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PREDICTIVE MODELS OF HUMAN VISUAL PROCESSES IN AEROSYSTEMS.(U)
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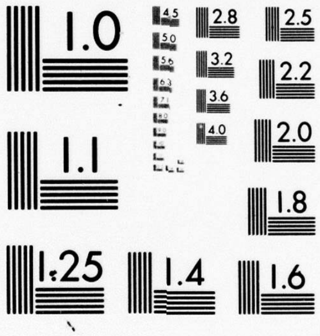

MICROCOPY RESOLUTION TEST CHART

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Summary

Over the past year a special eye-movement monitoring and visual display system has been used to investigate human acuity using computer-controlled psychophysical testing procedures. The system can accurately measure eye-movements of less than 1' of arc and with the same precision, control the movement of visual targets relative to an observer's retina. The theoretical reconstruction of the response profile of a visual target is complicated by the fact that under ordinary viewing conditions, even during fixation, the population of active elements in the visual pathway changes constantly. Using the special visual apparatus, it was possible to maintain a target on a fixed set of retinal receptors facilitating an orderly experimental analysis of visual response patterns. Some of the main experimental findings are the following:

(1) The detection of slowly moving targets of high spatial frequency is superior to the discrimination of the direction of movement and this difference between detection and recognition performance is intrinsic to the visual system since it is not produced by small saccadic eye-movements present during fixation.

(2) The control site, i.e. locus of rate-limiting step, for the mechanism responsible for the selective loss of pattern sensitivity following exposure to high contrast targets is primary visual cortex; the loss and spontaneous recovery follow exponential time courses whose time constants increase with adapting target spatial frequency.

(3) Targets stabilized on the retina undergo a decrease in visibility that is inversely related to their spatial frequency.

(4) High frequency noise vibrating a target produces a proportionate loss in contrast sensitivity at all spatial frequencies but low frequency noise such as that present in normal eye-movements has little effect.

The problem of how the human visual system detects oriented targets was examined using a mathematical model whose basic elements are spatial filters representing the receptive field response profiles of visual cortical neurons in the supragranular layers of Area 17. The population response profile proved a useful predictor of visual sensitivity for foveal targets in the absence and in the presence of simple pattern adaptation. Work is currently in progress on extensions of the model to motion and spatial interactions.

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I. Introduction

Contemporary research on the organization of the visual cortex in the brain of primates suggests a new conception of visual information processing in human vision. Of the 10^6 retinal ganglion cell axons that exit from the eye and form the main pathway between eye and brain, a certain fraction bifurcate and send collaterals to the superior colliculus, a portion of the brain stem critical for eye-movements, but the majority terminate onto cells in the lateral geniculate body, a part of the thalmo-cortical system (Bunt *et al.*, 1976). The axons of the lateral geniculate neurons form the optic radiation that projects to the primary visual cortex, Area 17. The primary visual cortex projects in turn subcortically to the superior colliculus and the pontine reticular formation, another brain stem region but one concerned with eye-hand coordination and the inferior pulvinar, an intrinsic relay nucleus of the thalmus, as well as cortically to prestriate visual cortex, Area 18, and STS. Many of these connections were known at least in part from classical degeneration studies but the recent techniques have indicated that reciprocal connections exist as well: from Area 17 to lateral geniculate nucleus, from Area 18 to Area 17, and from STS to Area 17 (Kaas, 1978). The classic view of a serial elaboration of visual processing giving rise to a single internal representation, a view which has served as the basis of several conceptual schemes and algorithms of visual processing, can no longer be maintained as valid. The recent research suggests a distribution processing model for vision in which particular action-oriented functions may be segregated early in the network.

In the light of the new anatomical findings it is clear that the properties of only particular subpopulations of neurons within a given cortical region may be relevant in developing predictive models of human visual function. Fig. 1 shows a simplified schema for the organization of primary visual cortex. The input from the geniculate arises from two main types of neurons which project to different layers of the cortex, those with relatively small receptive fields, more sustained responses, and sensitivity to low velocities and high spatial frequencies (parvocellular neurons); those with relatively large receptive fields, more transient responses, and sensitivity to high velocities and low spatial frequencies (magnocellular neurons). The two classes of neurons project to separate layers in the visual cortex. The outflow of visual information also arises from distinct layers with the upper layers projecting transcortically, but the lower layers projecting subcortically. From such a segregation it is clear that at least to a first approximation the receptive field properties relevant to high visual acuity are to be found in the upper layers but those relevant to visually-guided movements are to be found in the lower layers. A recent survey of

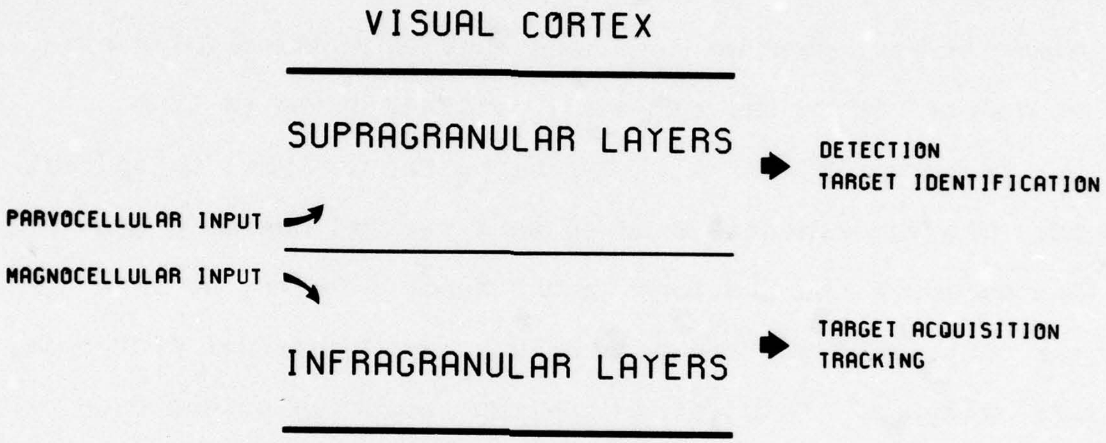


Figure 1. Schematic diagram of primary visual cortex in the primate visual system illustrating geniculate input and functional segregation of outflowing information.

the properties of such neurons (Mansfield, Ronner and Daugman, 1978) has provided detailed quantitative information concerning orientation tuning and other receptive field characteristics which served as a basis for modelling human performance and for motivating experimental analysis.

Over the past year we have been engaged in developing predictive models within the framework outlined above in line with our research objective of extending the analysis to spatial targets. The experimental studies were carried out on a system (described in the previous annual report) having on-line computer-controlled pattern generation, psychophysical protocols, and data analysis. This system has the presently unique capability of stabilizing an arbitrary pattern on the observer's retina which permitted the isolation of eye-movement effects in visual acuity experiments. We have been very fortunate in attracting to the project two outstanding visual scientists presently on sabbatical from their home institutions: Professor Jacob Nachmias of the Department of Psychology at the University of Pennsylvania and Professor Kent Higgins of the Division of Visual Sciences at the Pennsylvania College of Optometry.

II. Experimental Studies

1. Detection and Discrimination of Movings Targets (with J. Nachmias)

One class of cortical cells found in the primary visual cortex of primates is that consisting of cells driven preferentially by movement of an appropriate target in one direction but not in the opposite direction. Since velocity sensitive cells are not found at lower levels in the primate visual system, these cells undoubtedly form the initial filter of the mechanism for detecting the movement of small targets with high acuity. In the experimental analysis of these mechanisms we employed a temporal 4-alternative forced choice procedure in which two targets were sequentially presented on the face of a CRT: one was a target of uniform luminance; the other had the appearance of a sine wave grating drifting to the right or left. To generate a frame of the moving pattern, the Data General Eclipse S/200 read the appropriate 512 word list at the rate of 144 kwords/sec using its 12-bit D/A converter synchronized to the onset of a frame; successive word lists were made identical except for a 1-word offset producing sinusoidally varying voltage levels for the Z-axis that on successive frames were phase shifted. The observer's task was to respond to a given presentation pair by pressing one of four switches to indicate (1) which interval (first or second) contained the grating target and (2) in which direction

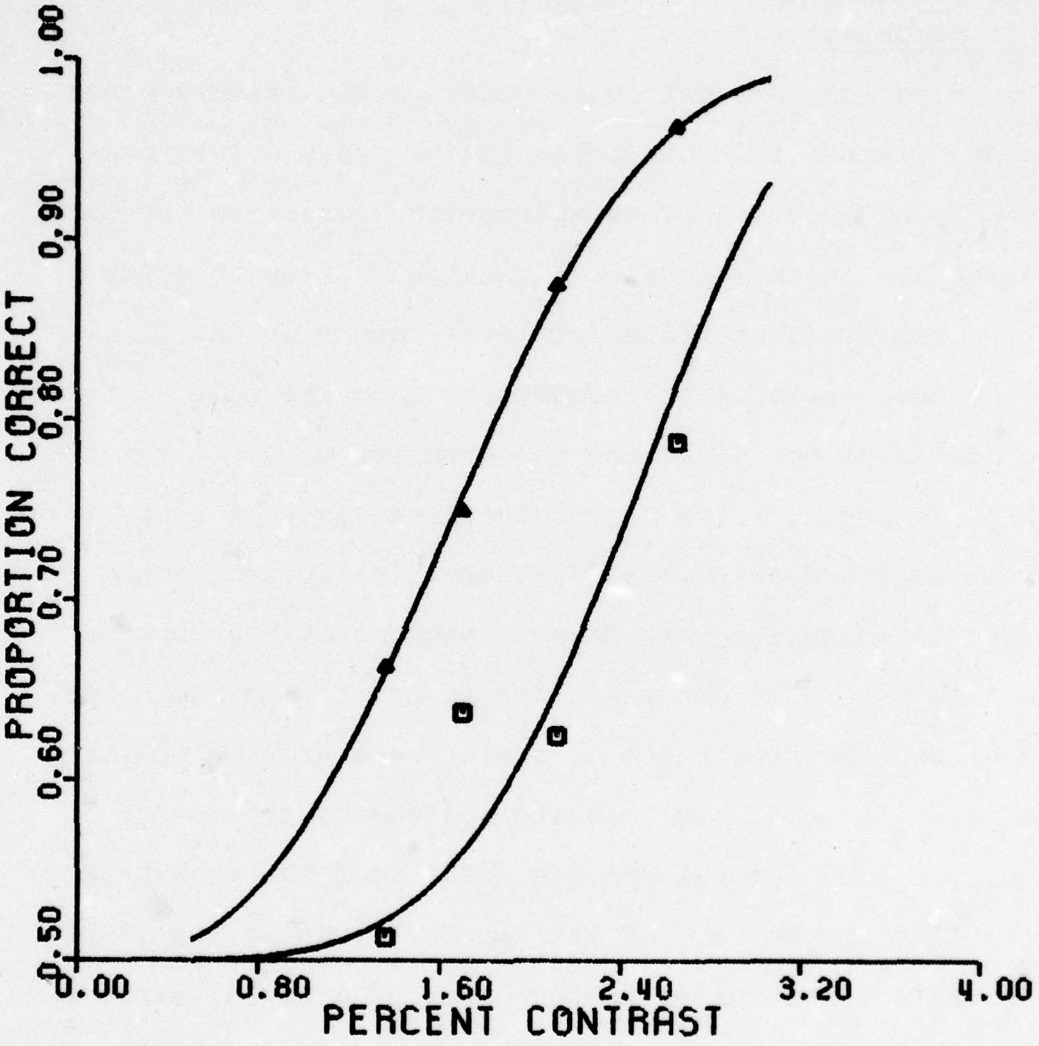


Figure 2. Psychometric functions for detection (filled symbols) and recognition (unfilled symbols) of 8 cycle/degree grating moving at the rate of 1.5 Hz.

(left or right) the target appeared to move. Results from a typical experiment are shown in Fig. 2.

For targets of high spatial frequency and low drift velocities, detection performance was better than direction discrimination. To rule out the possibility that under our conditions, i.e. isolated CRT viewed in darkened room, an observer's eye-movements produced the direction confusion, we stabilized the target images on the observer's retina. This finding may have implication for target acquisition in an operational environment with human observers or man-machine systems. A distant target, i.e. one with a high spatial frequency content and low apparent velocity, could be spotted but its direction erroneously reported.

2. Adaptation of Pattern Detecting Mechanisms (with J. Daugman)

Following exposure to a high contrast pattern, an observer's threshold for targets of similar orientation and spatial frequency is elevated by a considerable amount up to 300%. This effect has been used operationally to define the visual filters in the human visual system dealing with spatial frequency and orientation (e.g. Blakemore and Campbell, 1969) but little is known of the dynamic characteristics of this form of pattern-specific adaptation (Bodinger, 1978) and the mechanism is unknown.

There are three unresolved issues: (1) the locus or control site in the visual system of the adaptation; (2) whether the time course is governed by a long time constant as well as by a short time constant; (3) whether the mechanism involves long-lasting cortical inhibition as Tolhurst and Barfield (1978) and Vautin and Berkley (1976) have speculated or involves a form of synaptic habituation.

For the first issue several lines of experimental evidence rule out the retina or lateral geniculate as a locus of pattern-specific adaptation. We found (1) that adaptation to a high contrast grating target presented to one eye only, elevated an observer's threshold in the unstimulated eye by approximately the same amount as if the stimulated eye were tested and (2) that the recovery from adaptation followed a similar if not identical time course in both eyes (see Fig. 3). Since an observer cannot voluntarily move his eyes smoothly across the grating target but rather fixates salient peaks or troughs, Kelly (1978) has argued that adaptation to an oriented grating target can be localized to the retina which has become differentially sensitized; it could be further argued that if the pattern specific adaptation had a retinal locus then interocular transfer could be produced by cortical interference arising from a signal from the stimulated eye. To rule out a retinal site we produced adaptation using a counterphase presentation which would produce uniform retinal stimulation providing there were no eye-movements then tested with and without retinal image stabilization and found equivalent threshold elevation. A non-retinal locus is also consistent with known neurophysiological findings. No evidence for pattern specific adaptation has been reported for

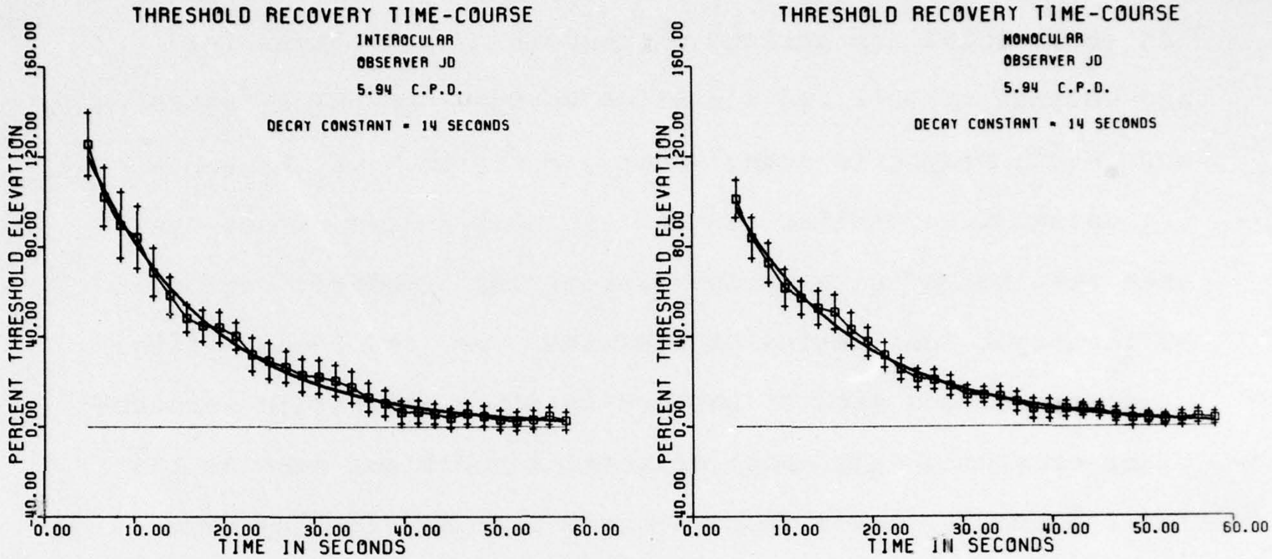


Figure 3. Threshold recovery time-course for observer JD with foveal grating target of 5.94 cycles/degree. Each data point is the average of 5 measurements determined by threshold tracking techniques. The vertical bars indicate 1 s.e.m.

A. Interocular transfer condition.

B. Monocular test condition.

The thick solid line drawn through the data points is an exponential function of the form $Ae^{-t/\tau} + B$ fitted to the data by the method of least squares. In both cases the best fitting time constant has the value of 14 seconds.

retinal ganglion cells or for lateral geniculate neurons but it is found for striate neurons in Area 17 (Mansfield and Daugman, 1978). To establish an upper bound we tested for interhemispheric transfer of adaptation, i.e. presenting an adapting grating to the left hemi-retina of one eye then testing in the corresponding mirror symmetric region of the right hemi-retina of the other eye, and found little or none. If the site of pattern-specific adaptation were regions receiving many cross callosal connections such as the inferotemporal cortex whose neurons are described by Gross and his colleagues as having large receptive fields that cross the midline and always include the fovea then interhemispheric transfer should be significant. No such transfer was found. This is consistent with Legge's thesis work (1976) showing that adaptation to a spatial impulse does not elevate at all spatial frequencies, a finding which implies a local rather than a global adaptation mechanism. In addition, the small size of the space domain profile derived from spatial frequency data (e.g. Stromeyer and Klein, 1974) would be consistent with a locus in Area 17.

On the second issue, we have found no evidence for a long-lasting component as did Bodinger (1978) which reflect a difference in the stimulus conditions employed or the methods for measuring threshold; a difference that is being further examined. For the short-term component we found strong evidence for an exponent process with both adaptation and recovery with a single

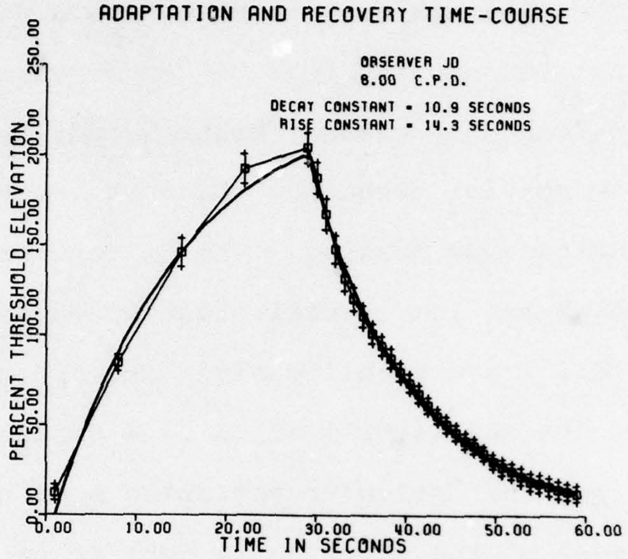


Figure 4. Adaptation and recovery time course. Threshold elevation of time in cycle (30 sec adaptation; 30 sec recovery) for observer JD with a 8 cycle/degree grating target. Each data point is the average of 5 measurements determined by a threshold tracking technique. The vertical bars indicate ± 1 s.e.m. The thick solid line drawn through the data represents a least squares fit of exponential functions to the data. The best fitting time constant of the rising phase is 10.9 seconds; and 14.3 seconds for the recovery phase.

(possibly lumped) time constant on the order of 10 seconds for high spatial frequency targets. For low spatial frequencies, adaptation and decay appear to be more rapid which is consistent with the findings of both Blakemore and Campbell (1969) that it was not technically feasible to measure by adaptation a spatial frequency channel below 3 cpd, and of Legge (1978) that low spatial frequency channels are readily revealed by near simultaneous masking. The difference in time scale between high and low spatial frequencies was also apparent during retinal image stabilization (see Effects of Eye and Target Movements and Stabilization). A parametric study of the effect of other stimulus variables such as luminance and contrast level of the adapting targets is in progress.

On the third issue, psychophysical experiments do not suggest the type of mechanism involved but parallel neurophysiological experiments in monkeys indicate that the activity in individual neurons in Area 17 of the rhesus monkey also adapts following exposure to high contrast grating targets and recovers following removal of the target with an exponential time course for adaptation having a time constant on the same order of magnitude as that obtained psychophysically in human observers (Mansfield and Daugman, 1978). Such evidence does not provide compelling localization because of the rich complexity of interconnections described in the introduction. To test for a mechanism intrinsic to Area 17, perfused slices of monkey visual cortex sectioned normal to the pial surface and to the Area 17/Area 18 border to preserve functionally intact synaptic connectivity of the visual cortex were examined _in vitro_. Adaptation to synaptic activation was found to have a recovery time constant of 14 seconds. Suggestive evidence for cortical inhibition mediated by the inhibitory neurotransmitter GABA (gamma amino butyric acid) and for cholinergic activation of a muscarinic synapse possibly involving the cyclic nucleotide cGMP, (3'-5' guanosine cyclic monophosphate) (Mansfield, Simmons and Daugman, 1978) favors Area 17 as the control site of adaptation, i.e. the locus of a rate-limiting step in the reduction and recovery of sensitivity to oriented targets possessing medium and high spatial frequencies. Moreover, the results suggest a general principle: since cellular adaptation (habituation) is a common property shared by a wide class of central neurons, and since adaptation is optimized for the class of stimuli that maximally activate the cells, the site of adaptation is also the site at which particular type of visual information is filtered. In addition, the mechanisms may be similar since the basic unit of cortical organization is repeated from one cortical region to the next (Mountcastle, 1978). The results have practical implications for target acquisition in situations involving visual clutter; the general principle indicates that similar inference would be encountered in visual attention tasks.

3. Effects of Eye and Target Movements and Stabilization (with K. Higgins and J. Daugman)

Under ordinary viewing conditions, an observer's eyes move constantly even during fixation so that the population elements of the visual pathway activated by a given target changes constantly. Under special conditions the consequences of such eye-movements can be observed. When a target is viewed with the peripheral retina, particularly at night or as a low contrast object with poorly defined contours (e.g. no sharp edges), and the observer fixates, the target fades from view but visibility can be restored by eye-movements, or by the movement of the target. One means of experimentally investigating the consequences of eye-movements on target visibility is to maintain the target image on a fixed set of retinal receptors. Approximately 25 years ago two groups working independently developed one means of stabilizing retinal images on the retina using either a contact lens to support a small first surface mirror thus changing the optical path length and angle of incidence as the eye moved in an optical system that directed the image onto the retina (Riggs _et al._, 1953) or by using the contact lens to support a small projector that focussed an image onto the retina (Ditchburn and Pritchard, 1953). Studies arising from the application of these methods found that stabilized images tended to fade sometimes in a complicated fashion; however, the techniques were difficult to apply if not dangerous and could not be applied to a large subject population because of the necessity for a close fitting (i.e. non-slipping) schleral contact lens. The development of the SRI Dual Purkinje Eye-movement Monitor capable of measuring continuous eye motion with an accuracy of 1' of arc or less without contact but simply using infrared reflection from the front surface of the cornea (1st Purkinje image) and the back of the lens (4th Purkinje image) suggested a new means of retinal image stabilization. By using the vertical and horizontal eye movement signals with appropriate gain and offset to drive small mirrors in an optical system for horizontal and vertical deflection of a target image (a concept suggested to SRI by B. Wooten) image stabilization might possibly be achieved. This approach has an additional advantage in that any target of arbitrary configuration or target of arbitrary complexity or chromatic composition can be viewed in this manner. As described in the previous annual report, we have assembled such a system and over the past year employed this unique system for retinal image stabilization.

Fig. 5 shows a photograph of an observer in the apparatus. The observer views the target through the optical system with his right eye and a patch over his left eye. Although reasonably precise tracking of eye movements was possible over a short run using only a chin rest, long sessions under image stabilization necessitated a bite bar constructed with a hard wax compound. By means of a Bidel prism the optical distance of the target could be changed to bring it into focus for our observers many of whom were myopic; variations in accommodations which were reflected on occassion by variability in threshold settings could be eliminated by the application of a cycloplegic drug. Contrast sensitivity functions were used as a measure of the effects of eye-

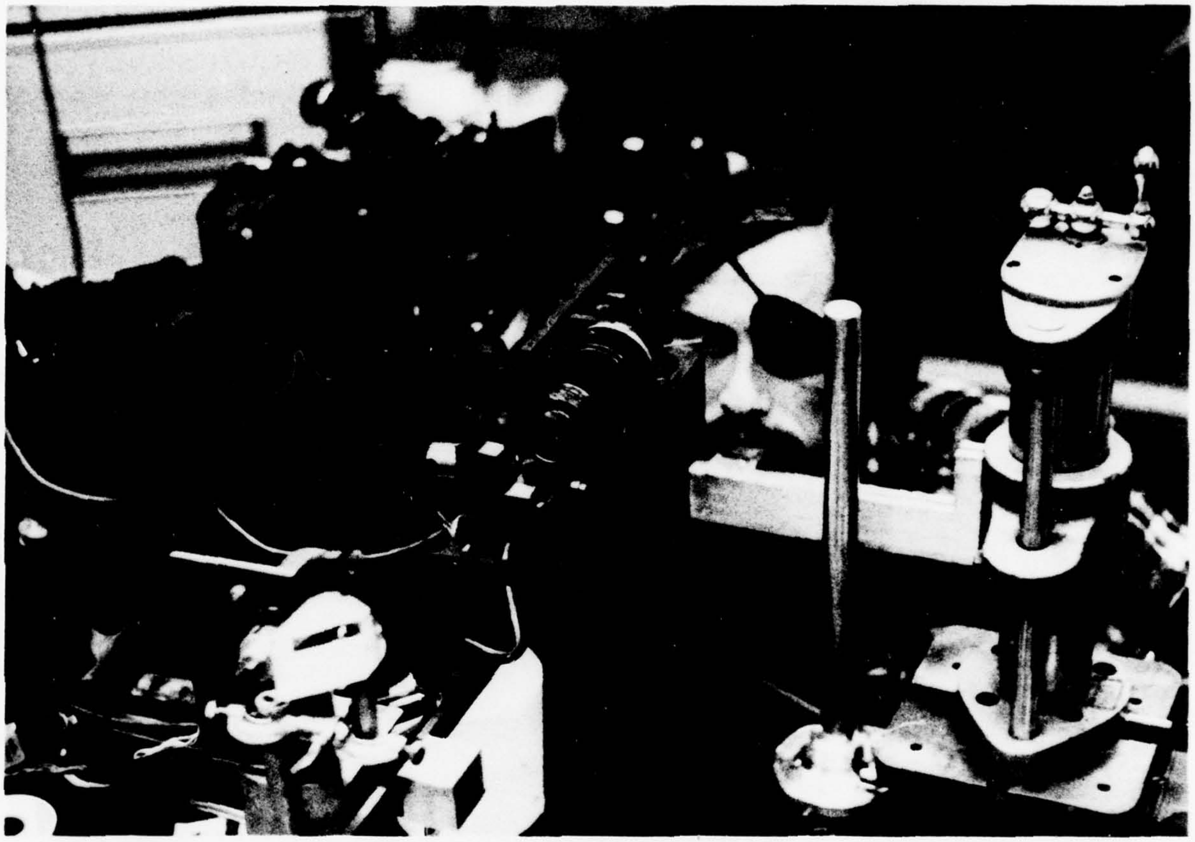


Figure 5. Photograph of observer KH viewing target under retinal image stabilization produced by using the outputs of the SRI Dual Purkinje Image Eyetracker to drive small mirrors on the Stimulus Deflector seen in the foreground.

movements and two procedures were employed to assay different aspects of the stabilization paradigm. A temporal two-alternative forced choice staircase procedure was used for brief presentations in which the contrast for the target was ramped on and off in a Gaussian manner. The experiment was under computer control so that the computer kept track of the 16 independent contrast staircases, one for each spatial frequency tested, sequenced with random complete permutations. Alternatively, the spatial frequencies were tested with random complete permutations but a modified von Békésy tracking procedure was employed with the computer sampling the voltage to the Z-axis as the observer tracked threshold. The first method yields the benefit of stabilization without significant fading and could be used by naîve observers. The second method could assay the effect of long term exposure to stabilized images but required experienced observers to achieve stable results. In the latter method, the observer continued during a search period while the computer did not measure threshold to increase the contrast level of the target until the target ceased to fade and remained near the threshold of visibility. Fig. 6 shows an example of the contrast sensitivity function obtained using this latter procedure for a single observer under two conditions: without stabilization and with stabilization. The observer has normal acuity and this is reflected by the shape and amplitude of the upper curve. However, the lower curve obtained under image stabilization conditions shows a much lower sensitivity

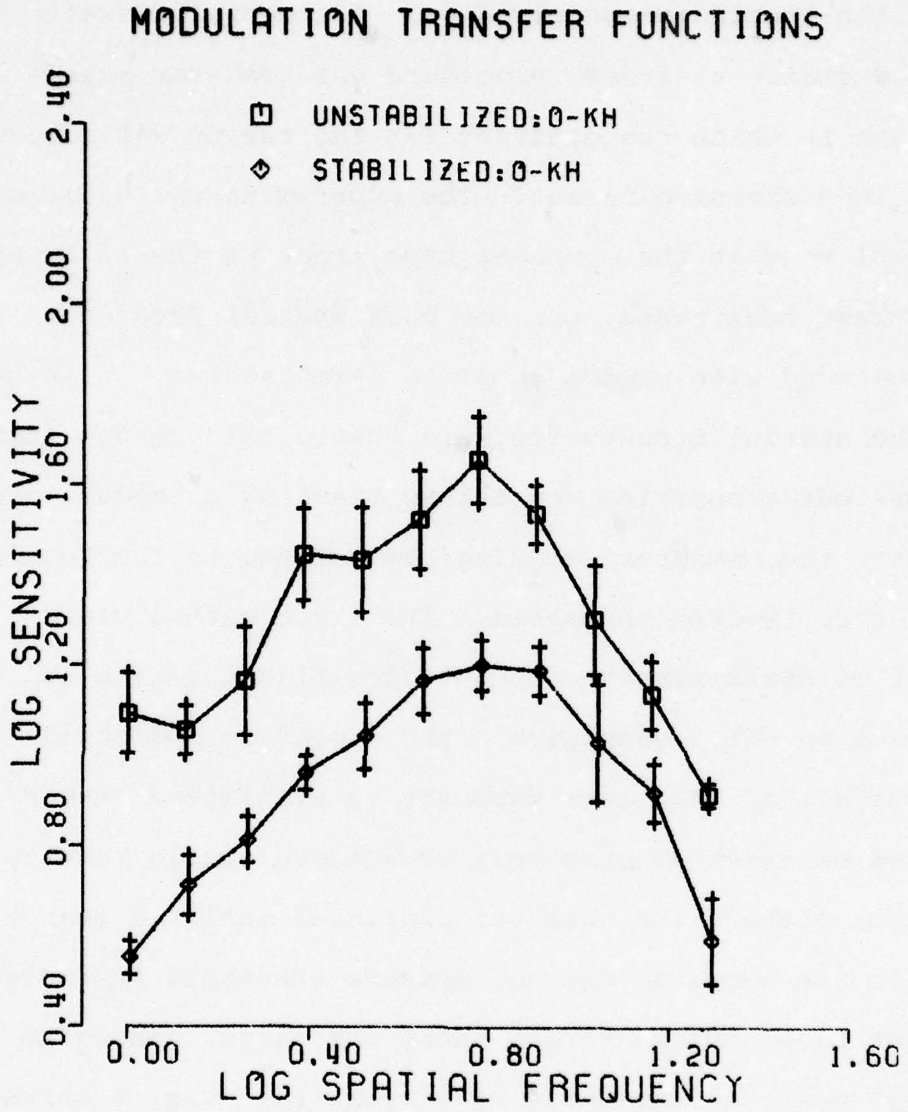


Figure 6. Effect of retinal image stabilization on contrast sensitivity function determined by the method of adjustment.

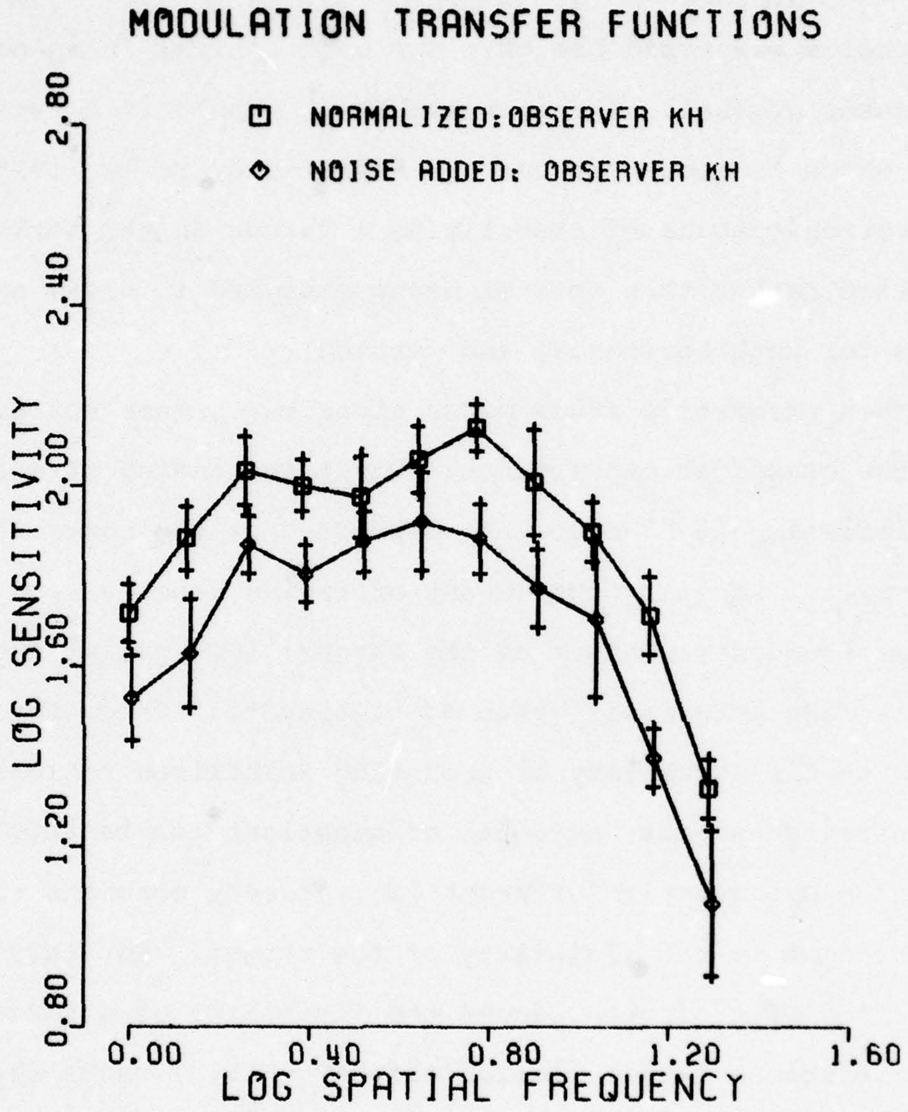


Figure 7. Effect of high frequency vibration on contrast sensitivity function determined by the method of 2AFC.

(higher threshold) for low spatial frequencies. As is consistent with the adaptation studies, the fading for low spatial frequencies was rapid but that for high spatial frequencies was rather gradual. The increase in threshold is a factor of three which is about the average reported by Kelly (1975) using an electronic means of stabilizing a target in the horizontal direction rather than optical means employed in these experiments for both horizontal and vertical.

This parametric study makes clear two points not evident from the classical experiments. First the fading of a stabilized image is not absolute but depends upon the contrast of the target. Secondly the amount of fading depends upon the spatial frequency content of the target: low spatial frequency targets fade more easily than do high spatial frequency targets.

With the capability of producing stabilized retinal images of arbitrary targets, a number of questions can be supplied with answers. One question of practical interest concerns the effect of vibration on the visibility of the target. Entirely stopping the motion of a target reduces the visibility of a target but do vibrations have a similar effect? Fig. 7 shows the effect of high frequency vibration on the contrast sensitivity function. The result is a fairly uniform decrease over all spatial frequencies tested rather than a selective decrease at the high spatial frequencies as might be predicted. An extension of this work would be to see if the erratic eye-movement patterns of amblyopic observers serve as a source of their loss of visual acuity.

III. Model of the Mechanism for Detecting Oriented Targets

(with J. Daugman and S. Ronner)

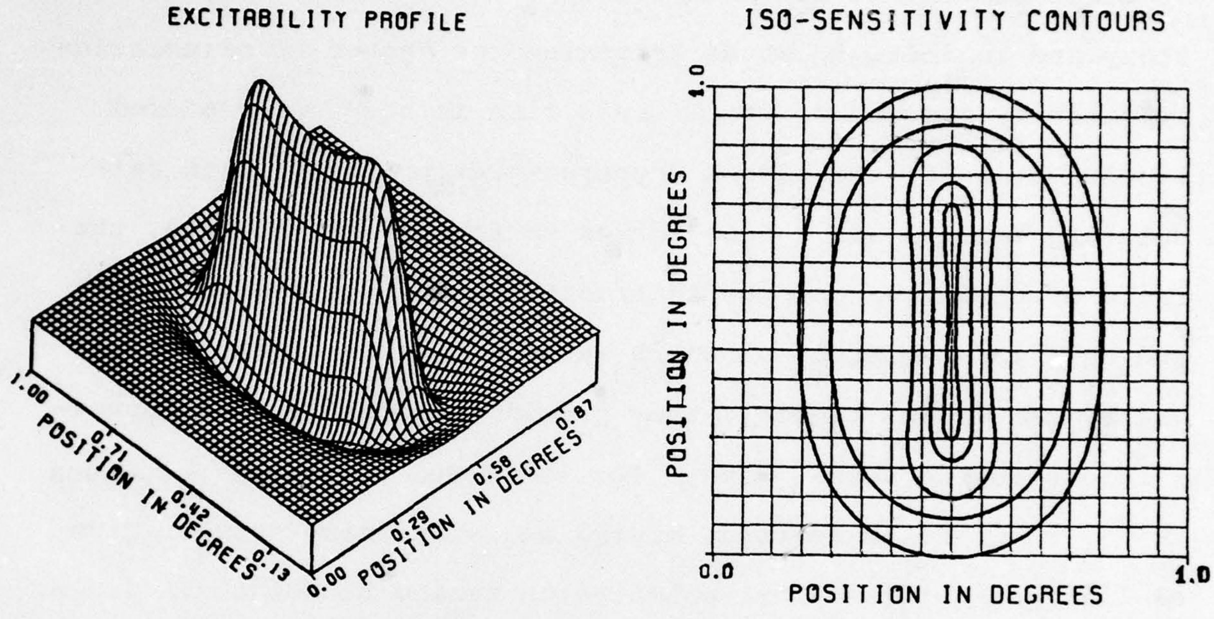
The primary visual cortex serves as a control site for a number of characteristics of visual acuity including orientation anisotropy (Mansfield, 1974; Mansfield and Ronner, 1978) and pattern-specific adaptation (Mansfield and Daugman, 1978). It is essential then to understand in quantitative terms the receptive field characteristics of neurons in this region particularly those as indicated in Fig. 1 that project transcortically. From parallel neurophysiological studies of these neurons (Mansfield, Ronner, and Daugman 1978), the results obtained from other laboratories (Hubel and Wiesel, 1968; Dow and Gouras, 1972; Poggio, Baker, Mansfield, Sillito and Grigg, 1975; Schiller, Finlay and Volman, 1976) as well as extrapolations from studies of cat visual neurons in Area 17 a number of principles of cortical organization can be stated:

1. Input from the geniculate is excitatory, all inhibition is generated intracortically.
2. All neurons in a given cortical column have receptive fields with similar retinal locations and similar orientation selectivity.
3. Interactions within a cortical column may be facilitatory or summative but between cortical columns the interactions are inhibitory.
4. Hypercomplex receptive fields are not a separate

class but the properties of length sensitivity is found in both simple and complex receptive fields.

5. Neurons with simple receptive fields and complex receptive fields are not distinguishable in the upper cortical layers. Such neurons might be termed simplex cells.

The first step was to consider a cell at the level of the individual striate neuron in the supragranular layers. Fig. 8a and 8b show the excitability profile for the receptive field of an idealized visual cortical neuron. The receptive field is composed of a linear array of excitatory zones, identical in all respects except location, together with an equal number of similarly arranged inhibitory zones. Each zone is given mathematically by a 2-dimensional rotationally symmetric Gaussian distribution and every zone of excitation is paired with a concentrically organized inhibitory zone. The inhibition is considered to arise at different levels: first by the off-zones of geniculate neurons whose afferents project directly onto the cell in question; secondly by silent intracortical inhibition. The excitability profile represents the net excitation or inhibition produced by illumination at any point in the field. The response measure applied to the idealized neuron is the integral of the rectified convolution of the excitability function with the luminous target pattern; such a measure would correspond to the sum of the action potenial discharge from the neuron, the measure employed in a parallel neurophysiological study (Mansfield,



(A)

(B)

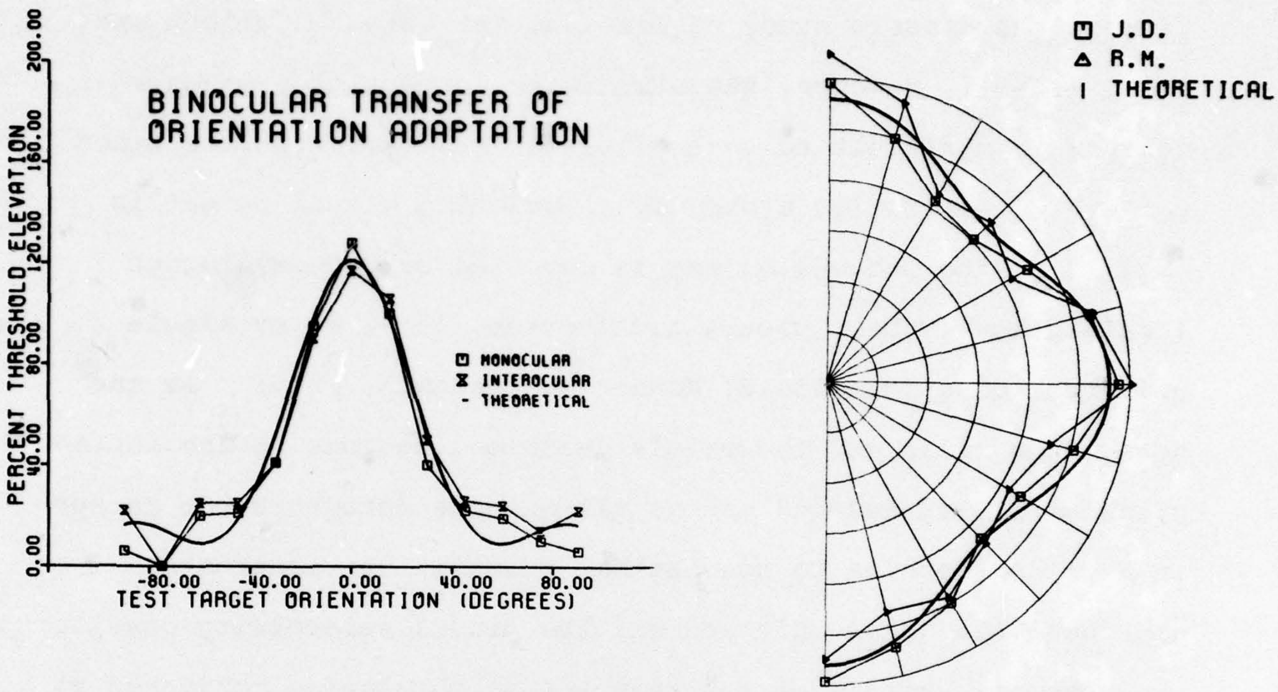
Figure 8. Synthesized response of striate neuron in supragranular layer.

A. Excitability profile of synthetic neuron of median orientation tuning bandwidth.

B. Iso-sensitivity contours for the same synthetic neuron.

Ronner and Daugman, 1978) and most likely the signal of interest to the central nervous system. The number and spacing of subunits as well as the ratio of the diameters of the excitatory and inhibitiory zones determine the degree of orientation selectivity and the degree of reduction in response produced by elongation of the target (hypercomplex property). In calculating orientation tuning curves to fit the neural data, the ratio of variances and the interunit spacing was held constant and only the number of subunits varied. The resulting curves are symmetric and bimodal; they provide reasonably good approximations to the neural data. For the model of neural responses as for the striate neurons, moving and stationary stimuli give similar but not identical orientation tuning bandwidths. Since the model involves specific assumptions it was important to note that the results regarding orientation tuning bandwidths are robust and not sensitive to the detailed assumptions, presumably because of the integration step involved.

The second step in developing the model is to relate the activation in individual neurons to psychophysically measured performances. Attempts to relate perceptual processes of neural events have frequently relied upon apparent trigger features of single neurons. Such an approach asserts that an aspect of a visual scene (geometric contour or particular spatial frequency) is detected and coded in a precise one-to-one fashion by the class of neurons for which that aspect serves as a "trigger feature" (or essential characteristic in the Aristotelian sense).



(A) (B)

Figure 9. Comparison of synthesized response of striate neuron population with human psychophysical data on orientation acuity.

A. Comparison of synthesized population response following adaptation to threshold elevation in monocular and interocular test conditions.

B. Comparison of synthesized population response in the absence of adaptation with detection threshold for 8 cycles/degree grating target subtending 2° foveally.

The concept of a trigger feature is best exemplified in animals with a limited repetoire of visually guided behaviors, e.g. the frog in the classic study of Lettvin, Maturana, McCulloch and Pitts (1959). However, the simplified concept of a trigger feature is difficult to reconcile, for example, with the broad pattern of activation evoked by an oriented visual target in Area 17 of the macaque monkey as revealed by 2-deoxyglucose localization (Hubel, Wiesel and Stryker, 1978) or by single unit recording (Mansfield, Ronner and Daugman, 1978). As the data makes clear and the models describe, neurons in the supragranular layers respond not as all-or-none detectors but rather in a graded fashion to non-optimal stimuli. An alternate approach that takes into account the graded selectivity considers the response profile of the relevant subpopulation activated by the stimulus as a principal determinant of the visual code. Since the control site is Area 17 for many aspects of visual acuity, the relevant subpopulation may be modelled simply by neurons with characteristics similar to those in the supragranular layers of Area 17. As a continuous approximation, the function $f(\mu,\omega,\theta)$ describing the response of the class of activated neurons to a target of orientation, θ, of a given bandwidth, μ, centered at orientation, ω is convolved both with the function $g(\mu)$ describing the distribution of orientation bandwidths and the function $h(\omega)$ describing the distributions of neurons optimally responsive to targets or orientation, ω. The resulting function, $R(\theta)$, represents a quantity proportional to the total response of the population of supragranular striate cortical neurons activated by a target orientation of θ. The function, $R(\theta)$, is given formally by the following equation:

$$R(\theta) = k \int_{\omega=\theta-\pi/2}^{\omega=\theta+\pi/2} \int_{\mu=0}^{\mu=\pi} f(\mu,\omega,\theta)g(\mu)h(\omega)d\mu d\omega$$

where k is a scale factor. In making the computation, analytic functions which closely approximated the neural data were chosen. Specifically,

$$f(\mu,\omega,\theta) = e^{-((\theta-\omega)/\alpha\mu)^2}$$

$$\text{where} \quad = (\ln(\pi/2)^{1/2})^{-1/2}$$

$$g(\mu) = (\mu/\beta)^6 e^{-\mu/\beta}$$

$$\text{where } \beta = \pi/45,$$

i.e., a gamma function fitted to neural data

$$h(\omega) = 1 + (\lambda/2)\cos(4\omega),$$

i.e., for $\lambda = 1$, a function having an anisotropy ratio of 2:1 which fits data for foveal cortical neurons; for $\lambda = 0$, a function having an anisotropy ratio of 1:1 which fits data for parafoveal cortical neurons. The calculated response, $R(\theta)$, for a foveal target is shown in Fig. 9.

An obvious extension to the case of simple detection against a uniform background based on the evidence described above (see Adaptation) that Area 17 is the control site for pattern-specific adaptation is the case of prior adaptation. On the basis of neurophysiological evidence (Mansfield and Daugman, 1978) each class of neurons was considered to be attenuated or adapted in proportion to its level of activation by adapting the oriented target. That is to say, the attenuation function, $1(\mu,\omega,\eta)$ is given by

$$1(\mu,\omega,\eta) = e^{-((\eta-\omega)/\alpha\mu)^2}.$$

The difference between the population response to the test oriented target in the absence of adaptation and the population response to the same oriented target following adaptation corresponds in the model, assuming linearity near threshold, to the sensitivity of the psychophysically defined orientation channel. The theoretical predication is compared with the psychophysical data in Fig. 9 and the two are in reasonably good agreement. These results are of interest for target acquisition by human observers or by pattern recognition machines employing spatial filters.

IV. Projections

The understanding of vision in biological systems in terms of predictive mathematical models is a central problem from the scientific point of view whose solution is of great practical significance. At present our research has taken some initial steps toward answering the intriguing questions of how the human visual system detects, discriminates and recognizes two-dimensional patterns. Using the stabilization of the retinal images of visual targets to localize processing control sites, and assess the contributions of eye-movements, first-order models have been developed which will serve as building blocks for the synthesis of more complex visual processes. The next step will be to consider modelling the effects of inhibitory spatial interactions and moving targets.

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Over the past year a special eye-movement monitoring and visual display system has been used to investigate human acuity using computer-controlled psychophysical testing procedures. The system can accurately measure eye-movements of less than 1' of arc and with the same precision, control the movement of visual targets relative to an ob-

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server's retina. The theoretical reconstruction of the response profile of a visual target is complicated by the fact that under ordinary viewing conditions, even during fixation, the population of active elements in the visual pathway changes constantly. Using the special visual apparatus, it was possible to maintain a target on a fixed set of retinal receptors facilitating an orderly experimental analysis of visual response patterns. Some of the main experimental findings are the following:

(1) The detection of slowly moving targets of high spatial frequency is superior to the discrimination of the direction of movement and this difference between detection and recognition performance is intrinsic to the visual system since it is not produced by small saccadic eye-movements present during fixation.

(2) The control site, i.e. locus of rate-limiting step, for the mechanism responsible for the selective loss of pattern sensitivity following exposure to high contrast targets is primary visual cortex; the loss and spontaneous recovery follow exponential time courses whose time constants increase with adapting target spatial frequency.

(3) Targets stabilized on the retina undergo a decrease in visibility that is inversely related to their spatial frequency.

(4) High frequency noise vibrating a target produces a proportionate loss in contrast sensitivity at all spatial frequencies but low frequency noise such as that present in normal eye-movements has little effect.

The problem of how the human visual system detects oriented targets was examined using a mathematical model whose basic elements are spatial filters representing the receptive field response profiles of visual cortical neurons in the supragranular layers of Area 17. The population response profile proved a useful predictor of visual sensitivity for foveal targets in the absence and in the presence of simple pattern adaptation. Work is currently in progress on extensions of the model to motion and spatial interactions.