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PREDICTIVE MODELS OF HUMAN VISUAL PROCESSES IN AEROSYSTEMS (U)  
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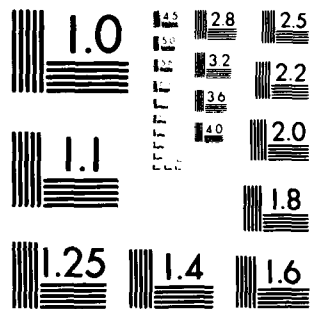
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| 20. ABSTRACT (Continue on reverse side if necessary and identify by block number)<br><br><b>Over the past three years a special eye-movement monitoring and visual display system has been used to investigate human acuity using computer-controlled 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.</b> |                                         |                                                                                   |  |

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✓ 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.

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 an accurate predictor of visual sensitivity for foveal targets.

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PREDICTIVE MODELS OF  
HUMAN VISUAL PROCESSES IN AEROSYSTEMS

Final Report

By

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I. Introduction

A central problem in the study of vision is the determination of the cellular neural mechanisms underlying behaviorally relevant functions. Unfortunately, no single approach or technique has proved sufficient by itself to unravel all the complexities involved and provide a complete understanding of visual behavior. Precise assessment of behavioral performance with well-defined tasks in the intact animal can yield a quantitative description of visual behavior but any inferences concerning causal neural mechanisms must remain speculative since the central nervous system of any species of interest is too complicated for a unique mechanism to be identified. As Dean describes in a discussion of the inferotemporal cortex elsewhere in this book, the same limitation applies to behavioral studies of lesioned animals. At the other end of the spectrum of approaches, neuronal activity can be measured directly at some level of the visual pathway by fracturing the integrity of the central nervous system with anesthesia, drugs or surgery, and with the application of techniques from the armamentarium of modern neurobiology, specific cellular mechanisms can often be identified. However, as several chapters in this book emphasize, visual processing in the central nervous system is distributive, that is to say there are multiple visual systems, so that a particular candidate mechanism may be irrelevant to the behavior of interest or may operate differently in the intact animal. However,

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converging evidence from different approaches to the study of the visual system can offer an effective strategy.

The primate striate cortex provides a model system to illustrate such a strategy. Considerable information has accumulated concerning the anatomy and physiology of the striate cortex and antecedent structures in the retinogeniculo-cortical pathway. In contrast to the afferent visual pathways of other species (see for example the afferent pathways in the cat as illustrated in Fig. 1 in the chapter by Berkley and Sprague) the striate cortex in Old World anthropoids is the major if not exclusive recipient of fine-grain visual information. For Old World anthropoids the cross-species similarity assumption appears valid, so that behavioral and neural data obtained for one species can be assumed to hold for all others. To explain visual performance in general, a reasonably complete if not exhaustive knowledge of the central nervous system is required, but for optimal performance such as that in a visual acuity task we need only focus on the relevant mechanisms that provide constraints on optimality. Strong evidence places the locus of such constraints in the striate cortex, and the quantification of striate receptive fields and visual performance on acuity tasks makes possible the development of a computational theory relating causal neural mechanisms to behavior. In this chapter a combined approach of neural and behavioral analyses and mathematical synthesis is applied to the role of the striate cortex in visual acuity. First those critical features of the primate visual system that are pertinent to the discussion are reviewed.

## II. Primate Anatomy and Physiology

Existing Old World anthropoids which includes a range of species from monkey (e. g. macaca mulatta) to man (e. g. homo sapiens) exhibit a number of special evolutionary adaptations in their visual systems. These species most probably having evolved from nocturnal, solitary visual predators (Cartmill, 1974; Polyak, 1957) into diurnal, social frugivores or omnivores possess frontally directed eyes with large degree of binocular overlap of  $150^{\circ}$ , high central visual acuity (Blakemore, 1970), well developed trichromacy (DeValois and Jacobs, 1968) and stereopsis to baffle natural camouflage and promote their precise eye-hand coordination, excellent visuospatial memory (Menzell, 1973) and acute perception of visual social cues (Savage-Rumbaugh, Rumbaugh and Boysen, 1978). Subserving these behavioral adaptations there are a number of neural adaptations not all of which are known or understood at the present time.

### A. Foveal specialization

The retina of Old World anthropoids and indeed of a number of other primates possesses a specialization corresponding to the center of visual fixation, the fovea. As in all vertebrate retinas the photoreceptors are located at the inner margin of the retina facing away from the light. However, in the primate retina at the region corresponding to the center of gaze the proximal neurons in the inner nuclear layer (amacrine and ganglion cells) are displaced laterally forming the foveal pit and allowing light more direct access to the transduction elements. Reduction in light scattering is also achieved by avoidance of the foveal region by the blood vessels on the

vitreal surface of the retina leaving intact only the choroidal circulation. Associated with the ciliary stocks of the photoreceptors in the fovea (cones) is the dense yellow pigment, the macular pigment, which serves to absorb shortwave light and reduce the chromatic aberration inherent in the simple lens system of the eye. Flicker photometry measurements (Wooten, Thawley and Knoblauch, 1980) indicate that the macular pigment is densest in the center of the fovea with its distribution dropping off sharply outside the fovea in parallel with the cone distribution. Microspectrophotometric measurements of cone outer segments have revealed a basis for trichromatic color vision in the differing absorption spectra with  $\lambda_{\text{max}}$  of 430nm, 535nm, 565nm (Marks, Dobell and MacNichol, 1964; Wald and Brown, 1965; Bowmaker, Dartnall and Mollon, 1980) described by a modified vitamin A<sub>1</sub> nomogram (Ebrey and Honig, 1977). Although the center of the fovea is rod-free the dense packing of the cones distorts the outer segment into slender rod-like shape (Dowling and Boycott, 1966) from their normal pyramidal shape found in the periphery. Although rods and cones probably do not differ significantly in intrinsic sensitivity (Fain and Dowling, 1973) they do exhibit substantially different saturation characteristics (Boynton and Whitten, 1970). The convergence necessitated by the existence of 200 million photoreceptors but only 1 million optic nerve fibers is not uniform but graded across the retina with the central region receiving a disproportionate share as reflected in the magnification factor in the retinotopic map of the dorsal lateral geniculate (Malpeli and Baker, 1975). In contrast to other vertebrate

species the retinal circuitry of Old World anthropoids is simple containing relatively few classes of amacrine cells and correspondingly the retinal ganglion cells fall into relatively few classes. Following terminology developed in the cat retina, ganglion cells have been classified into three classes termed X, Y and when specified, W (DeMonasterio and Gouras, 1975; Schiller and Malpeli, 1977; DeMonasterio, 1978a). X cells have small receptive fields, summate linearly across these fields, frequently have a sustained response to standing contrast and are found predominantly in the foveal region. Y cells have large receptive fields, summate nonlinearly across these fields, mainly exhibit a transient response to standing contrast and are found predominantly in the periphery. In quantitative terms the central fovea ( $1^\circ$ ) yields 90% X cells and 10% Y cells, but in the near periphery ( $11-20^\circ$ ) only 45-70% X cells and 30-50% Y cells (Schiller and Malpeli, 1977; DeMonasterio, 1978a). W cells, clearly not a homogeneous class, lack well defined center-surround organization, are distributed across the retina but mainly outside the foveal region, and project directly to the superior colliculus rather than through the geniculate with some exceptions (Wiesel and Hubel, 1966; Dreher, Fukada and Rodieck, 1976; DeMonasterio, 1978b) providing in the primate (in contrast to other mammals) a complete representation of only the contralateral half of the visual field. The actual proportion of the retinal ganglion cell distribution consisting of W cells is difficult to estimate since the recording techniques tend

to sample from the larger or more responsive X and Y cells. Rodieck (1979) estimates that possibly 50% of cat retinal ganglion cells are W cells, so that in monkey the proportion may be larger than the 10% encountered experimentally. The retinal segregation into separate functional classes undoubtedly has adaptive significance since it is retained at higher levels in the visual system.

B. Functional segregation in the dLGN

The axons of the retinal ganglion cells form the optic nerve which decussates at the optic chiasm before reaching its targets in the dorsal region of the lateral geniculate of the thalamus and the superior colliculus in the brain stem. Each hemi-retina has a geniculo-cortical target in a separate hemisphere except for a 1° vertical strip along the midline and a few ganglion cells around the rim of the fovea (Stone, Leicester and Sherman, 1973; Bunt, Minckler and Johanson, 1977). The primate dLGN is a 6-layered structure receiving in precise retinotopic register the inputs from the two retinas and maintaining them in separate laminae with a discrete functional organization as well (Schiller and Malpeli, 1978; Dreher, Fukada and Rodieck, 1976). The 4 parvocellular layers receive X cell input and have cells with concentric color-opponent receptive field organization (R+G- or G+R-); the blue-selective on-cells are found predominantly in the ventral pairs of parvocellular layers. The two magnocellular layers receive Y cell input and have cells that are concentrically organized but as might be expected have spectrally broad band or achromatic receptive fields.

### C. Cortical organization

In contrast to other mammalian species (e.g. see the chapter by Berkley and Sprague for a discussion of the multiple and parallel input pathways into the cortex of the cat) the dLGN of catarrhine monkeys, apes and man forms the major if not exclusive input into the cortex, and that entry is confined to the striate cortex (Area 17 of Brodman) as shown in Fig. 1.

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Insert Fig. 1 about here

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Moreover the functional segregation present in the geniculate is maintained though less strictly in this initial cortical stage. The axons of the X cells of the parvocellular layers terminate mainly in layer 4A and layer 4C $\beta$  of this 6-layered koniocortical region (Hubel and Wiesel, 1972). The field of termination is the spiny stellate neurons which project to layer 3B and 5A as well as within 4C (Lund, 1973; Lund and Boothe, 1975). The axons of the Y cells emerging from the magnocellular layers project mainly to layer 4C $\alpha$  (Hubel and Wiesel, 1972); however, they also bifurcate and terminate in the superior colliculus (Schiller, Malpeli and Schein, 1979). The field of termination is the spiny stellate neurons which contribute to laminae 4B and 5A but also distribute widely within 4C $\alpha$  (Lund, 1973; Lund and Boothe, 1975). Both anatomical evidence based on Golgi staining (Lund and Boothe, 1975) and electrophysiological evidence based on selective anesthetization of a specific geniculate lamina (Schiller, Malpeli and Schein, 1979) suggest that the input from the parvocellular and magnocellular geniculate neurons remains largely segregated with X cells being the dominant

influence for cortical neurons with cell somas in the upper or supragranular layers and Y cells being the major influence for the infragranular layers. Such a distinction has a definite functional significance since the efferent projections of the two regions are quite different.

Area 17 or V1 projects and receives reciprocal projections from both cortical and subcortical targets with the cortical targets receiving efferents predominantly from the supragranular layers and the subcortical targets receiving efferents from the infragranular layers (Lund, Lund, Hendrickson, Bunt and Fuchs, 1975).

The pyramidal cells in the upper regions of layer 6 project back inhibitorily to the parvocellular layers of the dLGN but the pyramidal cells in the lower portion of layer 6 project back to the magnocellular layers (Marocco, McClurkin and Farooqui, 1979). The pyramidal cells in layer 5 project retinotopically to both superior colliculus and pulvinar but receive a reciprocal projection to layer 2 only from pulvinar which also projects widely to the rest of the visual field (Diamond, 1979). However, the projection from the pulvinar to the more rostral regions of cortex does not contribute to the spatial selectivity of the cells in these regions (Gross and Mishkin, 1977). Both the pyramidal and stellate cells in layer 4A which exhibit strong directional selectivity (Dow, 1974) as well as the largest pyramidal cells in the upper portion of layer 6 project to MT which in turn sends a reciprocal projection to layers 4A and 6. This circuit

may contribute to visually guided movement rather than object vision since MT sends a heavy projection to the pontine nucleus which then relays the information to the cerebellum (Glickstein, 1979). The pyramidal cells in the supragranular layers project transcortically to V2 and V3 both ipsilaterally and near the V1/V2 border contralaterally as well; these regions reciprocate with a projection to layer 1 (Spatz and Tigges, 1972; Wong-Riley, 1979). In addition there is a recently discovered third cortical projection site in the most caudal portion of the interparietal sulcus (see chapter by Ungerleider and Mishkin for a review of the evidence for the site). The cortico-cortical pathways from the supragranular layers conveying the transformed input from the parvocellular X cells are undoubtedly the critical ones for pattern vision.

Since in primates but not other mammals V1 is the dominant if not exclusive entry site of visual information into the cortex, the supragranular layers of V1 as indicated in Fig. 1 are the gateway to an arena of rich cortical integration. The terminal target regions in the visual projection field have been implicated in different classes of visual behavior: (1) MT could play a role in visually guided movement (Glickstein, 1979); (2) Area TE of von Bonin and Bailey on the inferior convexity of the temporal lobe appears to mediate the acquisition of complex visual discriminations (Gross and Mishkin, 1977; see chapter by Dean in this book); (3) Area 8 in the frontal lobe serves as a second control center for saccadic eye movements in addition to the superior

colliculus (Schiller, True and Conway, 1979); (4) Area 7 in the parietal lobe appears to direct visual attention to objects in extrapersonal space (Lynch, Mountcastle, Talbot and Yin, 1977; Mountcastle, 1978; see chapter by Ungerleider and Mishkin in this book for evidence from lesion studies implicating this region in object localization). However, these more rostral regions of the visual system may be irrelevant or at least redundant for certain basic pattern detection tasks since all regions of the cerebral cortex project to the basal ganglia, the major motor control system. In particular, visual acuity is unimpaired by either infero-temporal lesions (Cowey and Weiskrantz, 1967; Blake, Jarvis and Mishkin, 1977; Weiskrantz, 1980) or by parietal lobe ablation (see chapter by Ungerleider and Mishkin in this book) which suggests that some relatively simple detection mechanism applied to the output of Area V1 may be sufficient for high level performance in a visual acuity task. It is of interest then to consider how visual information is processed in V1 and represented in the population profile of its efferents.

### III. Cortical Processing and Representation in V1

In order to analyze the contribution of V1 it is necessary first to consider visual information that remains essentially invariant so as to define more clearly the intrinsic processes.

#### A. Invariants of retinal and geniculate origin

The receptive fields of individual neurons recorded in the supragranular layers of striate cortex preserve invariant or only slightly transformed several properties encoded in more distal portions of the visual pathway. The minimum discharge receptive fields are discrete with excitatory cores only slightly greater in size than those of the dLGN (Schiller, Finlay and Volman, 1976a) maintaining approximately the same magnification factor as in the geniculate (Hubel and Wiesel, 1974) but with a somewhat less precise retinotopic organization. Light- and dark-adaptation have their major locus of control in the retina so that for example the inverse relation between discharge latency and the luminance of the background or target is determined up to an additive constant by retinal and in the dark-adapted case more likely by photoreceptor mechanisms (Mansfield, 1976b; Mansfield and Daugman, 1978). Object brightness which appears to be encoded by relative impulse density is established for isolated targets at the retinal ganglion cell level in a relation that is initially

linear up to one log unit above the background level but nonlinear at higher levels (Mansfield, 1976a,b; 1975). In the dark-adapted case, simple reaction time and the latency of cortical evoked potentials decrease as the inverse cube root of target luminance approaching asymptotically different but constant values. In the dark-adapted case, retinal ganglion cells, lateral geniculate neurons and supragranular striate cells (although only 10% of the population) increase their average discharge rate as the cube root of target luminance, a relation also found with numerical magnitude estimates in psychophysical tasks. However, the brightness or lightness of targets in more complex scenes is influenced by large range spatial interactions (e. g. Land and McCann, 1971) which undoubtedly reflect central convergence. Such global interactions of lightness may underlie object color perception but local spectral and achromatic differences are present more distally. The majority of neurons in the supragranular layers of the foveal projection region maintain a differential sensitivity to wavelength (Poggio, Baker, Mansfield, Sillito and Gregg, 1975; Crawford, Fagan, Borchert, Heston and Marc, 1979) but in the representations of the more peripheral regions the proportion drops sharply relative to that of the geniculate indicating some convergence. In addition, the constant criterion thresholds of the monkey spectrally broad band cells in both the foveal and parafoveal projection regions reflect the same balanced input from the three

classes of cone photoreceptors exhibited by behavioral measures of luminance threshold in the intact animal (Poggio et al, 1975). On the other hand, four attributes of cortical receptive fields represent intrinsic contributions of striate cortex.

B. Intrinsic cortical transformations

There are four major transformations carried out upon the incoming visual information by the synaptic circuitry of V1 and reflected in the discharge patterns of efferent neurons: (1) binocular convergence; (2) spatial frequency filtering; (3) pattern specific adaptation; (4) orientation and direction selectivity. For each visual hemifield V1 represents the first site of binocular convergence. With increasing distance from layer 4 the proportion of binocularly driven neurons increases in a manner suggesting independence of connectivity for orientation selectivity and ocular dominance (Poggio, 1972). Although the degree of orientation preference disparity, i. e. the amount to which the axis of orientation differs in the two eyes is small in primates, estimated to be  $4^{\circ}$  in the macaque monkey compared with  $9^{\circ}$  in the cat (Mansfield, Ronner and Daugman, 1980), there is also a binocular disparity in the retinal locus of receptive fields that probably serves a role in local stereopsis. Poggio and Fischer (1977) found that in the foveal striate projection region where receptive fields were small the majority of neurons were sensitive to location of stimuli in depth with the maximum discharge or shift in discharge occurring within  $\pm 0.4^{\circ}$  of disparity but the total range

of binocular interaction could extend to more than  $\pm 1^\circ$  of disparity. A second transformation that takes place is that the spatial frequency filtering present in the geniculate neurons becomes sharper (Poggio, Doty and Talbot, 1977; DeValois, Albrecht and Thorell, 1978). The third transformation is the adaptation or habituation of neural discharges to specific patterned stimuli (Mansfield, Ronner and Daugman, 1978) a feature not observed in the lateral geniculate (DeValois et al, 1978; Wiesel and Hubel, 1966; Schiller and Malpeli, 1978) but whose appearance at the cortical level reflects the initiation of a temporal filtering mechanism for visual salience and novelty. A fourth and major transformation is that instead of isotropic, concentrically organized receptive fields such as those found in the LGN the majority of striate neurons in the supragranular layers exhibit an orientation preference and are directionally selective (Hubel and Wiesel, 1968; Poggio, 1972; Dow and Gouras, 1973; Dow, 1974; Poggio et al, 1975; Schiller, Finlay and Volman, 1976a,b; Mansfield et al, 1980). From recent experiments quantitative estimates can be made of the population response characteristics in the efferent projection from V1.

#### C. Quantitative measurements of receptive field properties

In order to predict behavioral performance it is necessary first to know in quantitative detail the excitability profiles of the receptive fields of the efferent neurons in the supragranular layer and secondly to understand at least to a first approximation how the neural information is utilized in a particular behavioral task.

For the first problem the main obstacle is that of sample bias when recording from only a small proportion of neurons in the layers. One source of sample bias arises from the columnar organization for the attributes of orientation selectivity and ocular dominance (Hubel and Wiesel, 1968). The invariance of particular receptive field properties with cortical depth is a general principle of neocortical organization (Mountcastle, 1957; Mountcastle, 1978) probably reflecting the conservation of genetic information required for synaptic organization of the cortex using modular subunits. From the experimenter's point of view, however, microelectrode penetrations normal or nearly normal to the pial surface encounter neurons whose receptive field properties are not independent; oblique penetrations encounter similar problems of statistical dependence when the attributes like orientation selectivity exhibit sequential regularity (Hubel and Wiesel, 1974). One strategy for obtaining statistical independence is to count as a sample only a single neuron's receptive field (e.g. the first neuron encountered that could be studied) in a given penetration and to separate penetrations by at least some fixed distance (e.g. at a separation of 500 microns the mean serial correlation coefficient for orientation preference has dropped to chance levels) (Mansfield, 1974; Mansfield et al, 1980). A second potential source of sample bias with microelectrode penetrations is that the neurons with large cell somas will be more heavily weighted since their action potentials will be more easily isolated (Humphrey and Corrie, 1978). However, since the

neurons of interest are the pyramidal cells in layers 2-3 rather than the stellate cells such a bias will aid in selecting the population of interest. A third potential source of bias is the stochastic nature of the neuronal discharge; however, multiple and randomized stimulus presentation can provide objective, stable measures (Stryker and Sherk, 1975; Schiller, Finlay and Volman, 1976a; Mansfield et al, 1980). A fourth potential source of bias is that a particular choice of measure for neuronal discharge may not be relevant for further processing by the more rostral portions of the visual system; however, integrated discharge (pulse number) for brief stimulus presentations is a probable candidate code.

1) Excitability profiles

The majority of the receptive fields in the supra-granular layers of primate V1 have discharge characteristics resembling X cells in the geniculate but spatial characteristics of complex cells, i.e. a single activating region (Hubel and Wiesel, 1968; Poggio et al, 1975; Schiller et al, 1976a; Poggio et al, 1977; Mansfield et al, 1980). No receptive field type, e.g. simple cells, is distinguishable on the basis of receptive field size or breadth of orientation tuning (Schiller et al, 1976; Mansfield et al, 1980). At the descriptive level a central excitatory zone with flanking silent cortical inhibition of cortical origin is a first approximation.

2) Orientation tuning

As with orientation tuning curves in the cat when they have been examined in quantitative detail (Henry, Dreher and

Bishop, 1974), a symmetric bell-shaped curve provides an excellent fit to primate data as illustrated in Fig. 2 for a binocular cell.

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Insert Fig. 2 about here

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The shape of the orientation tuning curve does not change systematically with orientation preference or with retinal eccentricity at least between the central foveal projection ( $0-2^\circ$ ) (Mansfield et al, 1980) and parafoveal region ( $3-6^\circ$ ) (Schiller et al, 1976b; Mansfield et al, 1980) where it has been examined. However, as illustrated in Fig. 3 the distribution of tuning bandwidths (half-width at half-height)

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Insert Fig. 3 about here

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is broad but skewed toward the narrowly tuned neurons with a median near  $24^\circ$ , a value that is consistent across electrophysiological experiments (Schiller et al, 1976; Mansfield et al, 1980). One striking difference illustrated in Fig. 4 between foveal and parafoveal

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Insert Fig. 4 about here

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projection regions is that in the parafoveal projection region all orientations are equally represented (Hubel and Wiesel, 1968; Finlay, Schiller and Volman, 1976) but in the foveal projection region the horizontally and vertically selective receptive fields are over-represented (Mansfield, 1974; Mansfield and Ronner, 1978; Mansfield et al, 1980). The orientation anisotropy is probably innate and is not confined to primates (e.g. for the cat: Pettigrew, Nikara and Bishop, 1968; Levanthal and Hirsch, 1977; Kennedy and Orban, 1979; Orban and Vandenbussche, 1979).

### 3) Size or spatial frequency tuning

The size of receptive fields in the supragranular layers changes with two gradients. First the average size of receptive field increases with retinal eccentricity (Hubel and Wiesel, 1974). Second, the size of receptive field increases with distance from layer 4, the main input layer. So that at each location in the retinotopic projection there is a distribution of receptive field sizes. One method of quantifying the degree of size tuning of the cell is to measure the response of the cell to grating targets. When displayed along a log spatial frequency axis the response curves assume a shape that is approximately 1 - 2 octaves wide at half-maximal response (Schiller, Finlay and Volman, 1976c; Poggio et al, 1977) or at half-maximal sensitivity for a constant criterion response (DeValois, Albrecht and Thorell, 1978). The available samples of neurons from the supragranular layers for which optimal spatial frequency has been measured are relatively small but an approximation to the distribution is shown in Fig. 5. An additional factor is the degree to which neurons with

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Insert Fig. 5 about here

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different optimal spatial frequencies respond at their optimal frequency to contrast differences; however, there is essentially no quantitative data that can be brought to bear on this question.

### 4) Pattern-specific adaptation

A common observation is that neurons in the supragranular layers are difficult to activate repeatedly and habituate easily (Wurtz, 1969). The decrement in response is exponential with time and depends upon the cell's response, i.e. non-optimal stimulation does not produce habituation (Mansfield, Simmons and Daugman, 1979). The

exponential time constants vary across cells and are smaller for adaptation than for recovery in which case the average value is on the order of 10 sec. Direct synaptic activation of the supra-granular pyramidal cells produces habituation in vitro (Mansfield and Simmons, 1979) that follows a similar time scale for recovery.

5) Quantitative model of population response profile

In order to develop a computational theory of the function of the supragranular layers of V1 based on the population response profile, we need to consider first the excitation profile of a typical cortical receptive field in the supragranular layers; second, the local and global distribution of receptive field parameters; and finally a candidate algorithm for combining the neural output from V1 to produce a response.

i) Cortical receptive field excitation profile

The experimental studies reviewed above indicate that the cortical receptive fields in the supra-granular layers are shape-invariant with changes in preferred orientation and scale multiplicatively in the frequency domain. As a simplified but instructive approach to the question of the construction of a cortical receptive field, we can consider how the receptive fields at successive levels in the primate visual system are generated. For convenience, the on-center retinal ganglion X cell will be used as an example. The spatial domain weighting function describing the contributions of the photoreceptor input to the cell can be reasonably well approximated by a circularly symmetric Gaussian distribution, the expected limiting distribution as the number of photo-

receptors becomes large assuming isotropic and globally random connectivity. However, lateral inhibition is also contributed by the retinal circuitry and can be represented by the simplest isotropic form of spatial differentiation, the two-dimensional Laplacian operator,  $\nabla^2$ , defined as

$$\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} \quad (5.1)$$

or more simply as  $\frac{\partial^2}{\partial r^2}$  for circularly symmetric spatial functions in polar coordinates. The resulting excitation profile,  $E(r)$ , for the retinal ganglion cell is given by the equation

$$\nabla^2 G = \lambda \left( \frac{r^2}{a^2} - \frac{1}{2} \right) e^{-\left( \frac{r}{a} \right)^2} \quad (5.2)$$

representing central excitation with surround inhibition as depicted in Fig. 6. The profile is essentially similar to the empirically

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Insert Fig. 6 about here

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derived difference of Gaussians used by Enroth-Cugell and Robson (1966) to describe the structure of cat retinal ganglion cells. At the next level in the parvocellular layers of the lateral geniculate, the principal cells receive excitatory input from probably a very small number of retinal ganglion cells of the same type (on-center). No inhibition is directly transmitted but rather is supplied by inhibitory interneurons. The profiles would remain essentially isotropic and unchanged in shape except for stronger inhibition since the lateral inhibition is applied on the afferent side rather than on the efferent side. At the cortical level the geniculate input is probably exclusively excitatory and supragranular pyramidal cells probably receive direct monosynaptic contact from very few geniculate axons. Inhibition is supplied by di-synaptic or polysynaptic circuits. Since the intra-cortical inhibition is polysynaptic, the inhibitory subfields are

larger than the excitatory central zone as well as being slightly displaced. The inhibitory side lobes although silent could generate orientation selectivity and the width of the excitatory central zone could determine the optimal size or spatial frequency tuning for the cell. A second operation of lateral inhibition is suggested by the recurrent collaterals of pyramidal cells as are found elsewhere in the neocortex (Marin-Padilla, 1969; 1970) and by the difficulty in generating responses by electrical stimulation in the optic radiation below the cortex. Antidromic action potentials would serve to silence cellular activity by recurrent inhibition. Such pericolumnar inhibition as Mountcastle (1978) has described it would be by the sequential regularity of the orientation columns be directed orthogonal to the preferred orientation. Formally in terms of the simple theoretical receptive field profile described by Equation 5.2, the Laplacian operator takes the form  $\nabla_x^2$  if for convenient we let the y-axis be the axis of preferred orientation. When the operator is applied the equation for the receptive field profile becomes

$$\nabla_x^2 \nabla_y^2 G = \left[ \frac{8r^4 (\cos\theta)^2}{a^6} + r^2 \left( \frac{8(\cos\theta)^2}{a^6} - \frac{16r^2}{a^4} - \frac{4}{a^6} \right) + \frac{8}{a^4} \right] e^{-\left(\frac{r}{a}\right)^2} \quad (5.3)$$

The receptive field profile corresponding to Equation 5.3 is shown in Fig. 6. The pericolumnar inhibition would have the effect of sharpening orientation and frequency tuning.

## ii) Local and Global population parameters

At a given point in the cortex a typical receptive field can be described by an excitation profile such as that given by Equation 5.3. Such a receptive field then acts as a local spatial

filter with a particular center frequency and frequency bandwidth and preferred orientation and orientation bandwidth. Locally the center frequency is distributed as illustrated in Fig. 5, and the frequency bandwidths at half height are distributed in a small range between 1 and 2 octaves. Depending upon location the orientation preferences have distributions similar to those shown in Fig. 4, and the orientation bandwidths have a distribution similar to that in Fig. 3. More globally the distributions of orientation preferences and center frequencies change with retinal eccentricity. An important question is the degree to which orientation tuning and spatial frequency selectivity are interrelated. These two aspects appear to be functionally separable since orientation tuning bandwidth for supragranular neurons (Mansfield et al, 1980) or presumed supragranular neurons (Schiller et al, 1976b) does not appear to change with retinal eccentricity at least up to 20 degrees. On the other hand since receptive field size and center frequency are correlated; and bandwidth is roughly proportional to center frequency (1-2 octaves); and center frequency shifts with retinal eccentricity (Schiller et al, 1976c) there is a change in absolute bandwidth with retinal eccentricity. A deeper question is how the population response profile information is utilized for a particular task.

### iii) Detection mechanisms

The ensemble of supragranular pyramidal neurons forms an input array to the rest of the visual system that carries the necessary and sufficient information for optimal acuity performance. If  $I(x,y)$  denotes the luminance distribution in the retinal image, then the neural response of a particular class of orientation selective neurons at the corresponding retinotopic point,  $N_{\theta,f}(x,y)$  is given by the equation

$$N_{\theta,f}(x,y) = S[I(x,y)] \quad (5.4)$$

where  $S$  is the visual system operator. The operator can be considered to be linear if the input to the neurons is exclusively from  $X$  cells since by definition they respond linearly. The luminance distribution can be written in terms of the Dirac delta function,  $\delta(x - \xi, y - \eta)$ , as follows

$$I(x,y) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} I(\xi,\eta) \delta(x - \xi, y - \eta) d\xi d\eta \quad (5.5)$$

Then substituting this definition of  $I(x,y)$  in Equation 5.4 and using the linearity of the  $S$  operator since the input to the supragranular layers is dominated by  $X$ -cell input, we obtain

$$N_{\theta,f}(x,y) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} I(\xi,\eta) S[\delta(x - \xi, y - \eta)] d\xi d\eta \quad (5.6)$$

But the operation of  $S$  on the delta functions is simply to produce spatial filter functions  $h(x,y;\xi,\eta,\theta)$  which correspond to the excitatory profiles previously discussed so that

$$N_{\theta,f}(x,y) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} I(\xi,\eta) h(x - \xi, y - \eta, \xi, \eta, \theta) d\xi d\eta \quad (5.7)$$

That is to say the response of the neurons, the integrated discharge, is the convolution of the luminance distribution with the excitatory profile of the receptive field. Such detailed considerations based upon the present limited knowledge of synaptic circuitry in the central visual system cannot be extended with confidence beyond the striate cortex. How then can visual behavior be dealt with in a predictive quantitative manner: by choosing a visual task that requires optimal performance such as visual acuity and by considering what an optimal information processing system can do given the

output array from V1. As will be seen optimal or near optimal detection can be carried out by at least two neurally realizable mechanisms shown schematically in Fig. 7.

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Insert Fig. 7 about here

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In discussing the detection process involved in visual acuity we need to consider the issues of the independence of noise in different neural channels, the coherence or incoherence of the detection and the nature of the optimal detection mechanism. An important theorem of stochastic processes (Cinlar, 1972) states that the sum of point processes that are Poisson is itself Poisson. For this reason, the simplest random process, a Poisson process is a good first approximation to the stochastic nature of impulse trains for cortical neurons when suitably corrected for refractoriness which is intrinsic to neural activity (Teich and McGill, 1976; Teich, Martin and Cantor, 1978). On the other hand, the very multiplicity of sources guarantees the statistical independence of the noise in different channels, i.e. the noise is uncorrelated. On the issue of coherence of the detection process, the question is whether phase information between channels tuned to the same spatial frequency but at different retinotopic locations is preserved. With a coherent detector spatial frequency bandwidth and spatial summation area are inversely related but with an incoherent detector the two are independent. The studies of receptive fields in the more rostral portions of the visual system indicate that the fields are large but in general do not show correspondingly specific spatial frequency tuning so incoherent detection is the most likely form. In order to detect a pattern of interest presented to the retina the central mechanisms can be considered to monitor the output of  $M$  orthogonal channels and perform a decision process that is independent of spatial phase except locally. Optimal

detection arises from the application of the Neyman-Pearson criterion which maximizes the probability of detection with the probability of a false alarm constrained to a particular value as described by the theory of signal detectability (Peterson, Birdsall and Fox, 1954; Green and Swets, 1966). The general decision rule can be stated in terms of likelihood ratios but for a Poisson noise-counting distribution the decision rule reduces to a simple comparison of a pulse count to a criterion number of pulses, a threshold process readily realizable in terms of known neural mechanisms. In the case of small signals, the optimal detector is closely approximated by a multi-band detector, i.e. one that simply compares the sum of the outputs of the M channels to a criterion level (Cohn, 1978). Moreover, the optimal detector is also closely approximated by another suboptimal detector, one in which detection occurs if the activity in at least one channel exceeds a threshold (Nolte and Jaarsma, 1967; Green and Weber, 1980). Such a probability summation detector is readily realizable as a neural OR-gate and is computationally particularly convenient. The detection process in a visual acuity task then can be conceptualized in terms of a set of orthogonal spatial filters with uncorrelated Poisson noise followed by an incoherent but quasi-optimal detector.

#### IV. Behavioral Experiments

Behavioral performance reflects organized cellular, mainly neural, activity and for a detailed understanding requires precise information about the underlying neural activity. However, optimal performance can be considered within the context of a computational theory without complete information of all neural activity but rather

only the neural activity that sets constraints on optimality. In the case of simple visual acuity optimal performance is constrained by the spatial filtering carried out by the cortical receptive fields in the supragranular layers of V1. A comparison can be made between experimentally determined spatial visual acuity and the predictions of a computational theory based on an optimal incoherent detector constrained by M linear orthogonal spatial filters having characteristics like the cortical receptive fields for a particular set of stimulus conditions. However, there is a developing consensus that such a computational theory can be extended to a wide class of stimuli.

#### A. Comparisons under stabilized viewing

The close correspondence in behavioral capacity among Old World anthropoids makes possible the comparison of visual performance in man with predictions from a computational theory based upon neural parameters derived mainly from the macaque monkey. Visual acuity assessed by contrast sensitivity functions is essentially identical in man and macaque monkey when measured under the same stimulus conditions (DeValois, Morgan, and Snodderly, 1974). For oriented grating targets the cross-species similarity assumption for neural mechanisms is quite plausible but the experimental conditions under which the neural data were collected must be carefully considered.

Precise assessment of single unit receptive fields necessitated the control of eye movements typically by immobilizing the ocular and skeletal musculature with a curare-like drug, gallamine triethiodide (Schiller et al, 1976a; Mansfield et al, 1980). Even with drug-induced paralysis of the neuromuscular synaptic transmission there is some residual eye movement but it is on the order of only  $0.1^{\circ}$  over the

course of 10 minutes. Similar drug-induced paralysis in human observers results in a reduction in apparent contrast so that large uniformly illuminated objects disappear and edges fade (Stevens, Emerson, Gerstein, Kallos, Neufeld, Nichols and Rosenquist, 1976), a phenomenon observed in normal vision for peripheral targets viewed with steady eccentric fixation under dim illumination. Such Troxler fading is confined to the periphery since the small eye movements present in steady fixation are small relative to the dimensions of the receptive fields engaged by the stimulus. Steady fixation with foveal viewing does not achieve the same result since even in the best normal observers the direction of gaze about a fixated target is erratic having a mean radius of about  $0.1^{\circ}$  and microsaccades are not suppressed (Higgins, Daugman, and Mansfield, 1980). In order to examine visual performance under comparable conditions to the neurophysiological experiments in "any detailed psychophysical task would have required hours of total paralysis - a very unrealistic requirement" (Stevens et al, 1976). An alternate means of achieving retinal image stabilization is to compensate optically for image motion on the surface of the retina.

The conventional approach developed twenty five years ago involves the use of a contact lens either with a mirror attached to form one arm of an optical lever (Riggs, Ratliff, Cornsweet and Cornsweet, 1953) or to carry a miniature projector (Ditchburn and Pritchard, 1956). These methods, however, are limited both in the range of stimuli that can be presented and in the ease with which extended and detailed observations can be made in several observers because of the specially fitted scleral contact lenses involved. Recent innovations in the methods of accurate eyetracking which do not require physical contact

have set the stage for a new technique of retinal image stabilization.

The approach uses infrared light reflected from the eye to determine eye position. As shown schematically in Fig. 8 the novel feature is that the

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Insert Fig. 8 about here

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SRI Dual Purkinje Image Eyetracker monitors infrared reflections from both the cornea (1st Purkinje image) and the back of the lens (4th Purkinje image) (Cornsweet and Crane, 1973; Clark, 1975). By measuring the optical distance between the two images, the eyetracker achieves an accuracy of greater than 1' of arc. Such a high degree of accuracy suggested to B. R. Wooten of Brown University the possibility of developing a means of retinal image stabilization without contact lenses. In the Wooten modification a pair of fast response (1-2 msec risetime) galvanometer driven mirrors use the horizontal and vertical eye movement signals of the eyetracker to compensate optically for movement of the stimulus across the retina resulting from eye movements.

Figure 9 shows an observer in the apparatus and a typical stimulus pattern

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Insert Fig. 9 about here

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on the display oscilloscope. The observer views the target monocularly and holds his head steady by means of a hard wax bite bar. Typically mydriatic and cycloplegic drugs are used to maintain the pupil at maximal dilation and the lens in a relaxed state of accommodation. A television-like raster scan on the face of the display oscilloscope can be readily produced by waveform generators to yield a uniformly illuminated surface. The voltage on the Z-axis of the oscilloscope can be modulated in phase with each frame of the scan to produce patterns on the display face using electronic hardware for simple sinusoidal patterns or digital to analog read-out from a computer for more complex patterns.

The choice of a target stimulus with which to probe the visual system and test the range of validity of the computational theory

outlined above depends upon several characteristics of the primate visual system. By using low contrast patterns the response remains in the linear range. By choosing patterns with a small spatial extent a piece-wise isoplanatic approximation can be made to retinal inhomogeneity. A sinusoidally-modulated luminance grating such as that shown in Fig. 9B is easily generated and controlled and can be used to determine the frequency response which is related to the line-spread function by a Fourier transform. The case of foveal vision is of particular interest and Fig. 10 shows three results

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Insert Fig. 10 about here

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obtained for a small grating patch centered at the fovea ( $\pm 1^\circ$ ) surrounded by a broad border of approximately equal luminance to eliminate edge effects which could swamp the response of interest. Temporal transients also are avoided by the use of a relatively long display period.

The basic datum consists of an observer's contrast threshold setting but each data point is typically based on several observations to obtain an accurate average. Fig. 10A displays detection threshold as a function of target orientation for a grating of relatively high spatial frequency. The solid line drawn through the data points is the prediction from the computational theory scaled to the sensitivity level of the observer. The results show how the orientation anisotropy present in the neuronal population translates into a difference in the detectability of targets at different orientations. These results are generalized in Fig. 10B which shows detection threshold as a function of spatial frequency of the grating target for both a vertical and an oblique angle ( $45^\circ$ ). The solid line is again the theoretical prediction from computation. At low spatial frequencies the sensitivity is depressed beyond that inherent in the frequency response of the

central fovea because the limited number of grating cycles present in the small  $2^\circ$  target decreases the optimization of detection produced by the information pooling that can take place when multiple bars are present. However, the convergence of the vertical and oblique sensitivities reflects the dominance of the response by the Y cells which do not exhibit orientation anisotropy. The effect on detection threshold of prior exposure to a high contrast grating target is shown in Fig. 10C. The solid line represents the theoretical curve generated from the computational theory by taking the difference in the pooled neural response before and after adaptation. The selective elevation of threshold reflects the orientation selective nature of the pattern adaptation. Since the pooling operation in effect averages over the spectrum of orientation tuning curves the resulting curve resembles the tuning curve of the average receptive field.

#### B. Implications for pattern detection

There is accumulating evidence that the detection of a wide class of monochromatic patterned stimuli can be explained by a computational theory based on quasi-optimal incoherent detection applied to the output of an array of independent channels whose medium bandwidth filter characteristics resemble the receptive field excitatory profiles of efferent neurons in the supragranular layers of V1. Incoherent detection is consistent with the localized effects of pattern adaptation. Previous work from this laboratory (Legge, 1976) demonstrated that the adaptation is retinotopically localized. Legge found that adaptation to a high contrast fine line did not affect subsequent detection of spatially extended sinusoidally modulated grating patterns as would be predicted if the effect of

adaptation were local rather than global. Daugman and Mansfield (1979) found that the adaptation is not even transferred interhemispherically since no adaptation is produced by an eccentric high contrast grating patch placed in the homologous location in the opposite hemifield. Graham and her colleagues (Graham and Nachmias, 1971; Graham, Robson and Nachmias, 1978) have demonstrated independence of detection of separate components in a compound grating even when presented to a relatively homogeneous retinal region, a result consistent with the existence of independent channels. Variation with retinal eccentricity of several measures such as visual acuity (Aulhorn and Harms, 1972), summation area (Westheimer, 1967), Mach band locations (Shipley and Wier, 1972), contrast sensitivity functions (Hilz and Cavonius, 1974), and line spread functions (Hines, 1976; Limb and Rubinstein, 1977; Wilson, 1978) are consistent with an increase in receptive field size with distance from the fixation point. The work from Wilson's laboratory in particular suggests that the increase is linear at least up to  $4^{\circ}$ . The scatter in receptive field sizes and types at a given retinotopic projection point is reflected in the differences in detectability of different patterns presented at the same retinal locus (Kulikowski and King-Smith, 1973; Wilson and Geise, 1977). Experiments with frequency gradient patterns (Wilson and Geise, 1977) and with artificial central scotomas (Kelly, 1978) indicate that all receptive field sizes are represented in the foveal projection region but that there is a decline in the relative proportion of small receptive fields with retinal eccentricity. On the important issue of the estimate of the spatial frequency bandwidth of the receptive fields a growing consensus indicates that although several studies have been interpreted as implying extremely narrow bandwidths (1/4 octave)

(Sachs, Nachmias and Robson, 1971; Kulikowski and King-Smith, 1973; Quick and Riechert, 1975) subsequent work has shown that if an incoherent detection process such as probability summation across space is taken into account the data are consistent with medium bandwidths (Mostafavi and Sakrison, 1976; Stromeyer and Klein, 1975; Graham and Rogowitz, 1976; King-Smith and Kulikowski, 1975; Wilson, 1978; Wilson and Bergen, 1979; Bergen, Wilson and Cowan, 1979). The bandwidth estimates range from 1.5 to 2.1 octaves at half-height. The data of Blakemore and Campbell (1969) obtained using spatially selective frequency adaptation yields an estimate of 1.5 octaves full bandwidth at half-height but retinal inhomogeneity and probability summation are not taken into account resulting in an underestimation. Mostafavi and Sakrison (1976) obtained an estimate of 2.1 octaves using band-limited noise displays taking into account retinal inhomogeneity and spatial probability summation but not summation over channels resulting in an overestimation. Wilson and his colleagues (Wilson, 1978; Wilson and Bergen, 1979; Bergen, Wilson, and Cowan, 1979) using subthreshold summation to determine the line-spread function found 1.75 octaves taking into account spatial probability summation over channels and space. The monkey neurophysiology data as described earlier yields estimates of 1 - 2 octaves (Schiller et al, 1976c; Poggio et al, 1977; DeValois et al, 1978). De Valois et al's measurements made under conditions comparable to the psychophysical measurements gave a median value of 1.4 octaves and 1.2 octaves for the more orientation selective neurons. A similar situation holds for orientation selectivity. Early studies particularly those that employed subthreshold summation, e.g. Kulikowski, Abadi and King-Smith (1973) were interpreted as evidence for extremely narrow orientation bandwidths. e.g.  $\pm 3^\circ$ . Other measurement procedures using adaptation

(Blakemore and Nachmias, 1971) and masking (Campbell and Kulikowski, 1966) gave estimates of  $\pm 7^\circ$  to  $\pm 15^\circ$ . However, these studies did not take into account spatial probability summation. By taking spatial probability summation into account the data from subthreshold summation experiments are consistent with orientation bandwidths on the order of  $\pm 16^\circ$ . Mostafavi and Sakrison (1976) using two dimensional filtered noise and assuming a Gaussian shape, retinal inhomogeneity and a spatial probability summation index of 6 obtained an orientation bandwidth of  $\pm 14.4^\circ$ ; however, they did not take into account summation across channels or orientation anisotropy. As we have seen taking into account spatial probability summation, orientation anisotropy and probability summation across channels yields an estimate of  $\pm 20^\circ$  (see Fig. 10C). The neurophysiological data uniformly concur on an estimate of average bandwidth of  $\pm 20^\circ$  to  $\pm 25^\circ$  (Schiller et al, 1976b; Poggio et al, 1977; DeValois et al, 1978; Mansfield et al, 1980). The concordance of results from behavioral and neurophysiological studies particularly regarding orientation and frequency bandwidths carries a number of implications for visual processing. For example, the view that the visual system performs some type of Fourier analysis on a visual scene (Campbell and Robson, 1968; Blakemore and Campbell, 1969; Pollen, Lee and Taylor, 1971) is oversimplified at best since the channel bandwidths are too broad. The apparent sharp tuning is the result of the statistical nature of the incoherent detection process. On the other hand an alternative view consistent with experimental facts reviewed here is that the visual system analyzes target objects using an ensemble of medium bandwidth spatial filters whose characteristics match those of the receptive fields of supragranular striate cortical neurons.

### V. Future Prospects

The development of a truly computational theory of primate vision is an exciting prospect but one that can be realistically approached. Two guiding principles have emerged from the studies reviewed here. First the primate visual system is organized in terms of functionally significant channels. Secondly optimal visual performance can be analyzed into a critical transformation site and optimal utilization of the information from that site. The filtering operations performed by the visual system up to the level of the striate cortex and by the striate cortex itself give rise to a filtered neural image of the retinal stimulus represented by the population response profile of the efferent neurons, the trans-cortical projection of which consists of the pyramidal cells in the supragranular layers. This neural image contains all the fine grain information available to the more rostral portions of the visual system which operate upon the information in a manner similar to a noncoherent optimal detector. In the detailed example the stimuli were stationary, low contrast, monochromatic, monocularly presented targets and the task was one of detection. Each of these restrictions can be lifted or modified.

The neurons in the supragranular layers respond differentially to direction of target motion, but no quantitative comparison has been made with the directionally sensitive mechanisms revealed by prior adaptation in psychophysical experiments. One experimental finding which makes reasonable the suggestion that these neurons mediate the detection of target direction is that target detection is superior to detection of direction of motion even in the absence of eye movements achieved using retinal image stabilization

(Mansfield and Nachmias, 1980), a result consistent with the dominance of X-input over Y-input into these layers. Although the simplest cases to analyze are those at threshold, linearity extends about that level (Mansfield, 1976a). Indeed as Cannon (1979) has shown the entire contrast sensitivity curve remains parallel to those generated from equal apparent contrast up to at least a 70% contrast ratio. At suprathreshold levels in the linear range, the spatial filtering imposed by the striate cortex has predictable but not intuitively obvious consequences such as the distortions from veridicality epitomized by the familiar optical illusions (Ginsburg, 1979) or, for instance, the spatial distribution of eye saccades and fixations in free viewing of even a complex target such as a face (Ginsburg, Mansfield and Higgins, 1980). Saccadic eye movements also induce an adaptive suppression of retinal blur by masking that is spatially frequency tuned and can be modelled in terms of inhibitory interactions between fast and slow responding spatial filters (Breitmeyer and Ganz, 1976; Rogowitz, 1980). Within the same conceptual framework, binocular interactions such as interocular adaptation and masking or even local stereopsis can be usefully analyzed in terms of striate neuronal activity. On the other hand, successful extension of the approach of the cellular synthesis of behavior described here to more complex visual perceptual and visuomotor behaviors such as global stereopsis, object color determination and object tracking will require a more detailed understanding of the primate visual system particularly of regions beyond V1.

The basis for a new and detailed understanding of the primate extrastriate cortex will rest on three developments in cellular and behavioral neurobiology. First, information on

the general functional subdivision of labor among the different regions. A recurrent theme of the chapters in this volume is the existence of visual subsystems, and a premier goal of behavior analysis must be that of fractionating an animal's repertoire into units that optimally engage a particular subsystem. Insights into causal sequences in the dynamic unfolding of a behavioral script are now possible with single and multi-unit recording from alert animals in well defined behavioral tasks with eye movements closely monitored (e.g. the study by Lynch, Mountcastle, Talbot and Yin (1977) of the initiation and control of visual grasping of an object of motivational significance). On the other hand, anatomical labelling of a subsystem by its elevated metabolic activity when engaged can be accomplished by using  $^3\text{H}$ - or  $^{14}\text{C}$ -2 deoxyglucose which accumulates in cells since it does not substitute for glucose beyond a certain point in the Krebs cycle (for example, Frost (this volume) using this technique has localized the region of a pigeon's brain dealing with relative motion). In the living animal positron emission transverse tomography will soon both supplement the resolution of metabolic activity on the cortical surface now possible with gamma emission and provide resolution in three dimensions eventually down to the millimeter level. Secondly, an extensive knowledge of the interconnections between cortical regions and the interactions with subcortical structures. Area V1 is the simplest visual cortical area in terms of its connections and yet it is reciprocally interconnected with at least four other structures: dLGN, the pulvinar complex, and Areas V1 and MT. Although

connections can sometimes be inferred from disconnection syndromes produced by lesions, such an approach, applied to a distributed processing system such as the visual system, particularly in advance of anatomical investigations, can frequently yield paradoxical results (see chapters by Dean and by Levine for a discussion of such inferences for infero-temporal lesions). Fortunately, recent advances in neuroanatomical labelling by axonal transport have brought this question within the range of experimental analysis so that precise information is accumulating (see Van Essen (1979) for an excellent recent review). Since the function played by a particular region is determined not only by the intrinsic operations it performs but by the pattern of its afferents and efferents in the circuit of which it forms a part, even a first approximation to the necessary circuit diagram such as the one illustrated in Fig. 1A provides a rational basis for identifying functional subsystems (see the chapter by Ungerleider and Mishkin discussing two cortical visual subsystems: one terminated by the infero-temporal region TE and the second by the inferior parietal lobule, area PG). Thirdly, an understanding at the synaptic level of the functioning of cortical columns, the modules of organization of the neocortex. Although a connectional diagram even as detailed as Fig. 1B together with recording and lesion studies can illuminate the role of a particular region, for example that of the striate cortex as a preprocessor of object information but the mechanism by which the cortex operates upon its afferent input requires a more fine grain analysis. As Mountcastle (1976) points out: "the central problem of the

intrinsic physiology of the cerebral cortex is to discover the nature of the neuronal processing within the translaminar chains of interconnected cells (in columns)." Techniques are now available to determine the synaptic circuitry of morphologically identified neurons in functional modules of neocortex using in vitro recording from brain slices (Mansfield and Simmons, 1979; Mansfield, in preparation). Anatomical and physiological evidence (see review by Mountcastle, 1978) suggests that cortical modules may have a unitary organization so that detailed knowledge of the synaptic organization in one cortical region could serve as a paradigm for the cortex as a whole. The present and continuing challenge will be to synthesize the results from these three lines of development into a coherent computational theory of visual behavior.

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Zeki, S. M., 1971. Convergent input from the striate cortex (area 17) to the cortex of the superior temporal sulcus in the rhesus monkey. Brain Research, 28:338-340.

Figure Captions

Figure 1. Anatomical organization of the primate visual system.

Nomenclature: R is the retina; X, Y, W designate the axons of three classes of ganglion cells or at the geniculate the projections to and from the parvocellular and magnocellular layers, see Fig. 1B; DLGN is the dorsal lateral geniculate nucleus; PT is the pretectum; SC is the superior colliculus; PL is the lateral pulvinar; PI is the inferior pulvinar; V1 is the striate cortex; V2 etc. are the prestriate visual areas (See Van Essen, 1979); IT is the inferotemporal cortex (cytoarchitectonic areas TEO and TE of von Bonin and Bailey); FEF are the frontal eye fields in the region of the arcuate sulcus consisting of cytoarchitectonic areas 8A, 8B and posterior 9 in the terminology of Brodmann; MT is a region at the posterior end of the temporal sulcus described as the visual area of the superior temporal sulcus by Zeki (1971) but probably homologous to the middle temporal area in the owl monkey; IPS(OA) is a region delineated by Ungerleider and Mishkin (this volume) using anterograde transport from V1 of radioactive amino acids in area OA (von Bonin and Bailey) at the depth of the posterior extent of the intraparietal sulcus; IPS(PG) is a region delineated by Mesulam, van Hoesen, Pandya and Geschwind (1977) using retrograde transport of horseradish peroxidase from PG and is located in the intraparietal sulcus anterior to IPS(OA); TF is a region described by von Bonin and Bailey on the medial surface of

the temporal lobe adjacent to TE and OA; IPL(PG) is the region PG described by von Bonin and Bailey on the inferior parietal lobule and corresponds approximately to the posterior half of area 7 of Brodmann.

- A. Schematic representation of the main structures showing the principal pathways with arrows indicating the direction of flow of information and control. For clarity of presentation only ipsilateral connections have been shown and the detailed structure of the limbic and motor systems and that of the prestriate visual cortical field has been omitted. For purposes of this diagram area 6a $\beta$ , premotor cortex, which receives a projection from area 9p in FEF is included in the motor system along with the pons (which receives input from IPL(PG), MT and intervening regions (Glickstein, Cohen, Dixon, Gibson, Holland, Labossie and Farrel, 1980)) and the interstitial nucleus of Cajal (which receives input from the superior colliculus). Major sources of evidence for the newly described projections in the cortical visual field: projections to IPL(PG) are based on Mesulam et al. (1977) and Divac, LaVail, Rakic and Winston (1977); projections to and from limbic system based on Nauta and Domesick (1980); projection from motor system to visual cortical field based on Johnston, McKinney and Coyle (1979); projections from FEF (areas 8 and 9p) based on Kunzle and Akert (1977) and Kunzle (1978); projection to IPS(OA) based on Ungerleider and Mishkin (this volume); connections to and from VI based on Lund et al. (1975). The dashed

rectangles indicate structures whose substructures are not indicated or not known in detail, e.g. prestriate visual areas. Arrows to dashed rectangles indicate projections to more than one substructure; arrows from such rectangles indicate projections from more than one substructure.

B. Schematic representation of the main structures in the retino-cortical pathways with arrows indicating the direction of information flow. For clarity of presentation only the connections from one hemi-retina and to one hemisphere are shown. The brackets on the left-hand side of the lateral geniculate nucleus indicate feedback distributed over the parvocellular (upper bracket) or magnocellular (lower bracket) layers. Major sources of evidence: for the existence and distribution of X, Y and W type retinal ganglion cells (DeMonasterio, 1978a, 1978b; Schiller and Malpeli, 1977); for the projections from retina to superior colliculus and pretectum (Schiller and Malpeli, 1977; Bunt, Hendrickson, Lund, Lund and Fuchs, 1975); for the connections from retina to dorsal lateral geniculate nucleus (Dreher, Fukada and Rodieck, 1976; Schiller and Malpeli, 1978); for the projections from geniculate to striate cortex (Hubel and Wiesel, 1972; Rezak and Benevento, 1979); for the projections from striate cortex to cortical and subcortical structures (Lund et al., 1975; Van Essen, 1979; Maunsell, Bixby and Van Essen, 1979; Ogren and Hendrickson, 1976; Rezak and Benevento, 1979); for feedback connections to

striate cortex (Van Essen, 1979; Ogren and Hendrickson, 1977; Wong-Riley, 1979); for connections among superior colliculus, pretectum and their projections (Benevento and Fallon, 1975; Rezak and Benevento, 1977; Berman, 1977 (cat); Benevento, 1980); for feedback from V2 and MT to geniculate (Lin and Kaas, 1977 (owl monkey)).

C. Schematic diagram of anatomically segregated visual processing in striate cortex (after Mansfield, 1979).

Figure 2. Orientation selectivity in binocular bidirectional striate neuron in monkey. (After Mansfield et al., 1980)

- A. Anatomical reconstruction of microelectrode track. On the left side of the diagram the nomenclature for each distinguishable lamina of the striate cortex is indicated. The solid black circles represent the locations of 4 marking electrolytic lesions. The short line segments perpendicular to the solid line marking the track represent the recording sites of isolated single units. The solid black arrow indicates the recording site of Unit 8T107 described more fully in Figures 2B and 2C.
- B. Receptive field map and response profile. The solid black rectangle represents the minimal discharge receptive field of the neuron in the right visual hemifield. The receptive field measured  $1/2^\circ$  by  $1^\circ$  and was located approximately  $6^\circ$  from the fovea. Arranged around the receptive field map are peristimulus discharge histograms generated by a long slit subtending  $0.1^\circ$  in width moved through the discharge zone at a velocity of  $5.6^\circ/\text{sec}$  at the orientation indicated. Each peristimulus histogram is based upon 15 stimulus presentations.
- C. Orientation tuning curves. Integrated discharge as a function of target slit orientation. Each data point is the average calculated from

15 stimulus presentations. The solid squares represent the responses from the receptive field in the right eye; the open circles represent the responses from the receptive field in the left eye. The error bars represent  $\pm$  one standard error of the mean integrated discharge. The solid lines fitted to the data points represent theoretical functions for orientation tuning derived from a simple model of orientation determination.

(Modified from Mansfield, Ronner and Daugman (1980)).

Figure 3. Frequency distribution of orientation selectivity in striate neurons. Orientation selectivity was measured as the half-bandwidth at half-maximal response on an orientation tuning curve as shown in the insert. The measurements were obtained from 96 independently sampled neurons. (From Mansfield et al (1980)).

Figure 4. Distribution of axes of orientation preference for striate cortical neurons. Each neuron was sampled from a single penetration with multiple penetrations separated by at least 500  $\mu$ m across the cortical surface.

A. Polar histogram of distribution for receptive fields of independently sampled neurons with foveal receptive fields. (N=82). The deviation from uniformity is statistically significant ( $\chi^2 = 15.94$ ,  $df = 8$ ;  $p < 0.05$ ).

- B. Polar histogram of distribution of independently sampled neurons with parafoveal receptive fields ( $N = 128$ ). The Chi-squared test for departure from a uniform distribution was not significant at the 5% level ( $\chi^2 = 1.66$ ,  $df = 8$ ;  $p > 0.5$ ). (From Mansfield et al (1980)).

Figure 5. Frequency distribution of optimal spatial frequency of striate cortical neurons in the foveal and parafoveal projection regions. The curve to the left represents the parafoveal striate neurons from the projection region  $4^\circ$ - $6^\circ$  from the fovea. The curve to the right represents the foveal striate neurons from the projection region covering the central  $2^\circ$ .

Figure 6. Schematic diagram of a candidate mechanism for receptive field organization of supragranular neurons.

- A. Excitatory profile generated by retinal lateral inhibition.
- B. Candidate neural network in supragranular region of striate cortex exhibiting recurrent lateral inhibition.
- C. Excitatory profile generated by operating on profile in A. by neural network in B.

Figure 7. Schematic diagram of two quasi-optimal neurally realizable pattern detector mechanisms.

- A. Pooling detector. In this case the luminance corresponding to the visual stimulus distribution is processed by linear spatial filters and the responses of the filters summed or pooled in a detector which responds if the combined input exceeds some criterion level. For clarity of presentation the independent noise sources for the spatial filters have been omitted.
- B. Probability summation detector. In this case the luminance distribution corresponding to the visual stimulus is processed by linear spatial filters but the response of each is handled by an independent detector which responds if the input exceeds a criterion level. So the action of the effector depends on the action of one or more of the detectors. For clarity of presentation the independent noise sources for the spatial filters have been omitted.

Figure 8. Schematic diagram of Dual Purkinje Eyetracker and Retinal Image Stabilization System. In determining eye position, a low intensity invisible beam of infrared light from a light emitting diode is reflected from the eye and the images of the first Purkinje image (corneal reflection) and fourth Purkinje image (posterior surface of the lens) are separately focussed on quadrature photodetectors. The error signals from the quadrature photodetectors drive mirrors in the optical path via servo motors. The output of the second quadrature photodetector (fourth Purkinje

image) then corresponds to the difference between the first and fourth Purkinje images, a measure of eye position that is relatively invariant under lateral movement of the head. For retinal image stabilization the eye position signal is used to operate galvanometer driven mirrors in the optical path of the viewer which compensate for vertical and horizontal eye movements by appropriate movements of the visual target, a computer-controlled video display on a CRT. Independent of the stabilization a set of visible LEDs serve as fixation targets. In addition the observer's responses are accessible to the computer and can be used in interactive psychophysical procedures.

- Figure 9. A. Photograph of observer viewing target under retinal image stabilization by using the outputs of the SRI Dual Purkinje Image Eyetracker to drive small mirrors on the Stimulus Deflector seen in the foreground.
- B. Photograph of target on CRT at high contrast.

- Figure 10. Comparison of calculated response from synthesized striate neuron population with human psychophysical data on orientation acuity. The theoretical curves have been scaled in amplitude to fit best the experimental data.
- A. Detection threshold as a function of target orientation for a 8 cycle/degree sinusoidally modulated luminance grating subtending  $2^\circ$  foveally. The circles represent the data points; the solid line represents the computed values.
- B. Detection threshold as a function of grating spatial frequency. The circles represent the data points for the vertical target; the squares represent the data

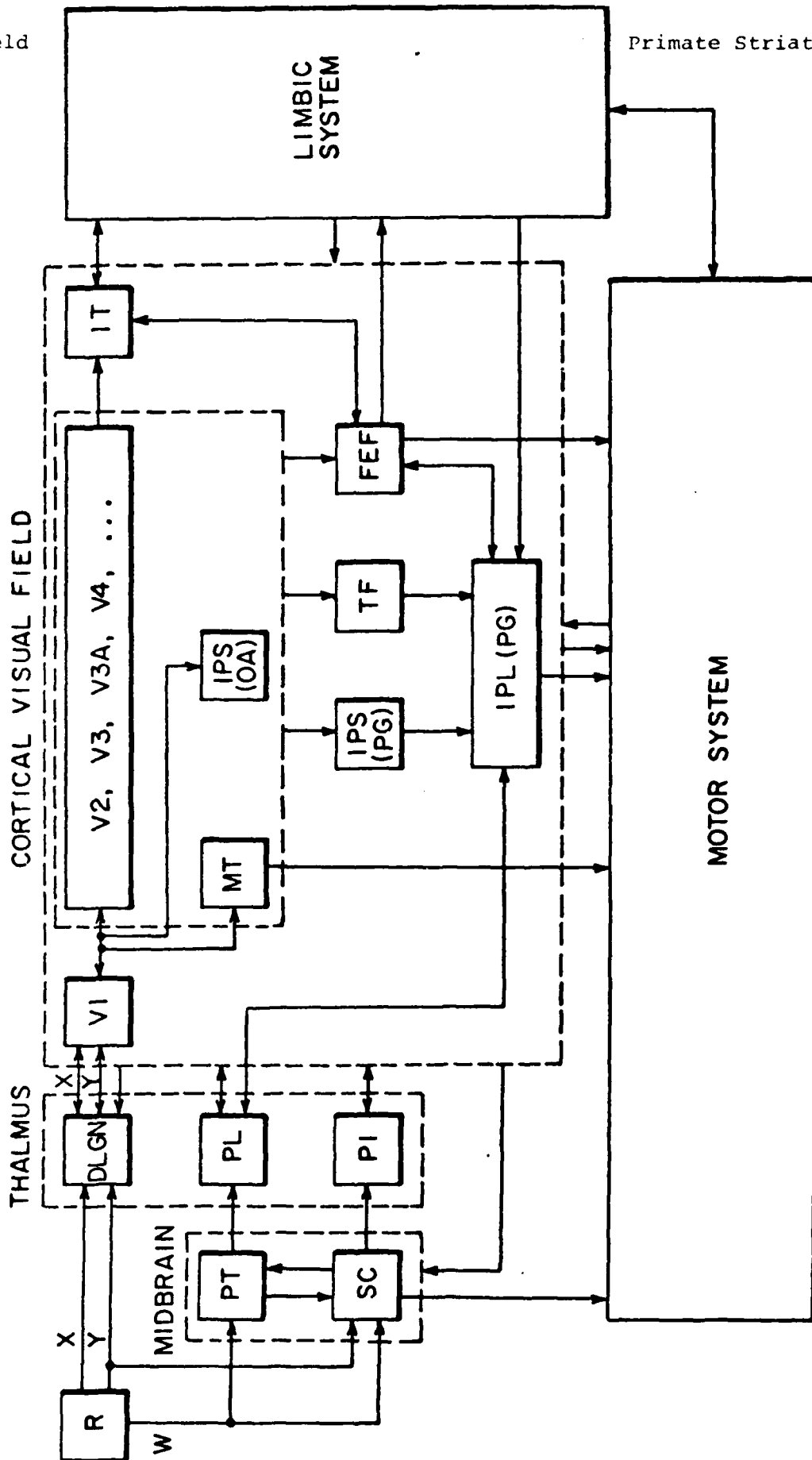
for the oblique ( $45^\circ$ ) target. The solid lines represent the computed values.

- C. Detection threshold elevation following adaptation to 8 cycle per degree grating subtending  $2^\circ$  foveally. The squares represent the data obtained with adaptation and testing in the same eye. The x's represent the data obtained with testing in the contralateral eye. The solid curve represents the computed values with adaptation proportional to neural response.

A

# PRIMATE VISUAL SYSTEM

Mansfield

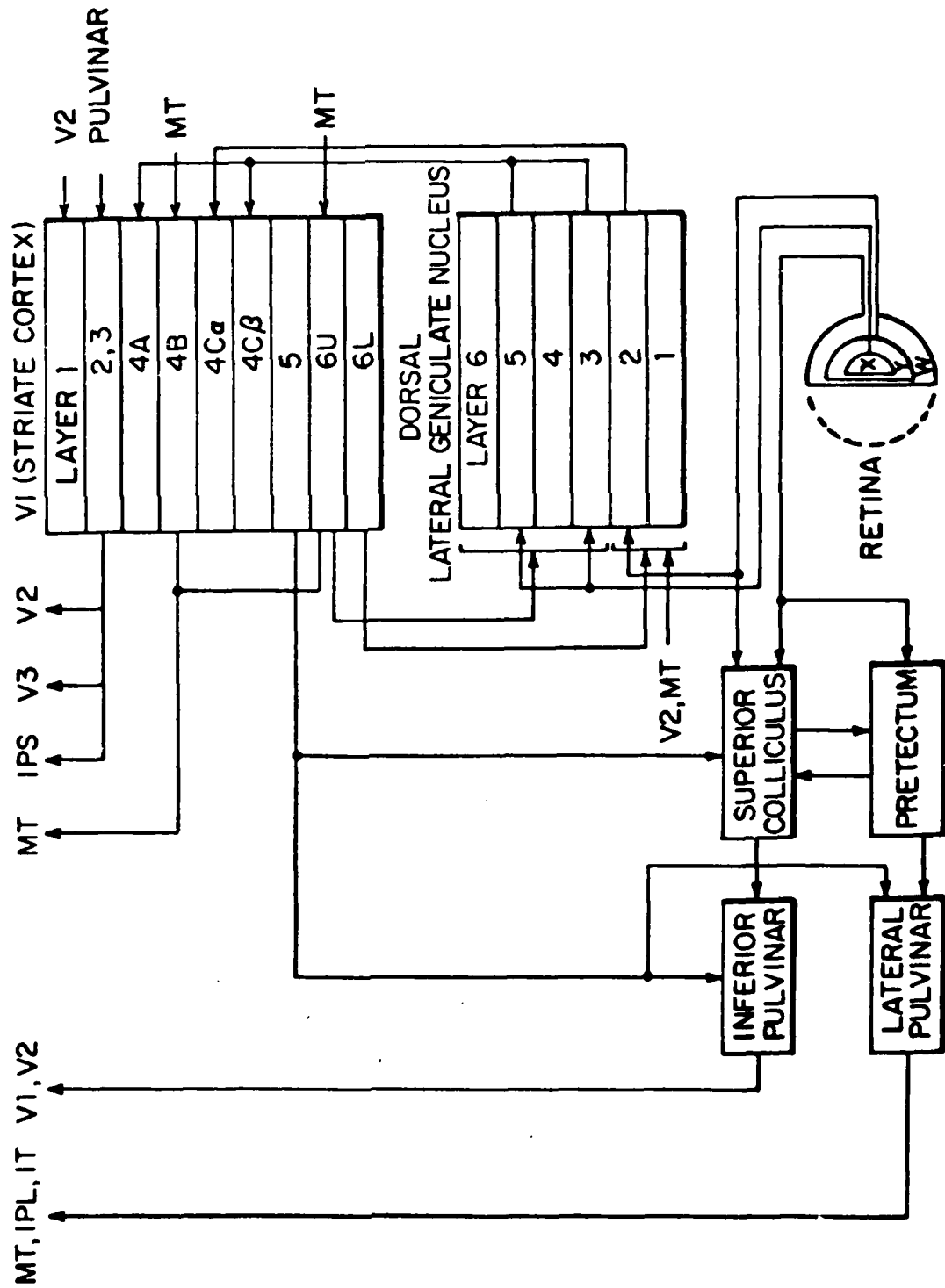


Primate Striate Cortex-69

VISUALLY GUIDED BEHAVIOR

Figure 1

# B PRIMATE RETINO-CORTICAL PATHWAYS



NASAL TEMPORAL

Figure 1

C

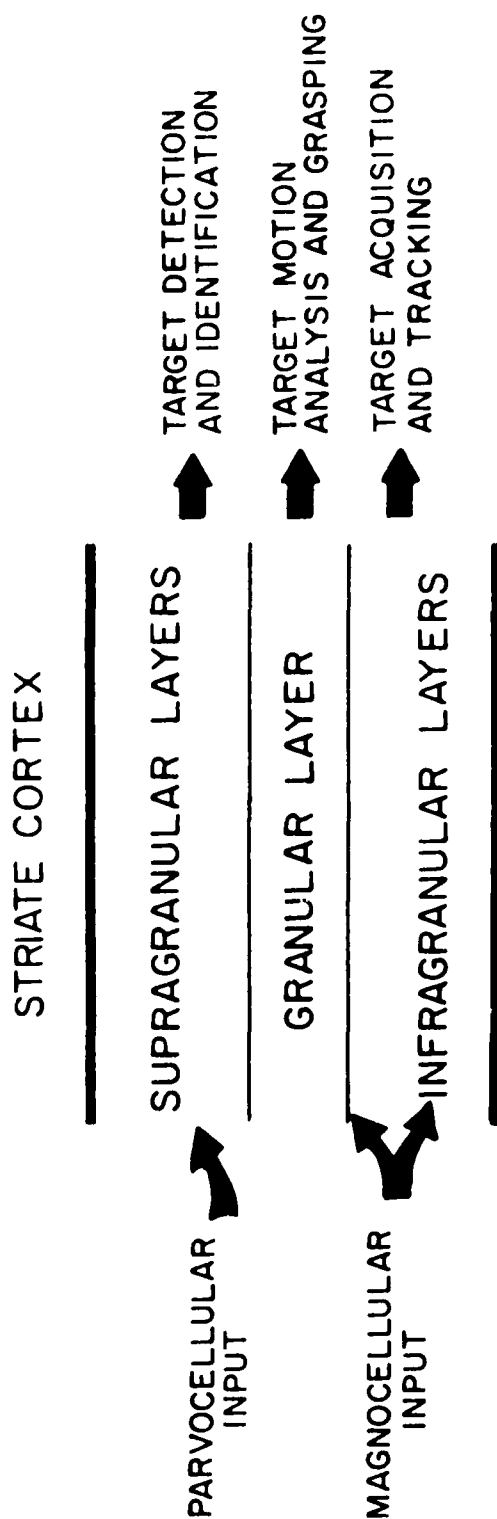


Figure 1

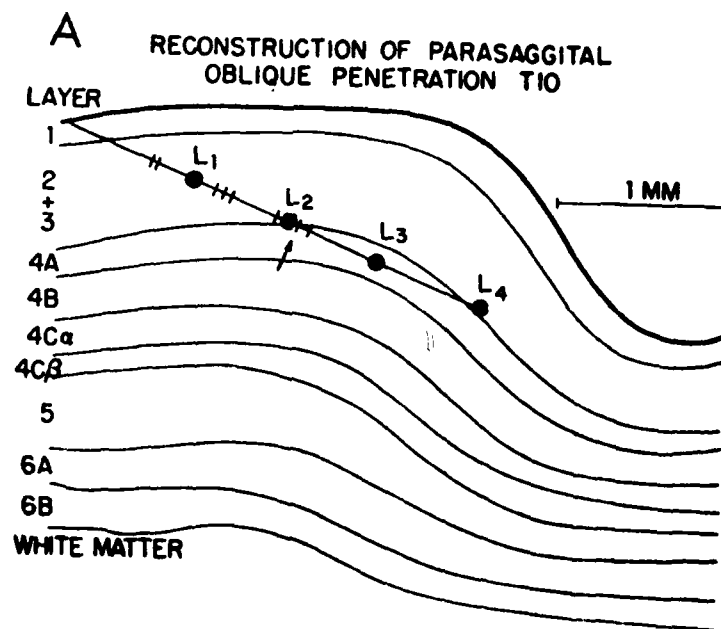


Figure 2

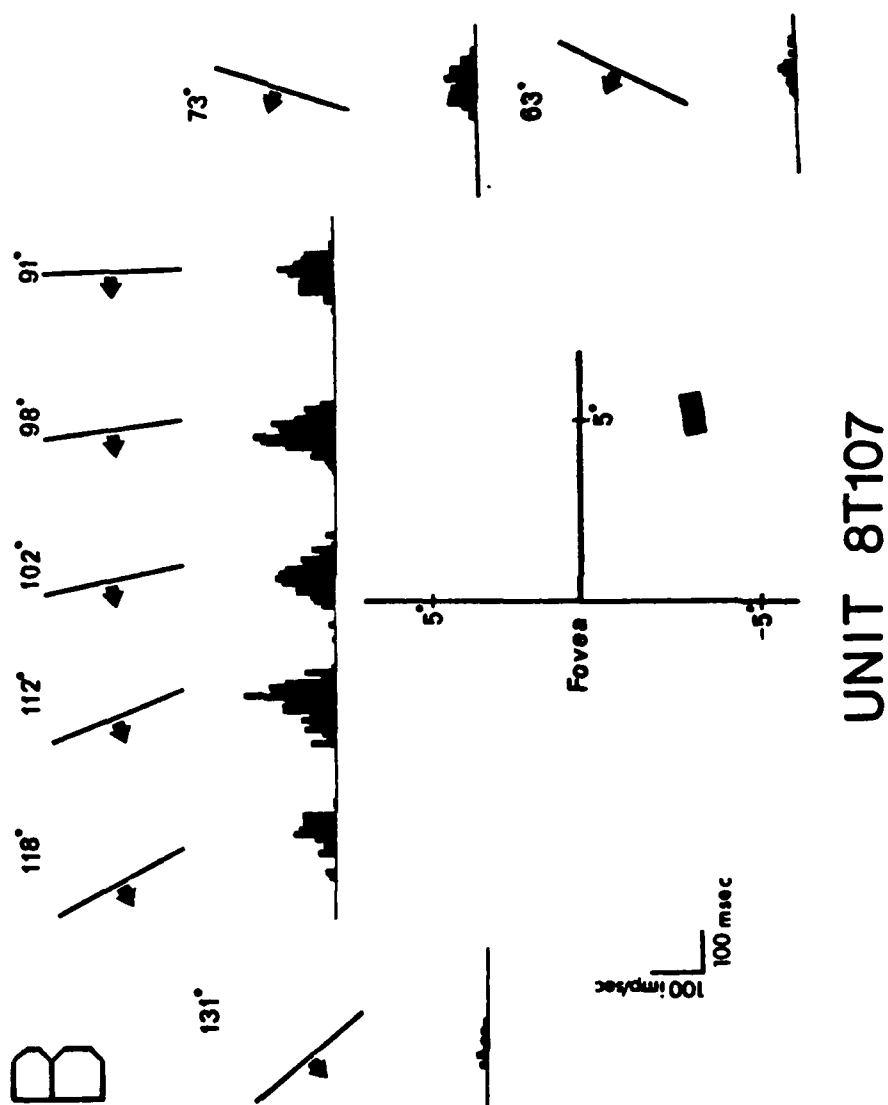


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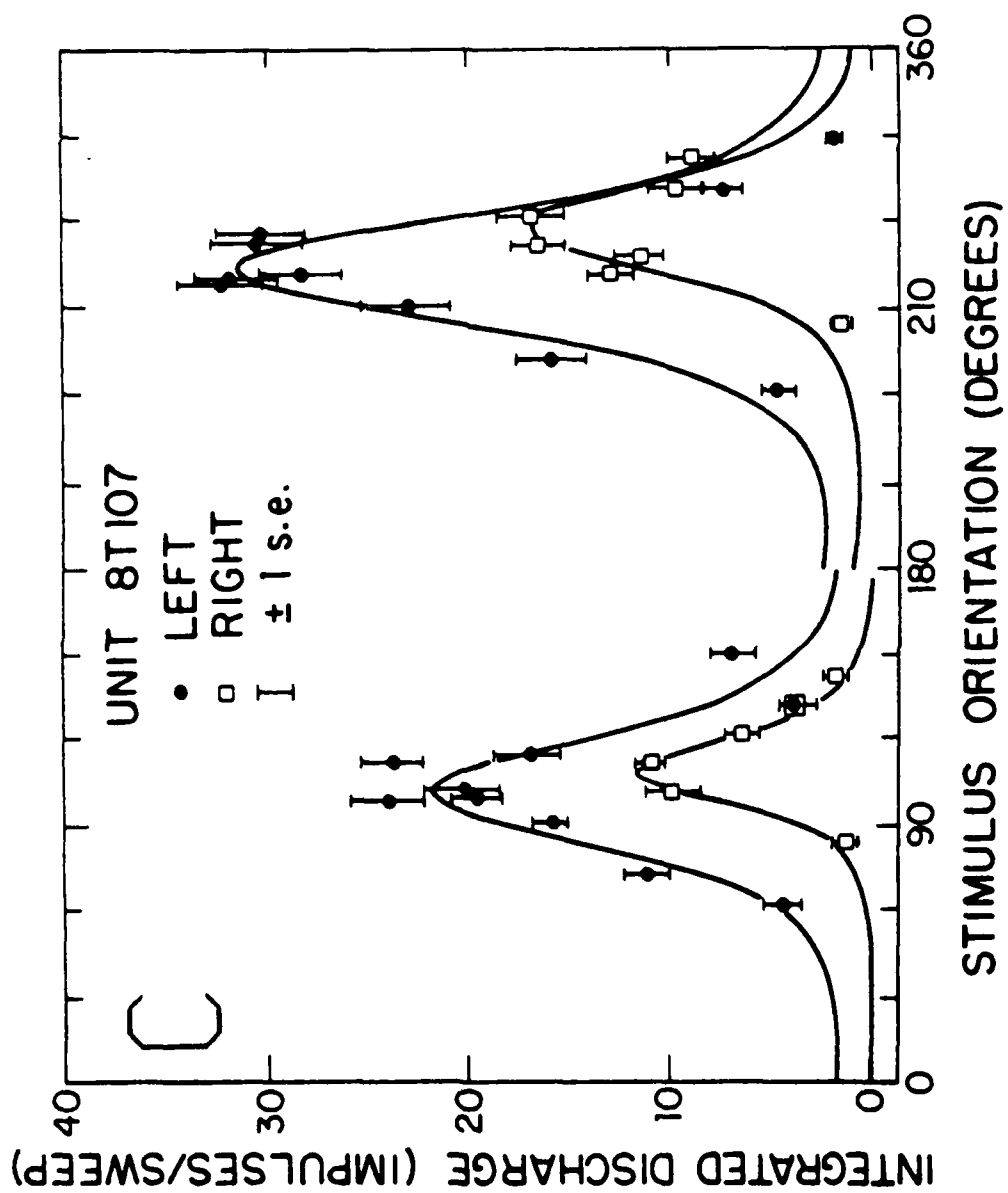


Figure 2

# DISTRIBUTION OF ORIENTATION SELECTIVITY

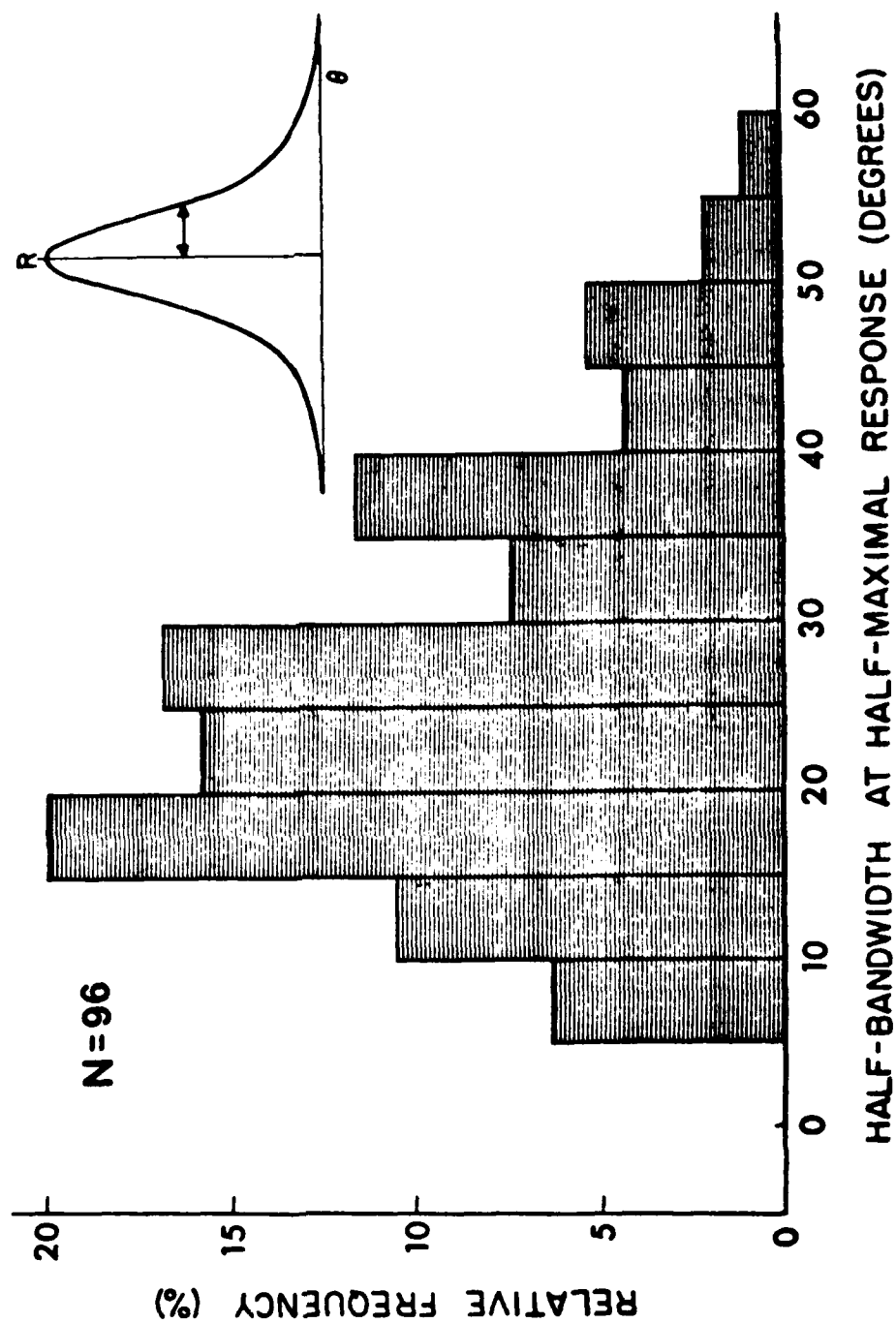


Figure 3

DISTRIBUTION OF AXIS OF ORIENTATION PREFERENCE

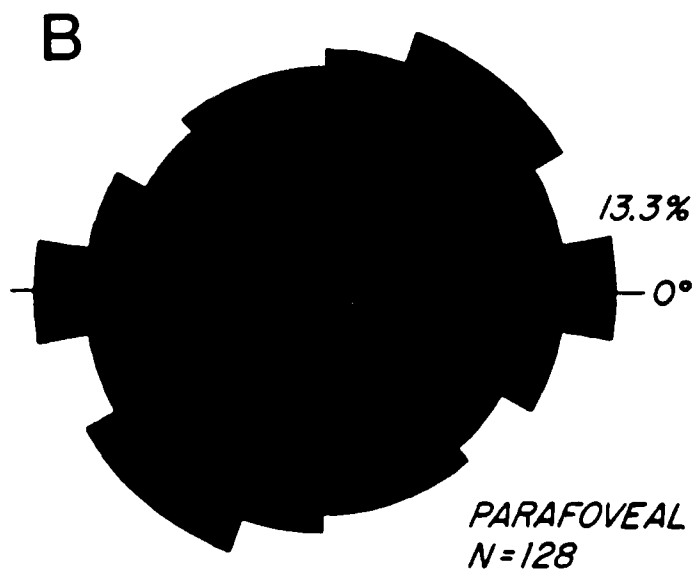
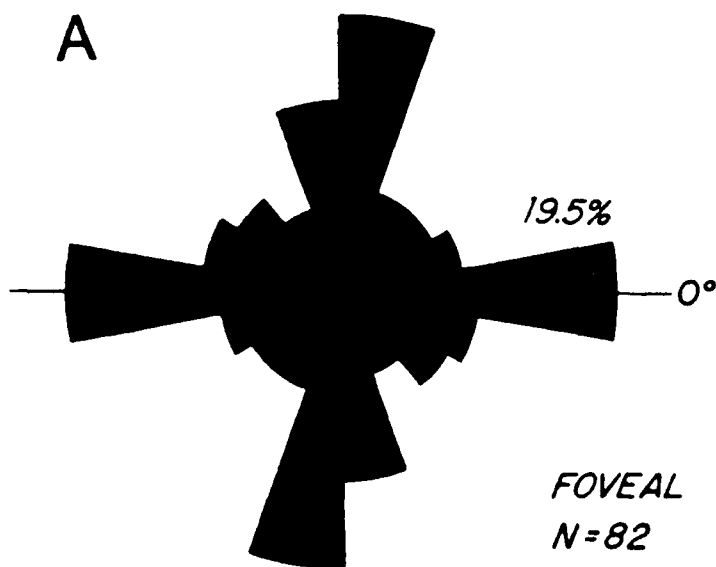


Figure 4

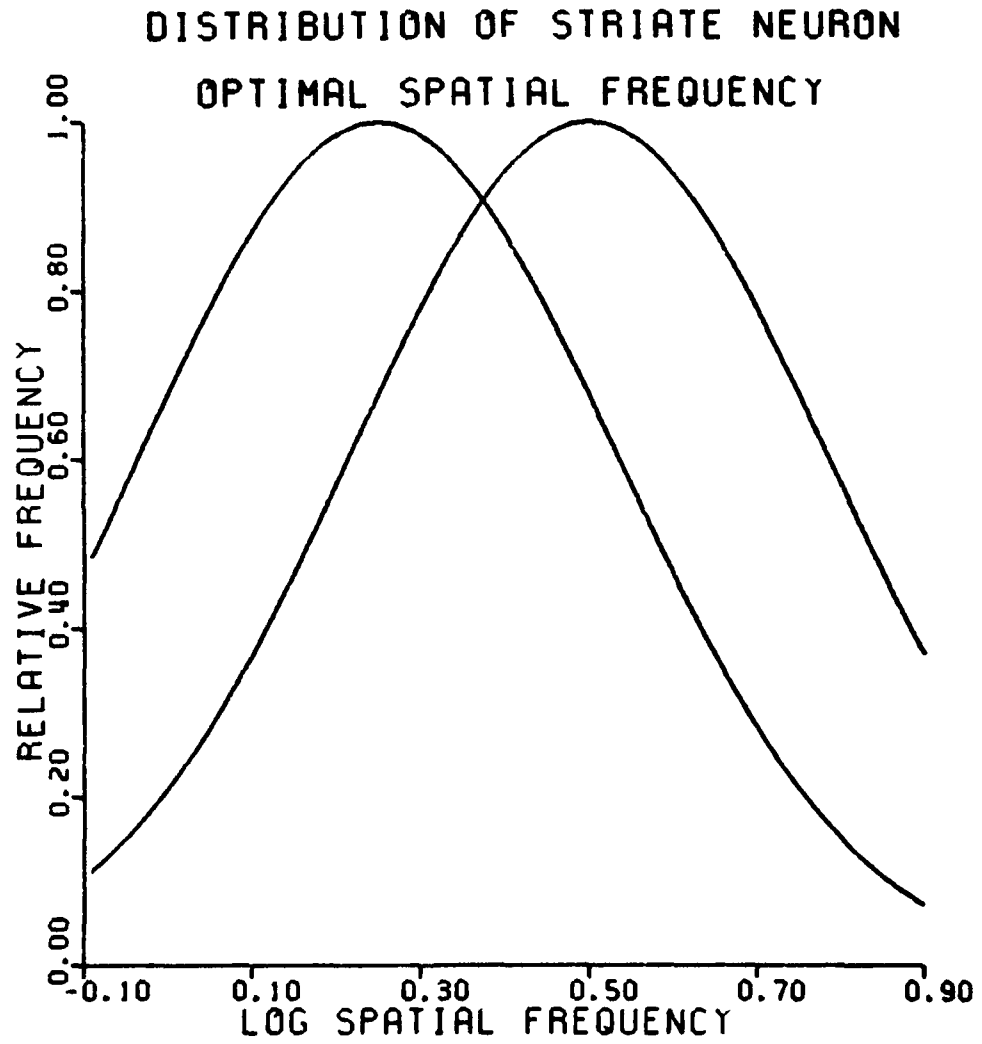
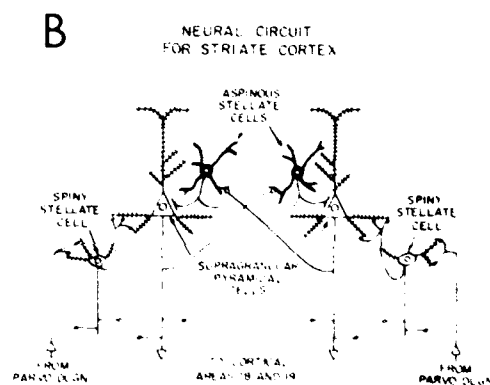
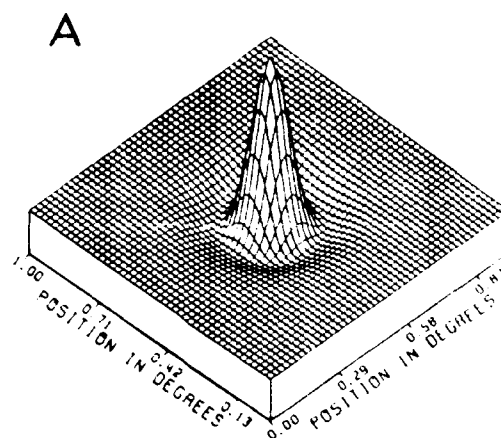


Figure 5

EXCITABILITY PROFILE



EXCITABILITY PROFILE

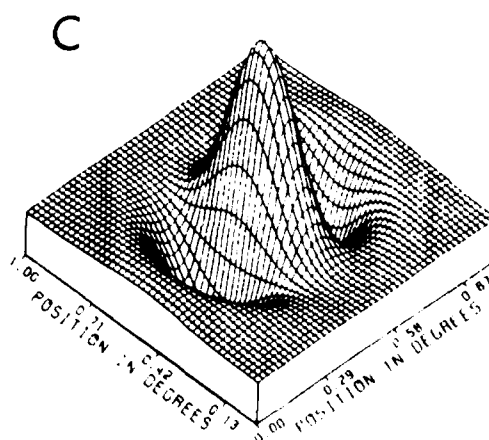


Figure 6

A

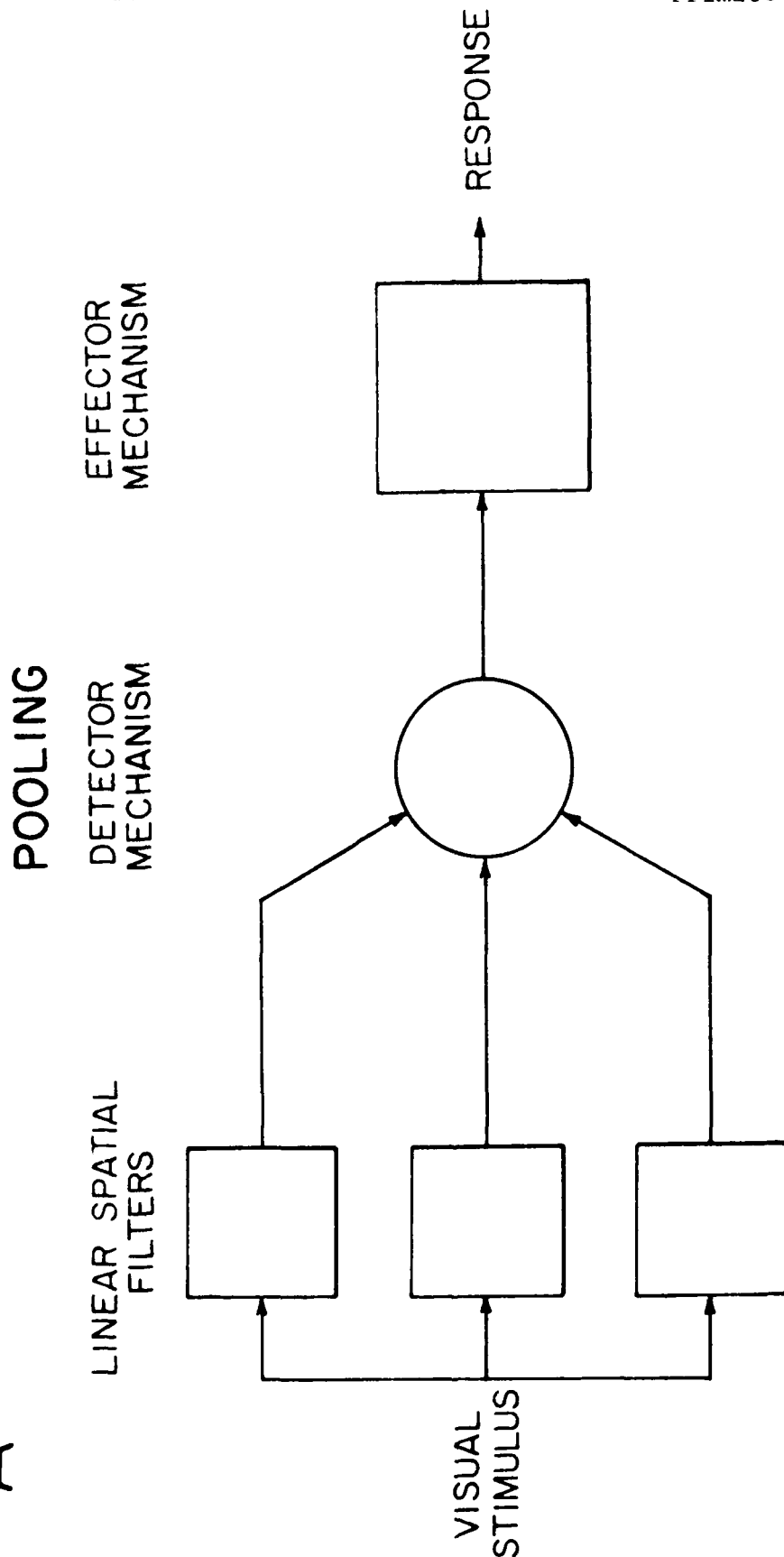


Figure 7

B

# PROBABILITY SUMMATION

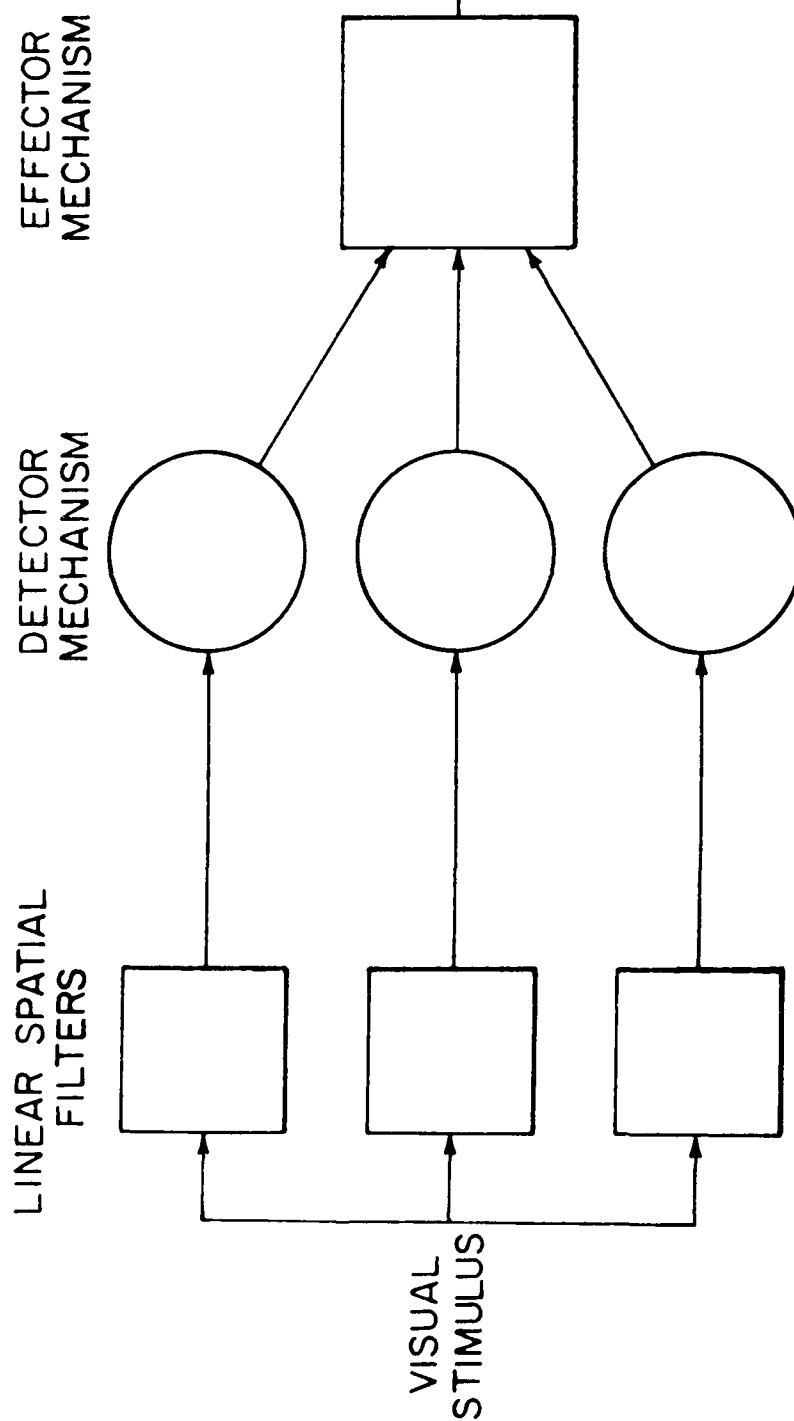


Figure 7

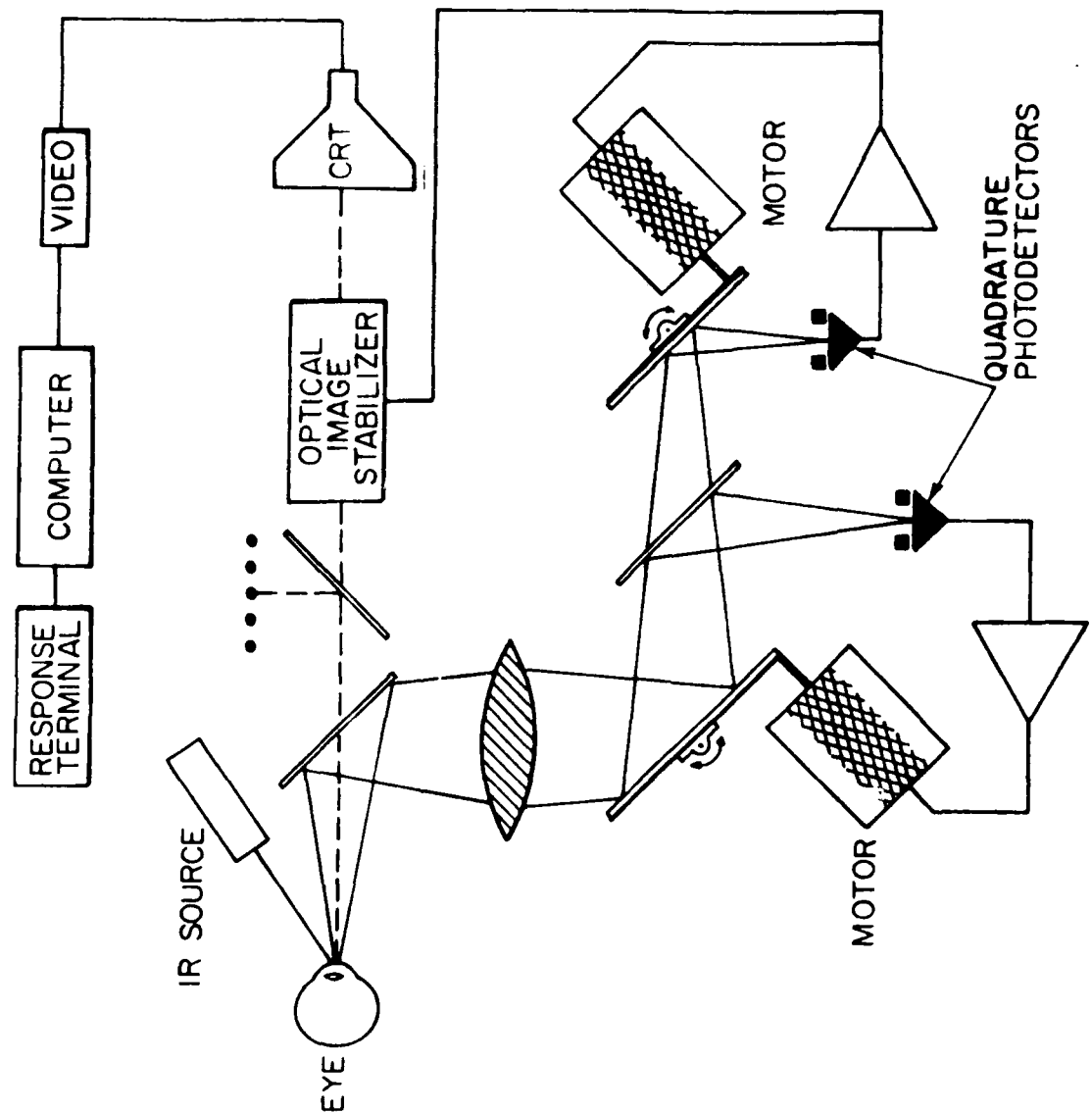


Figure 8

A



B



Figure 9

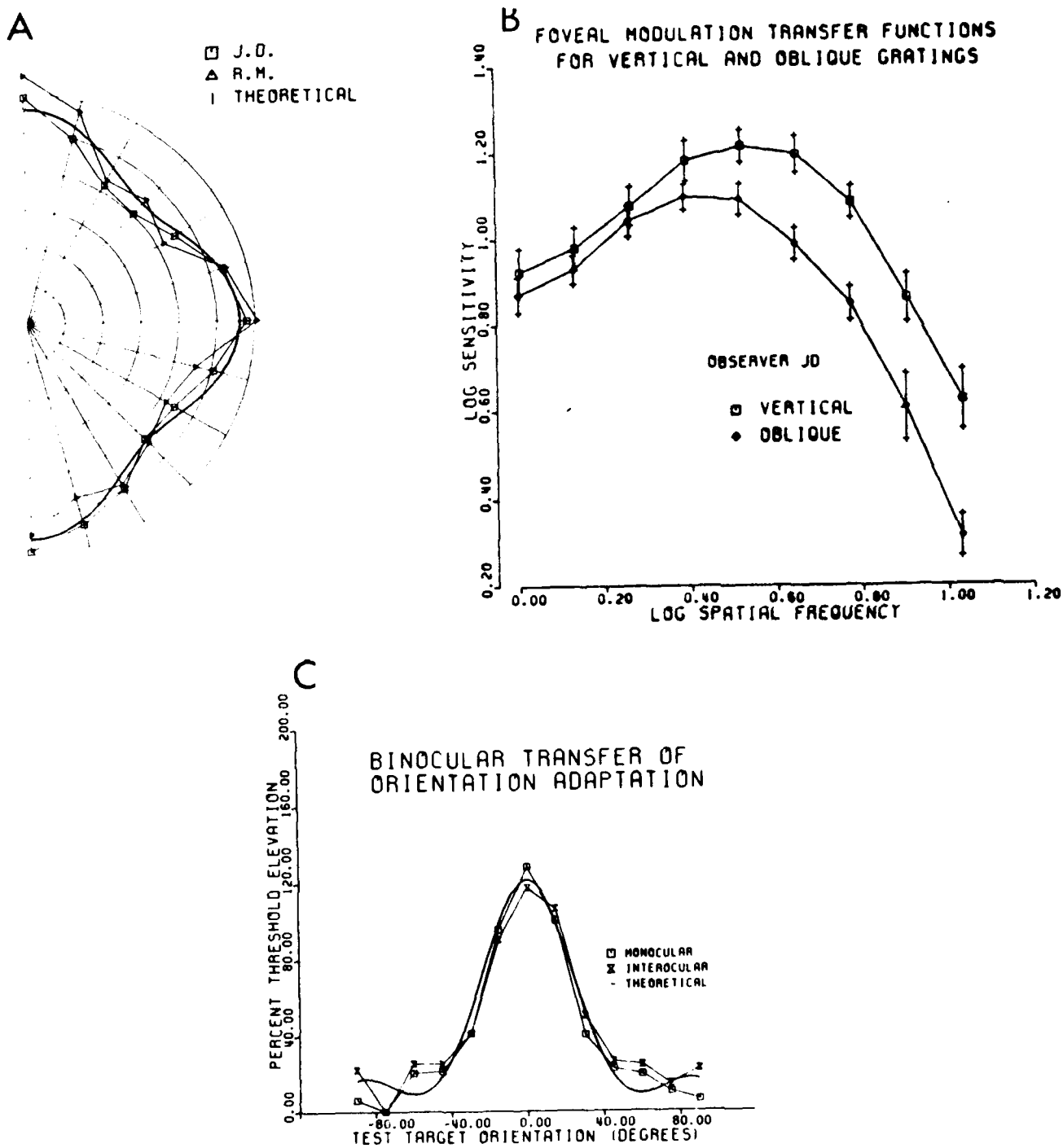


Figure 10

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