel surround effect.

surround. For other subjects (JC and TD), thresholds with a parallel surround were the same for both depth conditions. When the group thresholds were compared, there was not a significant improvement in orientation discrimination when a parallel center and surround were separated in depth ($p > 0.05$; Fig. 30). Presenting the center and surround components at different depth planes does not eliminate the effect of a parallel surround on orientation discrimination. This suggests that the context effect observed in the present paradigm is specific to the orientation domain, and that orientation-specific pooling is not segregated by disparity.

Discussion

These results suggest that the orientation-specific context effects observed behaviourally are based on the activity of early stages of cortical processing. Orientation discrimination thresholds with a parallel surround remained elevated when the center and surround components were presented to separate eyes, providing strong evidence that the underlying mechanisms of orientation-specific pooling are binocular in nature and thus cortically located. Moreover, thresholds with a parallel surround were still elevated when the center and surround were presented on different depth planes. This indicates that the center-surround effect observed in the present experiments are specific to the orientation domain, and signals are not pooled in a disparity-specific manner.

Neurons do not receive binocular information until visual cortex. Similarly, orientation-selectivity is a property not observed until V1. There is evidence, however, that monocular neurons in dLGN can be modulated in an orientation-specific manner. These modulatory effects likely arise from inhibitory feedback from orientation-selective regions such as V1 (Sillito, Cudeiro, & Murphy, 1993).

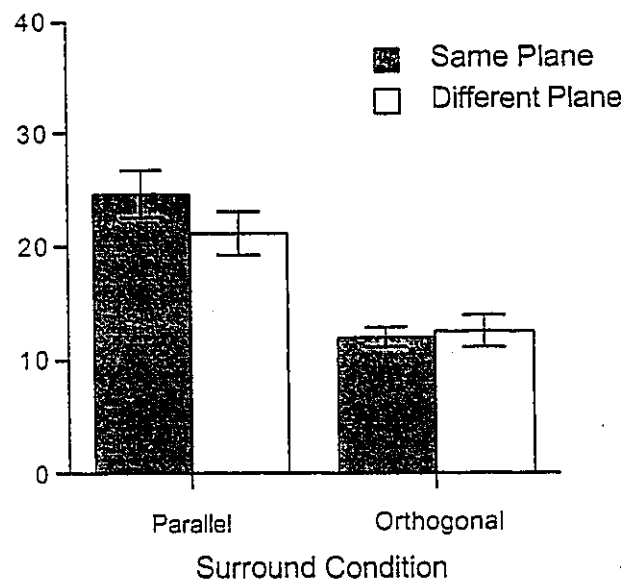


Figure 30. Effect of stereoscopic center-surround presentation on orientation discrimination thresholds. Mean thresholds for observers in Figure 29. Axes and bar labels are the same as in Fig. 29.

The finding that orientation-specific pooling is not affected when the center and surround are presented dichoptically provides strong evidence that this subcortical modulation does not underlie the parallel surround effect.

Center-surround effects observed in some other visual domains have been shown to depend on pre-cortical mechanisms. When an unoriented texture is presented in the presence of a high contrast surround, the perceived contrast for the center texture is lower. Presenting the center and surround texture components to separate eyes eliminates this suppression, suggesting that contrast modulations reflect a gain control that occurs pre-cortically (Chubb, Solomon & Sperling, 1989). Furthermore, cross-orientation suppression, where detection thresholds for an oriented grating increase in the presence of a superimposed orthogonal grating, also occurs before cortical processing, reflecting operations in the retina or thalamus, or depression of thalamocortical synapses (Meier & Carandini, 2002). Our results instead indicate that orientation-specific pooling occurs purely in cortical regions. This suggests that the mechanisms that mediate orientation-specific context effects are located after mechanisms mediating cross-orientation suppression and texture contrast modulation in visual processing.

Orientation information is not segregated by disparity. The orientation-specific pooling that underlies performance in this center-surround task operates over different disparities and therefore reflects a modulation that is likely specific to the orientation domain. This result is surprising, given evidence that the response of some neurons in V1 is different when the surround is at a different disparity rather than the same depth plane (Zipser, Lamme, & Schiller, 1996). Moreover, electrophysiological evidence reveals a response component that is specific for texture segregation including depth boundaries (Bach &

Meighan,1997). If orientation-specific modulation reflects activity from a more general texture segregation mechanism, then introducing a difference between the center and surround through a dimension other than orientation should break the parallel surround effect. The results from this chapter suggest that in the present center-surround paradigm, orientation signals are pooled regardless of differences in disparity or eye of origin, and therefore reflects activity only from the orientation domain.

Chapter 6

General Discussion

In this thesis, I describe a new orientation-in-noise paradigm that was used to investigate orientation discrimination (Chapter 2). Results from this paradigm show that oriented signals are pooled over visual space to support perceptual performance. With larger stimuli, human observers reached a performance limit of approximately 11% orientation signal. This limit is remarkably similar across subjects, and is not affected by practice with the orientation-in-noise paradigm. Furthermore, this limit cannot be overcome by further increasing the stimulus size and likely reflects noise in later stages of visual processing. I also explored the temporal nature of orientation pooling and demonstrated that oriented signals are pooled over time in addition to space to support better performance (Chapter 3). Temporal pooling operated independently from spatial pooling, and performance was captured by a model designed to account for early and late stages of intrinsic noise. When independent signals were presented over time in addition to space, orientation discrimination thresholds were as much as 2x better than thresholds with static stimuli. Taken together, these results suggest that oriented signals are pooled over time and space to reduce the signal-to-noise of underlying neural mechanisms.

I have studied the nature of orientation discrimination when the target is surrounded by parallel or orthogonal stimuli. These experiments demonstrate that oriented signals are pooled in an orientation-specific manner and can, under appropriate conditions, suppress responses (Chapter 4). When a strong parallel signal was presented in the surround, orientation discrimination thresholds increased two-fold. Discrimination thresholds with an unoriented noise surround were slightly elevated relative to thresholds with no surround, and thresholds

with a strong orthogonal surround were slightly lower than thresholds with an unoriented noise surround. The results probing the spatial extent and strength of the center-surround interaction show that the parallel surround effect depends on the amount of oriented signal in the surround, and that oriented signals are pooled over a very large spatial area. This orientation-specific pooling depends on cortical mechanisms that likely operate before stereoscopic information is processed (Chapter 5).

I also present a computational model that describes human performance in terms of the activity of low-level orientation-selective filters. Within the model framework, oriented signals were filtered and pooled over space within separate orientation channels, and the model decision was based on the orientation of the channel that produced the stronger response (Chapter 2). To account for the effect of a parallel surround, an additional pooling step was introduced where the pooled activity from surrounding filters modulated responses (Chapter 4). A key feature of the model is that signals from within the *same* orientation channel were used to suppress the filtered responses. This was a necessary restriction for capturing the human parallel surround effect. Orientation-specific modulatory connections are a biologically plausible assumption because neurons that share the same orientation preference are functionally connected via long-range horizontal connections in V1 and orientation-specific feedback connections (Gilbert & Wiesel, 1979;1989; Angelucci et al., 2002). For both orientation discrimination tasks, this model framework captures human performance remarkably well.

Taken together, these results demonstrate that there is obligatory orientation-specific pooling of low-level responses to support perceptual

performance. Orientation pooling is a proposed mechanism for oriented texture tasks, where the perceived tilt of an array of oriented patches can be described as the averaged orientation of the individual tilted elements (Dakin & Watt, 1997; Parkes et al, 2001; Dakin, 2001). In these tasks, pooling operates over a range of oriented responses to provide a single, useful estimate of global orientation. Orientation pooling has also been implicated in tasks involving fine changes in the tuning bandwidth of orientation-selective neurons (Bonds, 1989; Schoups et al, 2001). This form of orientation pooling likely depends on short range connections between neurons preferring multiple orientations and that span no more than 500 μm in V1 (Das & Gilbert, 1995). In the orientation-in-noise paradigm, however, pooling operates within an orientation channel to provide better signal-to-noise in the response. Pooling within an orientation channel likely depends upon long-range connections in V1 that connect iso-orientation domains and span several millimeters in cortex and/or feedback from higher cortical areas (Gilbert & Wiesel, 1979;1989; Angelucci et al, 2002). If both forms of pooling depend on different neural substrates, then the spatial extent of pooling in our task should be larger than the spatial extent of pooling observed in orientation tilt tasks. Indeed, thresholds improve for tilt discrimination tasks until the line length is increased beyond 0.5° , beyond which thresholds do not improve (Westheimer & Ley, 1997). In the orientation-in-noise task, thresholds continued to improve as the size increased beyond 10° under some conditions. The differences in spatial extent between tilt and orientation-in-noise tasks are consistent with the hypothesis that these two forms of pooling are mediated by different underlying mechanisms.

Temporal aspects of orientation discrimination are typically investigated

by changing the length of the stimulus presentation time in a temporal summation paradigm. Tilt discrimination thresholds improve as the presentation time of lines is increased to approximately 50 ms, beyond which presentation time does not influence performance (Andrews, 1967a; Watt, 1987; Zlatkova et al., 2000). Furthermore, tilted line segments that are presented asynchronously can be integrated over a 50 ms window in a tilt discrimination paradigm (Westheimer & Ley, 1997). To measure temporal *pooling* in a manner analogous to spatial pooling, however, requires a stimulus that contains multiple independent samples over time. In this thesis, I present the first research investigating the perceptual consequences of temporal orientation pooling using stimuli that are independent across the temporal domain. As with pooling in the spatial domain, presenting more independent temporal samples promotes better discrimination thresholds, likely by reducing the noise in the underlying neural mechanisms. These results show that spatial and temporal pooling are fundamental aspects of low-level visual processing, and likely depend on activity in early cortical neurons.

The influence of a parallel surround on orientation discrimination provides further evidence for orientation-specific pooling and illustrates that the nature and function of pooling depends on the spatial characteristics of the surround. With a strong parallel surround signal, orientation discrimination is worse than discrimination with an orthogonal or no surround orientation. This is similar to context effects that have been observed in other spatial vision tasks, where detection and discrimination thresholds are worse for stimuli presented in the context of a surround with similar elements (Chubb et al, 1989; Cannon & Fullenkamp, 1991; ElleMBERG et al, 1998; Snowden & Hammett, 1998; Xing & Heeger, 2001). This raises the possibility that the parallel effect may be an example

of a general suppression principle in visual processing that functions for a variety of visual dimensions. Suppressing redundant spatial information could be advantageous because neural resources could focus on information that provides more information about the visual environment, namely changes in boundaries due to texture or contrast differences.

While the parallel effect may reflect a global principle of visual information processing, context effects across different visual dimensions are not guided by a single mechanism. Presenting the center and surround components on different depth planes did not break the parallel effect. If the parallel effect reflected activity from a single mechanism responsible for suppression in all dimensions, then introducing a center-surround difference through another visual dimension should break the parallel effect. Instead, these results show that oriented information from the surround is pooled independent of depth or eye of origin.

The stimuli that I have presented in this thesis are ideal stimuli for investigating the link between single neurons and behaviour. In a manner similar to that used to relate the responses of MT neurons and motion discrimination (Britten et al., 1992), neurometric and psychometric functions for orientation-in-noise discrimination could be measured concurrently in an awake behaving animal. If the majority of orientation-selective neurons possessed a spike threshold at 11% orientation signal, this would provide evidence for a direct relationship between the performance of the animal and performance of single neurons. This would also provide insights into the nature of orientation pooling. If pooling is mediated by activity at or before V1, or by feedback to V1 from higher cortical areas, then the responses of V1 neurons should match the performance of the overall organism. Alternatively, if pooling is accomplished by

the convergence of V1 signals at a later cortical stage, neurons that would support overall behavioural performance would be located in higher visual areas, likely where orientation-selectivity is still maintained. It is also possible that pooling with the Local and Global stimuli may be mediated by activity at different cortical stages. Neurons in V1 may support performance with the Local stimuli which are only pooled over a small visual region, whereas neurons in later stages may support performance with the Global stimuli, where more “long-range” contour integration is accomplished.

The orientation-in-noise stimuli are also ideal for investigating the functional organization of orientation in V1 when stimuli are presented near the orientation discrimination threshold. Historically, orientation maps measured using optical imaging techniques have been measured using high contrast oriented sine- or square-wave gratings. Reducing the amount of oriented signal in a sine- or square-wave grating is typically accomplished by reducing the contrast of the grating. Measuring orientation maps with low contrast stimuli is difficult, however, because of contrast-dependant reductions in the strength of the elicited optical signal. Orientation maps measured to date, therefore, reflect patterns of cortical activity for stimuli that are easily discriminated in a perceptual task. Whether or not these functional maps change when viewing stimuli that are presented at threshold is a question that remains unanswered. The orientation-in-noise stimuli presented in this thesis are ideal stimuli for probing the selectivity of orientation preference maps because they are high contrast and will therefore elicit a strong cortical signal, yet perceptually difficult so responses at threshold levels can be measured.

A significant contribution of this thesis towards understanding orientation

processing is the description of a computational model based on orientation-specific pooling and surround inhibition. This model shows how orientation signals can be integrated to overcome external noise in the stimulus and internal noise in early stages of processing to support improved perceptual performance in most situations. One intriguing exception is that making a subtle discrimination about a noisy orientation signal within a small region becomes more difficult when it is surrounded by a large texture with a strong parallel orientation signal. This suggests that our visual system makes a trade-off, optimizing performance for some circumstances, while sacrificing performance in other less significant situations. The real goal of visual perception is to see beyond the raw sensory inputs to understand properties of objects in the world. Thus, when analyzing the orientation of a texture on an extended surface, it makes sense to integrate local orientation signals to overcome uncertainty and to provide a more accurate estimate of the orientation on the surface, even though this pooling may lead to a loss of positional information and finer variations of the texture within the surface. At the same time, the orientation-specific nature of surround inhibition leaves our visual system exquisitely sensitive to orientation differences that enable us to detect boundaries between surfaces. These principles of visual analysis are not unique to orientation processing and are repeated at different stages and on different scales for various aspects of vision, such as double-opponent colour processing in the retina and center-surround motion processing in cortical area MT.

This thesis presents a new orientation-in-noise stimulus that was used to measure orientation discrimination. The findings show that oriented signals are pooled over space and time by early cortical mechanisms, and that performance is

limited by two stages of intrinsic neural noise. Orientation discrimination is dramatically influenced by the orientation of a surrounding texture, and separating the center and surround dichoptically or in depth does not eliminate the parallel surround effect. These conclusions are strengthened and quantified by the results of computational modeling designed to account for human performance based on orientation-specific pooling and suppression. These orientation-in-noise stimuli will likely prove to be an excellent tool in future experiments using simple cell recording and optical imaging to draw links between physiology and behaviour in the orientation domain, and should therefore provide valuable insights into the nature of orientation processing in the brain.

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