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VISUAL MECHANISMS CONTROLLING OCULAR STABILITY

by

© Keith L. Grasse

A thesis submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June 11, 1984

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ABSTRACT

Visual responses were examined quantitatively in 173 units in the lateral (LTN) and dorsal (DTN) terminal nuclei of the normal and visually decorticate cat accessory optic system (AOS). In both preparations the receptive fields were quite large, with an average diameter of approximately 60 deg. Large moving textured stimuli provoked optimal modulation in all cells.

The present results demonstrate that 1) the normal LTN contains almost equal numbers of cells which prefer either upward or downward vertical motion; 2) in contrast, the DTN contains cells which predominantly prefer horizontal stimulus toward the recorded hemisphere; 3) on average, the majority of upward direction selective LTN cells prefer faster stimulus velocities than the downward direction selective LTN units; 4) despite the virtually complete crossing of the retinal projection, most LTN and DTN units may be driven through both eyes; 5) following visual cortex lesions which deprive the AOS nuclei of a substantial cortical afference, most LTN and DTN cells display much slower velocity tuning and show much less upward direction selectivity; 6) the normally highly binocular LTN and DTN cells become almost completely dominated by the contralateral eye after visual cortex lesions.

Throughout the life of an organism there will be many types of eye, head or body movement which will generate whole field motion information in the visual system. The direction and velocity selectivity of cells in the cat AOS, along with their large receptive fields, render these units well suited to detect the visual consequences of some of these movements.

ABBREVIATIONS

LTN	- lateral terminal nucleus
DTN	- dorsal terminal nucleus
AOS	- accessory optic system
cd/m^2	- candelas per square meter
deg	- degree
uA	- microampere
usec	- microsecond
um	- micron
mm	- millimeter
ml	- milliliter
mg	- milligram
ms	- millisecond
m/sec	- meters per second
kg	- kilogram
W	- watt
DC	- direct current
i.v.	- intravenous
N_2O	- nitrous oxide
CO_2	- carbon dioxide
O_2	- oxygen
cc	- cubic centimeter
C	- centigrade (degress)
A	- anterior
L	- lateral

ACKNOWLEDGMENTS

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GENERAL INTRODUCTION

Most physiological investigations of vision employ types of stimulation which are relevant to the issue of how moving objects in the world may be detected and perceived by the nervous system. An important but often neglected aspect of visual perception is the way in which the visual system deals with the visual consequences of the organism's own motion which may accompany eye, head, or body movements during orientation and locomotion. Whenever an organism moves in the environment, an optical flow-field is generated across the retinal surface which provides valuable information concerning the direction and rate of whole-field motion, change in perspective, and even future position. Gibson (1966) has pointed out that the region in space toward which the organism is moving, occupies a unique position in the optical array which distinguishes itself as a focus of expansion from which the flowing lines of texture appear to emerge.

Neurons in the principle optic pathways (i.e., the geniculostriate and retinotectal systems), display physiological response properties which indicate that these cells perform local operations within only a restricted region of the visual field. Since a shift in position of the eye or head results in image displacement across the entire retina, a radically different form of receptive field is required to detect the visual consequences of self-induced motion.

There is, however, a third relatively unknown branch of the primary visual system which contains cells whose response functions are better suited for the task of whole field motion detection: the accessory optic system (AOS). Because of its relatively small size and

obscure significance, the AOS has only recently received the prolonged attention of neurophysiologists. In mammals, the AOS consists of a tri-nucleate system in the anterior brainstem innervated by fibers from the contralateral eye: the medial (MTN), lateral (LTN) and dorsal (DTN) terminal nuclei. In addition, in mammals like the cat (Berson and Graybiel 1980, Marcotte and Updyke 1982), these sub-nuclei receive a substantial input from the visual cortex. Single unit recording from cells within each of the three nuclei of the cat AOS reveals a provocative picture. AOS units display a high degree of selectivity for the direction, velocity and size of visual stimuli. It is of special interest that the receptive fields of these cells are extremely large (sometimes as much as 100 deg in diameter). The most effective stimulus for AOS units is a large textured pattern moving across the receptive field along a particular direction. AOS receptive fields exhibit no obvious center-surround organization. These properties of AOS cells make them well suited to detect the visual consequences of self-motion generated by an organism moving around within its environment.

In this thesis the physiological responses of cells in the AOS of the cat have been investigated using quantitative methods. Part I contains the electrophysiology of the normal LTN and DTN of the cat AOS. Part II describes the effects of visual cortex lesions on the response properties of LTN and DTN cells.

PART I

ELECTROPHYSIOLOGY OF THE LTN AND DTN IN THE NORMAL CAT ACCESSORY OPTIC SYSTEM

INTRODUCTION

Detailed anatomical studies of the accessory optic system (AOS) in the cat began with Hayhow (1959) who distinguished three retinal terminal zones in the anterior midbrain which he named the dorsal (DTN), lateral (LTN), and medial (MTN) terminal nuclei. A subsequent degeneration study by Laties and Sprague (1966) confirmed Hayhow's observations and further emphasized the almost entirely crossed character of the retinal projection to the AOS. The terminal nuclei of the AOS are also depicted in the cat midbrain atlas of Berman (1968) as three sparse, bilateral networks of cells forming synaptic contacts with the fibers of the accessory optic tract (AOT).

Single-unit extracellular recording in the AOS of the rabbit by Simpson, Soodak, and Hess (1979) demonstrated that cells in this system are direction selective, display slow excitatory and inhibitory velocity tuning, and have extremely large receptive fields. Simpson et al. observed that the preferred and null directional axes of rabbit AOS neurons are not separated by 180 deg (noncolinear), and that both axes appear to be aligned with the planes of rotation of the semicircular canals of the vestibular system. The studies of Simpson and coworkers provided the first articulation of the hypothesis that the AOS may be involved in signaling the visual consequences of self-motion which arise from movements within the rotational planes of the vestibular system.

Burns and Wallman (1980) examined the single-unit behavior of cells in the chicken AOS. Their findings show that cells in the chicken nucleus of the basal optic root (NBOR), a nucleus presumably

homologous with the MTN of mammals, usually display direction selectivity. These units can be divided into two groups distinguished by their preference for either upward or downward vertical motion of large textured targets. Receptive fields were reported to be very large. The major excitatory and inhibitory axes of, most notably, cells displaying downward direction selectivity, were found to be noncolineal. This finding is very similar to the directional tuning properties of rabbit AOS neurons (Simpson et al. 1979). Burns and Wallman also postulated that the excitatory and inhibitory directional axes may be aligned with the planes of the semicircular canals.

The AOS has been implicated in the neural control of optokinetic nystagmus (OKN), a bi-phasic oculomotor reflex induced by rotation of large parts of the visual world. Impairment of OKN has been observed following lesions of the AOS (Conley and Fite 1980, Fite, Reiner and Hunt 1979, Lazar 1973 and Gruberg and Grasse, unpublished observations). Similar findings have been obtained following lesions of the nucleus of the optic tract (NOT) and neighboring pretectum in the rabbit (Collewijn 1975) and cat (Precht and Strata 1979). NOT/pretectal lesions preferentially effect OKN induced by horizontal whole-field motion, a finding consistent with the horizontal direction selective visual responses observed in NOT units in rabbit (Collewijn 1975 a & b) and cat (Hoffmann and Schoppmann 1975, 1981).

Despite these investigations, the electrophysiology of the cat AOS has only recently been investigated (Grasse and Cynader 1982). In that study, visual responses of cat MTN cells were described: most cells exhibited marked direction selectivity in response to large stimulus targets moving slowly downward. An additional but much smaller popula-

tion preferred upward vertical motion. The receptive fields of cat MTN units averaged 60 deg vertically by 40 deg horizontally in extent, invariably included the area centralis and frontal visual field, and were driven most effectively through the eye contralateral to the recording site. In contrast to the non-colinear arrangement of preferred and null directions observed in the rabbit and chicken AOS, the mean angular separation between the preferred and non-preferred axes was 190 deg.

A comprehensive functional interpretation of the role of the cat AOS is not possible until a detailed physiological investigation is made of all three terminal nuclei, and, therefore, the previous studies of cat AOS have been extended by quantitatively examining the visual response features of single cells in the cat LTN and DTN.

METHODS

Recording preparation

Most aspects of the recording preparation employed in this study have been described previously (Grasse 1981, and Grasse and Cynader 1982). Briefly, cats were anesthetized with intravenous (i.v.) sodium thiopental (2.5mg/kg) as required, the trachea was intubated, and the animal was placed in a modified stereotaxic frame which minimally obstructed the field of view. Paralysis was induced and maintained throughout the experimental session with i.v. administration of gallamine triethiodide (10mg/kg/hr) during which time animals were artificially respired with a 70:30 mixture of N_2O and O_2. Halothane (1.5%) was introduced into the gas-mixture for the entire duration of surgery and discontinued thereafter. End-tidal CO_2 was monitored and maintained near 4.0%. Wound margins were generously infiltrated with a long lasting local anesthetic (Bupivacaine hydrochloride 0.25%). Body temperature was kept at 37.5 C and controlled by a thermostatic heating pad. Pupils were dilated with atropine (1%) and nictitating membranes retracted with neosynephrine (10%). Contact lenses with 4mm artificial pupils were selected by retinoscopy to focus images projected onto a tangent screen 46 inches from the eye. The location of optic discs and areae centrales on the tangent screen was determined by the reversing ophthalmoscope technique. A 6mm by 6mm bone flap was removed over Horsley-Clark coordinates A0.0 to A6.0, L2 to L8.

Electrical recording and stimulation

Single-unit recording methods were conventional and are described in more detail elsewhere (Grasse 1981 and Grasse and Cynader 1982). The procedure used to locate the LTN and DTN involved an initial determination of receptive field position on the surface of the superior colliculus. The electrode was repositioned until the collicular receptive fields were close to, or directly upon, the area centralis, and then laterally until the lateral extreme of the collicular surface was reached. The region lateral to the edge of the colliculus was distinguished by a deeper overlying ventricular space (an electrically "silent" zone). On most occasions, the first neuronal elements encountered were responsive to auditory stimulation, which probably reflected the activity of the fibers of the brachium of the inferior colliculus. In these cases the electrode was moved anteriorly in 0.5mm increments. The visual units described as DTN cells in this report were always found within 0.5mm anterior to this auditory region on the dorsal surface of the midbrain.

The LTN was found by advancing the electrode ventrally beyond the DTN region, through the auditory cells of the medial geniculate body, into the most ventral depths of the lateral midbrain. On many occasions, the LTN was located in the same penetration as the DTN, some 4.0 to 5.0mm ventral. Otherwise, the LTN was found immediately lateral, or slightly anterior (i.e., approximately 0.5mm), to the DTN. Once visual cells were isolated in either region, further electrode displacements were on the order of 0.1 to 0.3mm in any direction.

To verify electrode positions, electrolytic lesions were made at

the site of recorded units near the end of recording sessions by passing 3 uA of DC current through the recording electrode for 5 sec. The animals were overdosed with sodium pentobarbital and perfused through the heart, as previously described. Lesions and electrode tracks were compared with the location of AOS nuclei given by Berman (1968), and with autoradiograms of cat midbrain obtained following intraocular injections of [^{3}H] proline (Feran and Grasse 1982). Figure 1 shows a recording site taken from a brain in which cells were recorded in the DTN and the LTN. The track of the electrode is clearly visible on the left side of the section immediately lateral to the superior colliculus (SC). This is the precise location of the DTN and LTN given by Berman (Berman 1968, plate 29, p. 52).

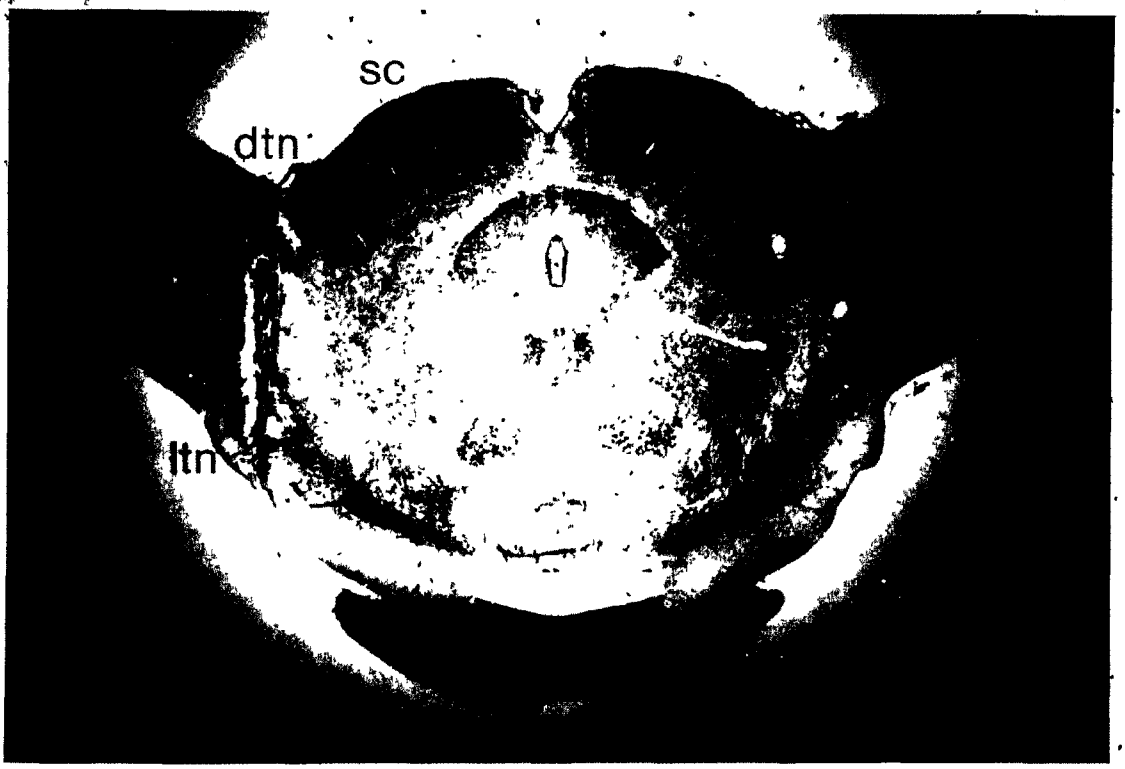
Conduction latency measurements were obtained by electrically stimulating units through bipolar electrodes implanted in the optic chiasm (Grasse 1981 and Grasse and Cynader 1982).

Visual stimulation and data collection/analysis

Unlike the previous study of the MTN (Grasse 1981 and Grasse and Cynader 1982), a random-dot pattern (Julesz 1964, figure 1) was employed as a stimulus target, rather than a square-wave grating, both as a search stimulus and for quantitative data collection. When a DTN or LTN unit was encountered, visual responses were first evaluated qualitatively by manual projection of a 40 x 40 deg random dot pattern onto the tangent screen. For quantitative assessment of visual responses, a larger random-dot pattern was employed which extended approximately 100 deg vertically by 80 deg horizontally (the angular subtense of each dot was equal to 1 deg on the retina). In all other

Figure 1

A coronal section through the midbrain of an animal in which cells were recorded in both the DTN and LTN. The track made by the recording electrode may be seen running from a point on the dorsal surface (DTN) immediately lateral to the superior colliculus (SC), through the entire thickness of the midbrain to the LTN at the ventral surface. Dorsal is up.


sc
dtn
ltn

respects, the computer controlled stimulus delivery system used to examine direction selectivity, velocity specificity, ocular dominance, diffuse light sensitivity, and the quantitative methods of data collection and analysis, were as previously described (Grasse 1981 and Grasse and Cynader 1982).

Vector Calculation

To determine an overall directional bias for individual cells and of large groups of cellular responses, a form of vector analysis was applied to the directional-response data. First, the mean spike rate values were segregated into two groups by dividing each vector magnitude by the resting discharge and treating ratios greater than 1.0 as excitatory and ratios less than 1.0 as inhibitory. Horizontal (x) and vertical (y) components were derived by multiplying the vector magnitude in the case of the excitatory vectors, and the reciprocal of the vector magnitude in the case of the inhibitory vectors, by the cosine and sine of the vector angle (the first direction on the far left in fig. 2A has been arbitrarily called 0 deg, the second clockwise direction 30 deg, and so on). The sum of these products furnished the x and y components of the excitatory and inhibitory vector sets. A resultant for each group was then determined by taking the arctangent of the ratio of y/x (for the angle). In a preceding study (Grasse 1981 and Grasse and Cynader 1982) the length of the resultant was determined by calculating the square root of the sum of the squares of the (x) and (y) components. In the present report, all vectors have been given unit-lengths. For convenience, all vector illustrations have been presented in polar coordinates referred to the vista of the

animal's left eye. Thus, "lateral" in the vector figures refers to the "temporal" aspect of the visual field, and "medial" to the "nasal" aspect.

RESULTS

The data presented in this report were obtained from 22 cats. Most frequently electrical recordings were made in both the LTN and DTN, and less frequently in both sides of the brain, of the same animal. A population of 96 single units was examined: 49 units in the LTN and 47 units in the DTN.

Direction selectivity

The direction selective responses of individual cells in the LTN and DTN were evaluated in the same manner as the previous study (Grasse 1981 and Grasse and Cynader 1982). In the LTN, direction selective responses fell naturally into two categories: units whose direction tuning profiles showed maximal excitation for downward vertical motion (23 of 49), and units whose direction tuning profiles displayed maximal excitation for upward vertical motion (25 of 49). Only one LTN cell displayed a preference for horizontal motion. Figure 2A shows the directional response profile of a LTN unit exhibiting maximal excitation for downward stimulus motion. Stimulus velocity was 10 deg/sec. The arrow on the ordinate indicates the resting discharge of this cell obtained while the random-dot pattern remained stationary within the receptive field.

Figure 2B illustrates the data of fig. 2A in polar plot form. The lengths of the arrows in fig. 2B are proportional to the mean spike rate elicited for stimulus motion along the arrow direction (note the arrows on the x-axis of fig. 2A). Maintained activity is not indicated in fig. 2B.

Figure 2A

Direction selective response of a cat LTN unit. In figs. 2A and 2D twelve directions of stimulus motion separated by 30 deg (as indicated by arrows on the abscissa) were presented 8 times each in a random sequence. The rate of firing in spikes per second, is represented on the ordinate. The resting discharge of this unit, sampled in the presence of a stationary stimulus pattern, is indicated by the arrow on the ordinate.

Figure 2B

Polar representation of directional response profile for the same unit as fig. 2A. The length of each arrow is proportional to the mean spike rate obtained for that direction of stimulus motion in space. All vector figures are presented in polar coordinates which have been, for convenience, referred to the vista of the left eye. The lateral visual field is on the left of each figure, medial on the right. Resting discharge is not indicated in this figure.

Figure 2C

Vector analysis of the LTN unit shown in figs. 2A and 2B. The polar plot vectors of fig. 2B were treated as described in the Methods to generate one E-vector (solid arrow) and one I-vector (broken arrow). Vectors have been given unit-lengths. Note that the E-vector points almost straight down and the I-vector points almost straight up.

Figure 2D

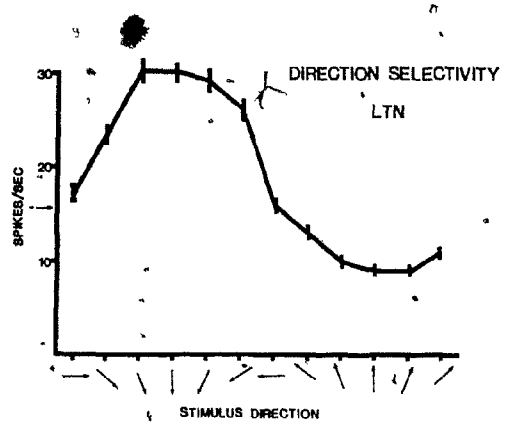
Direction selective response profile of another LTN unit. In contrast to the unit illustrated in fig. 2A, this unit displays maximal excitation for upward stimulus motion. Conventions are as in fig. 2A.

Figure 2E

Polar representation of LTN directional response (same unit as fig. 2D).

Figure 2F

Vector analysis of the LTN unit shown in fig. 2D and E. The polar plot of fig. 2D was treated as fig. 2C to generate the E- (solid arrow) and I-vector (broken arrow) shown in fig. 2F. These two vectors tilt slightly away from vertical.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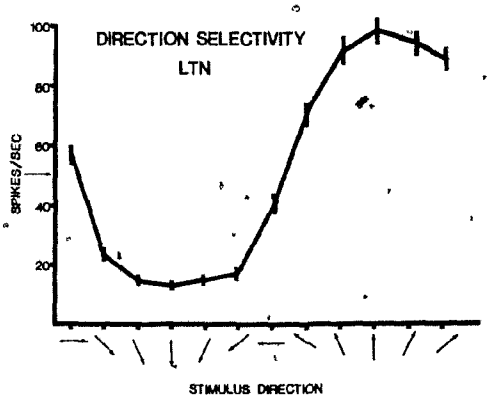
LTN
SPIKES/SEC
30
20
10
STIMULUS DIRECTION

A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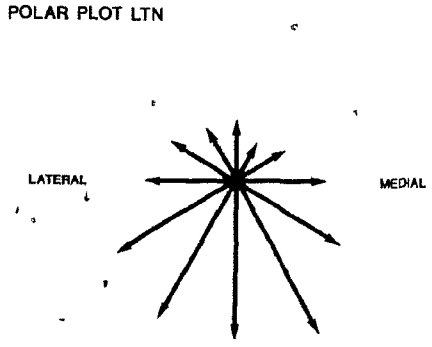
D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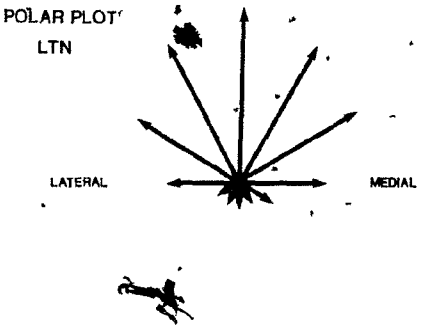
LATERAL
MEDIAL

B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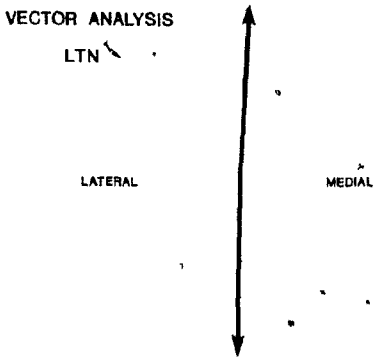
E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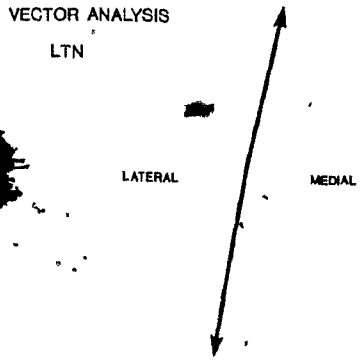
LTN
LATERAL
MEDIAL

C


VECTOR ANALYSIS
LTN
LATERAL
MEDIAL

F

A method of vector analysis was used to derive two vector quantities proportional to the major excitatory and inhibitory activity of AOS units (evaluated with respect to the resting discharge rate). This vector analysis has several advantages over conventional treatments of direction selective response profiles. First, it has the virtue of generating non-arbitrary estimates of the major excitatory and inhibitory directions for each response profile. Second, all available information is utilized in determining the two directions of greatest modulation. And lastly, the two vectors which emerge from this analysis are not constrained to fall onto one or more of the arbitrarily chosen directions employed in the testing procedure. A vector plot generated from the data of figs. 2A and B, is shown in fig. 2C. The excitatory vector (E-vector, solid arrow) of this unit points almost straight down, while the inhibitory vector (I-vector, broken arrow) points almost straight up. Both vectors have been given unit-lengths. Proceeding in a clockwise direction from the I- to the E-vector, the angular separation between these vectors is 179 deg.

A second class of direction selective LTN unit is represented in figs. 2D-F. This unit exhibits maximal excitation in response to upward stimulus motion and deepest inhibition for downward motion. Conventions for figs. 2D-F are the same as in figs. 2A-C.

Directional response profiles were also obtained for DTN cells. The response of a typical DTN unit recorded on the right side of the brain, is illustrated in fig. 3A. In contrast to the profiles of LTN cells, most DTN units displayed maximal excitation in response to horizontal stimulus motion directed toward the ipsilateral visual field (i.e., tempero-nasal motion relative to the eye contralateral to

Figure 3A

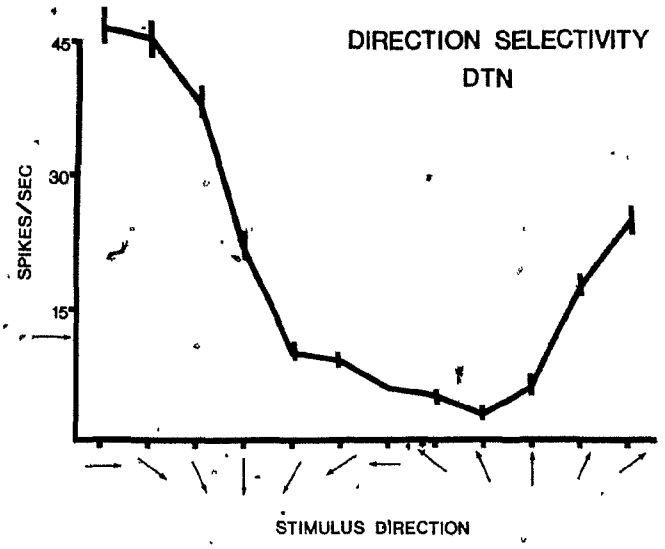
Direction selective response profile of a DTN unit. The overwhelming preference for horizontal stimulus motion of DTN cells is reflected in the response shown in fig. 3A. The resting discharge of this particular DTN cell is lower than that of the LTN units shown in figs. 1 and 2. On average, the resting discharge of DTN units was 11 spikes/sec, versus 21 spikes/sec for LTN cells.

Figure 3B

Polar representation of the direction selective response of the DTN unit shown in fig. 3A.

Figure 3C

Vector analysis of the DTN unit shown in figs. 3A and B. These vectors were generated by the same procedure as in figs. 2C and 2F. Note that the E-vector points in a horizontal direction into the medial visual field, while the I-vector points in a horizontal direction into the lateral visual field.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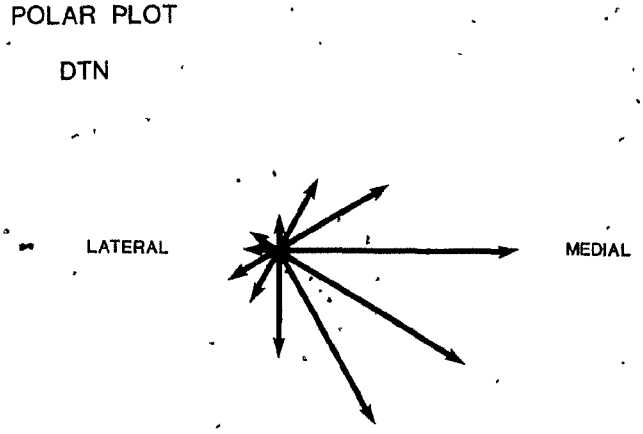
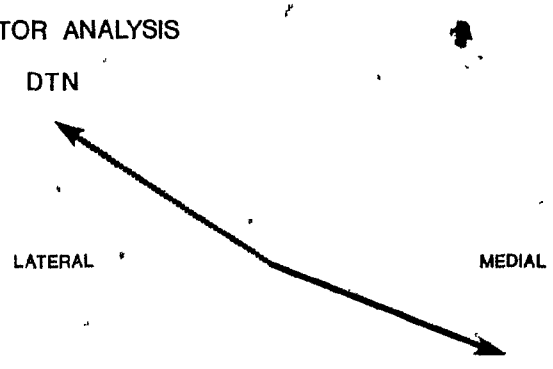
45
30
15
SPIKES/SEC
STIMULUS DIRECTION

A


POLAR PLOT
DTN
LATERAL
MEDIAL

B


VECTOR ANALYSIS
DTN
LATERAL
MEDIAL

the recording site). The polar plot display of this DTN unit is shown in fig. 3B, where the requirement for horizontal-medial stimulus motion is unequivocal. This same trend in directional tuning was also evident in the vector analysis for this cell, illustrated in fig. 3C. The E-vector in this case points approximately 20 deg off pure horizontal in the inferior-medial visual hemi-field, while the I-vector points approximately 31 deg off pure horizontal in the superior-lateral quadrant of the visual field. Angular separation between these vectors is 169 deg.

Distribution of direction selectivity in the LTN and DTN

To determine the total distribution of direction selective responses in the LTN and DTN, the results of the vector analyses of individual units were collected and plotted into a single circular distribution. Fig. 4A displays the total distribution of LTN E-vectors obtained in this study. As before, all vectors have been given unit lengths. Inspection of fig. 4A shows that LTN E-vectors fall naturally into two diametrically opposed groups of upward and downward directed vectors.

The total I-vector distribution for the LTN is displayed in fig. 4B. As in fig. 4A, the I-vector distribution divides into two groups of upward and downward directions. Within either the upward or the downward I-vector group, there is no obvious difference in the degree of clustering (i.e., relative dispersion) between the two groups of I-vectors and the two groups of E-vectors shown in figs. 4A and B.

E- and I-vector distributions for DTN cells examined in these

Figure 4A

Total distribution of E-vectors for the LTN. From the vector analysis of individual cells (e.g., figs. 2A and 2D), LTN E-vectors were collected and plotted together into a single circular distribution. All vectors have been given unit-lengths to emphasize dispersion. Two major sub-groups of vectors are apparent, showing an upward and downward trend respectively. Only one LTN unit was found to be sensitive to horizontal-lateral motion.

Figure 4B

Total distribution of I-vectors for the LTN. Similar to fig. 4A, I-vectors from individual LTN cells were collected into a single circular distribution. There are also two major sub-groups of I-vectors displaying the deepest inhibitory modulation for upward and downward stimulus motion. Two LTN I-vectors point in a horizontal-medial and horizontal-lateral direction. In other respects, the distribution is very similar to that of the E-vectors shown in fig. 4A.

Figure 4C, left panel

Hyper-E- and hyper-I-vectors for the upward-selective group of LTN cells. The hyper vectors representing the overall directional bias of an entire sub-group of unit responses, were derived by repeating the vector analysis on the upward directed E- and downward directed I-vectors from figs. 4A and B. All hyper-vectors have been given unit-lengths. The hyper-E-vector (solid arrow) points virtually straight up, while the hyper-I-vector points almost straight down.

Figure 4C, right panel

Hyper-E- and I-vectors for the downward-responding group of LTN cells. The hyper-E-vector (solid arrow) points 5 deg off vertical into the

inferior-lateral visual field. The hyper-I-vector (broken arrow) points 4 deg off vertical into the superior-medial quadrant.

Figure 4D

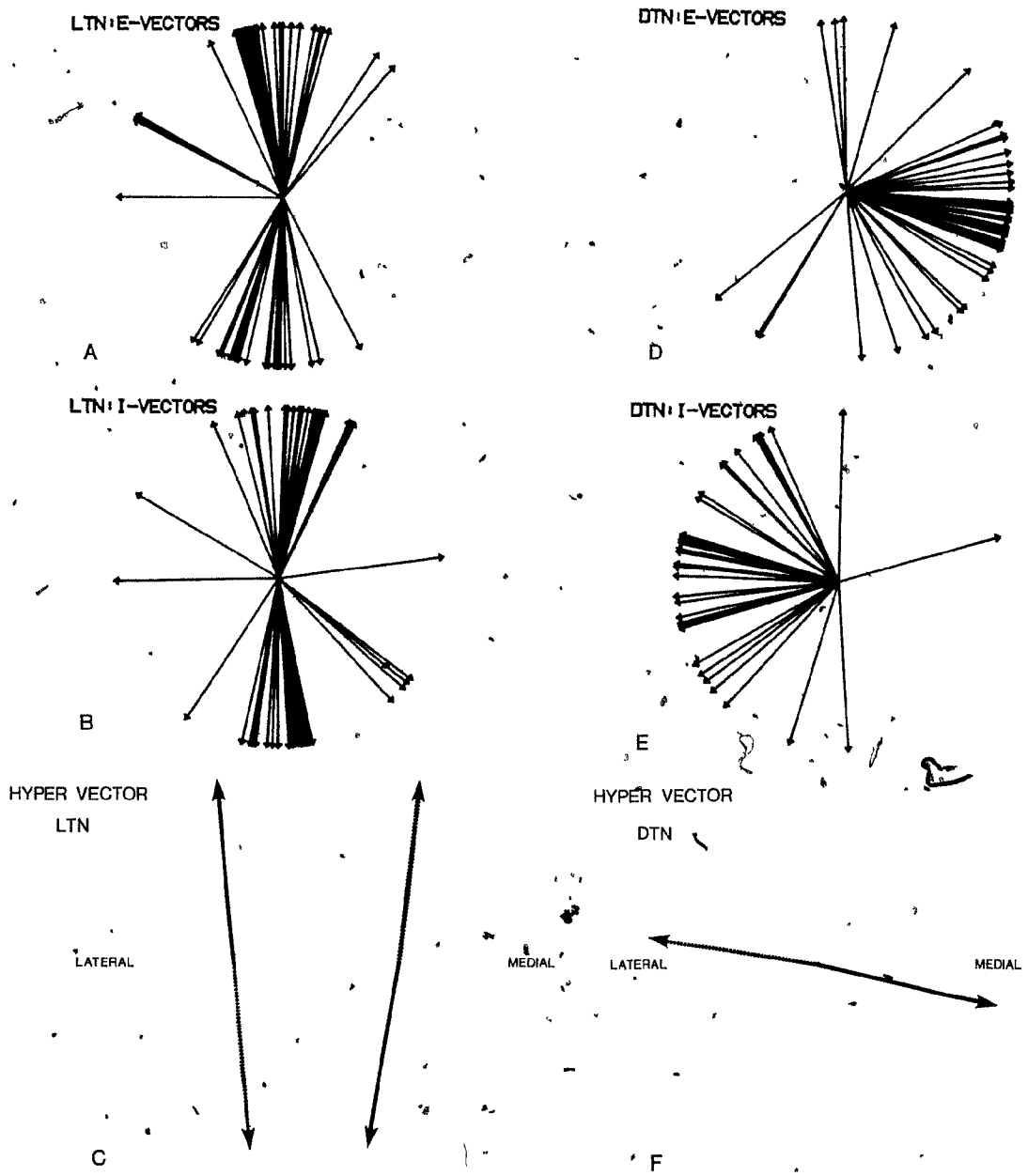
Total distribution of E-vectors for the DTN. Most DTN cells display greatest excitation for stimulus motion toward the horizontal-medial visual field. However, the E-vectors of 4 DTN units point almost straight up, while another 3 point down and lateral in visual space.

Figure 4E

Total distribution of I-vectors for the DTN. In contrast to the distribution of DTN E-vectors, most I-vectors are concentrated in the horizontal-lateral field. There are four exceptional DTN I-vectors, pointing either vertically up and down, or into the horizontal-medial visual field.

Figure 4F

Hyper-E- and I-vectors for DTN cells. Re-application of the vector analysis to the total distribution of E- and I-vectors shown in figs. 4D and 4E, yields a hyper-E-vector (solid arrow) pointing in a horizontal-medial direction, and a hyper-I-vector (broken arrow) pointing in a horizontal-lateral direction.


LTN: E-VECTORS
A
DTN: E-VECTORS
D
LTN: I-VECTORS
B
DTN: I-VECTORS
E
HYPER VECTOR
LTN
LATERAL
MEDIAL
C
HYPER VECTOR
DTN
LATERAL
MEDIAL
F

experiments, are shown in figs. 4D and 4E respectively. With few exceptions, most DTN E-vectors point in the inferior-medial direction. Fig. 4D also discloses a few DTN units which clearly do not display maximal excitation for horizontal-medial stimulus motion, but rather prefer either upward or downward diagonal motion.

The total I-vector distribution for the DTN unit population is shown in fig. 4E. In this distribution, the most frequently encountered direction is approximately 180 deg removed from the most frequently encountered vector direction observed in the DTN E-vectors of fig. 4D: i.e., most DTN I-vectors point in the lateral-horizontal direction.

By re-applying the vector analysis to the total distributions shown in figs. 4A and B, and 4D and E, a single non-arbitrary directional bias may be derived for an entire subset of response vectors. In any circular distribution of vectors there is no a priori rule by which subsets may be delineated for the purpose of calculating an average vector. The choice of subsets is, therefore, arbitrary. In the case of the LTN vectors shown in figs. 4A and B, two manifest subsets naturally emerge, pointing in an upward and downward direction. Thus, in fig. 4C two sets of hyper-vectors were calculated: one set for all those vectors pointing above (below) horizontal, and another set for all vectors pointing below (above) horizontal. For the upward direction selective LTN group, the left panel of fig. 4C shows the hyper-E-vector (solid arrow) pointing just off vertical toward the superior-lateral hemi-field. The hyper-I-vector (broken arrow) is likewise almost purely vertical except that it is deflected slightly into the inferior-medial quadrant. The right panel of fig. 4C illustrates the

hyper-E- and I-vectors for the downward group of LTN cells. These vectors approximate a polar reflection of the relationships shown in the left panel of fig. 4C.

The hyper-E- and I-vector for the distributions of preferred and non-preferred directions of DTN cells is displayed in fig. 4F. This panel illustrates the predominant preference for horizontal-medial stimulus observed in DTN cells, in that the hyper-E-vector points only 12 deg off pure horizontal into the inferior-medial visual field. Conversely, the DTN hyper-I-vector of fig. 4F is directed off horizontal into the superior-lateral quadrant.

Angular separation between E- and I-vectors

Electrophysiological studies in the AOS of the rabbit (Simpson et al. 1979), chicken (Burns and Wallman 1980) and pigeon (Morgan and Frost 1981) have revealed that very often the major excitatory and inhibitory axes of cells in this system are not separated by 180 deg (i.e., AOS cells are often non-colinear). To determine whether such non-colinearity obtains for the E- and I-vectors of LTN and DTN units in the cat, distributions of angular separation were compiled. Fig. 5A shows the distribution of vector separations for LTN direction selective cells. Unlike the results obtained in other species, the distribution appears remarkably Gaussian with the heaviest concentration of values at 175 and 180 deg (for individual examples see figs. 2C, 2F and 3C).

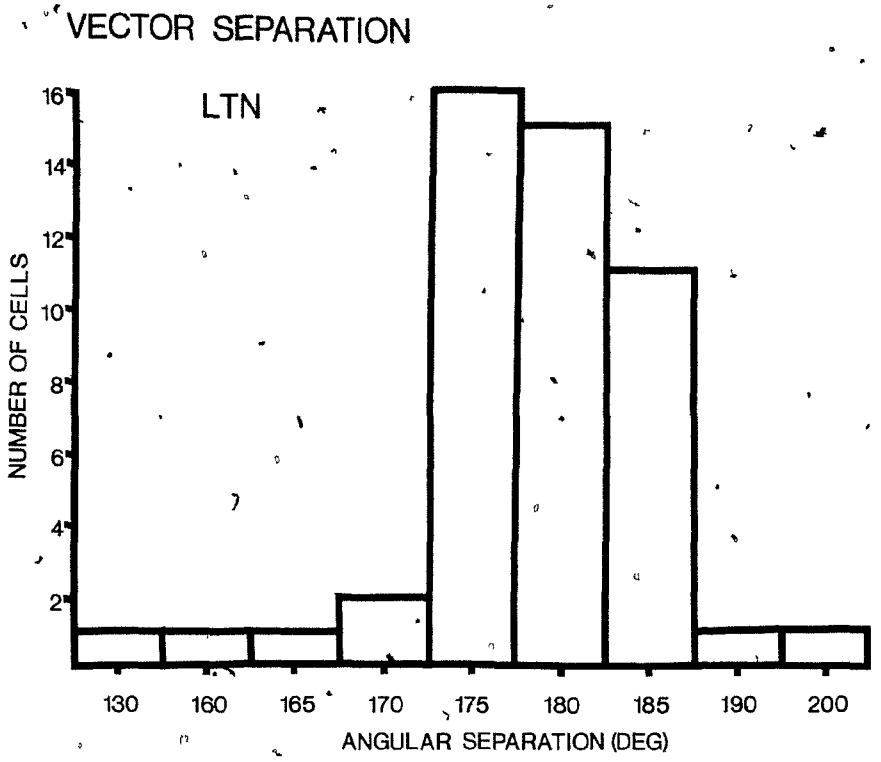
There was more spread in the range of values in the distribution of angular separations for DTN E- and I-vectors, which is shown in

Figure 5A

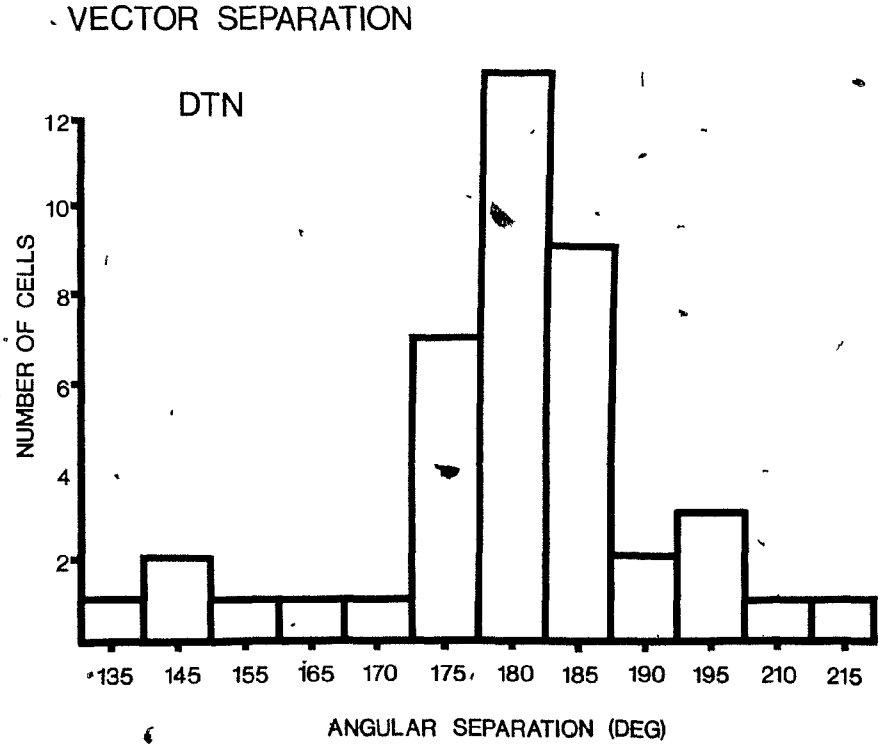
Distribution of angular separation for LTN E- and I-vectors. All measurements of angular separation between individual E- and I-vectors were made by proceeding in a clockwise direction from the I- to the E-vector. There is a broad range of values in this distribution extending from 130 to 200 deg, with most LTN vectors displaying separations of 175 to 185 deg. The mean of this distribution is 179.9 deg.

Figure 5B

Distribution of angular separation for DTN E- and I-vectors. Compared to the LTN distribution shown in fig. 5A, there is an even broader range of separation values for DTN vectors, extending from 135 to 215 deg, with a mean of 181.3 deg. However, like the LTN distribution, most vector separations fall between 175 and 185 deg.


VECTOR SEPARATION
LTN
NUMBER OF CELLS
16
14
12
10
8
6
4
2
130
160
165
170
175
180
185
190
200
ANGULAR SEPARATION (DEG)

A


VECTOR SEPARATION
DTN
NUMBER OF CELLS
12
10
8
6
4
2
135
145
155
165
170
175
180
185
190
195
210
215
ANGULAR SEPARATION (DEG)

B

fig. 5B. However, the overall shape of the distribution is normal with the majority of DTN E- and I-vector separations concentrated in the region of 180 deg.

Velocity specificity in the LTN and DTN

In addition to exhibiting a high degree of selectivity for the direction of stimulus motion, cat AOS units are also selective for stimulus velocity. Fig. 6A shows an example of a velocity tuning profile obtained from a LTN unit displaying a significant disparity in the tuning of the excitatory and inhibitory components of the response, roughly similar to what was observed in some cat MTN cells (Grasse and Cynader 1982, fig. 5). While the maximal excitation for this LTN cell occurs at 3.2 deg/sec, the deepest inhibition appears at a velocity of 25.6 deg/sec. The arrow on the ordinate of fig. 6A indicates the resting discharge rate sampled in the presence of a stationary stimulus pattern. With high stimulus velocities (> 100 deg/sec) this cell is inhibited with stimulation in either the preferred or non-preferred direction. This high velocity inhibition independent of the direction of stimulation was observed in 40% of LTN cells and 35% of DTN units.

The upward directed bar graph of figure 6B illustrates the distribution of stimulus velocities at which maximal excitation was elicited for all LTN cells. There is a broad range of preferred velocities, with most LTN units displaying maximal excitation for stimulus velocities between 0.8 and 12.8 deg/sec. The range of stimulus velocities which evoked the deepest inhibition in LTN units is shown in the lower inverted graph of fig. 6B. This histogram displays two peaks at velo-

Figure 6A

Velocity tuning profile of an LTN unit. This figure illustrates an LTN velocity tuning profile with different sensitivities for the excitatory (curve E) and inhibitory (curve I) components of the response function. At 0.2 deg/sec little excitatory response is observed, with values for the E curve being close to the resting discharge (arrow on the ordinate), while clear inhibition is already evident. Excitation increases with increasing stimulus velocity until 3.2 deg/sec, where the response peaks and thereafter begins a gradual decline. In contrast, the strength of inhibition is greatest at 25.6 deg/sec. Unlike excitation which is curtailed at 25.6 deg/sec and higher, inhibitory modulation in this cell is present at all stimulus velocities tested. Note that with very high stimulus velocities, both directions of stimulation result in firing rates which fall below that observed in the presence of a stationary stimulus pattern.

Figure 6B

LTN excitatory and inhibitory velocity tuning. Along two directions of stimulus motion aligned with the major excitatory and inhibitory axes obtained from direction response profiles (e.g., fig. 2A), units were tested with stimulus velocities ranging from 0.2 to 204.8 deg/sec. Each velocity was presented 8 times in a randomized sequence. Fig. 6B shows the velocity at which the major excitation (upper panel) and inhibition (lower panel) were obtained versus the number of cells. Most LTN cells achieved maximal excitation with stimulus velocities between 0.8 and 12.8 deg/sec. The remaining units displayed a preference for faster velocities (25.6 to 102.4 deg/sec). The lower inverted panel of fig. 6B shows the velocity at which the deepest inhibition

was obtained versus the number of cells. The range of inhibitory velocity tuning suggests a bimodal rather than a continuous distribution, with peaks at 0.8 and 12.8 deg/sec. Units showing deepest inhibitory modulation at relatively fast stimulus velocities (i.e., > 12.8 deg/sec) often displayed maximal excitation at much slower velocities (see fig. 6A, above).

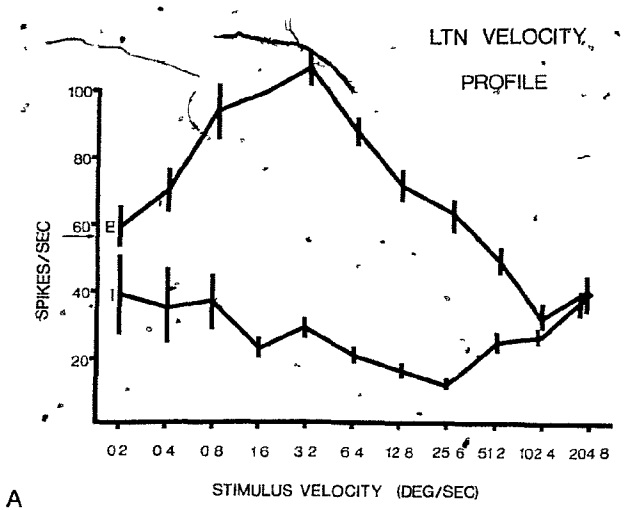
Figure 6C

Velocity tuning profile for a DTN unit. The velocity sensitivity of DTN cells was tested in exactly the same manner as described in fig. 6A. The DTN unit shown in this figure exhibits greatest excitation (curve E) at 6.4 deg/sec. As stimulus velocity is increased, the firing rate of this DTN cell steadily rises to a peak activity of 100 spikes/sec. Further increases in stimulus velocity cause a gradual decline in cellular discharge rate, until 102.4 deg/sec where excitatory response function descends to a level approximately equal to the resting discharge rate. Despite this neuron's relatively lower maintained rate (indicated by arrow on the ordinate, approximately 22 spikes/sec), clear inhibitory modulation (curve I) is seen for most velocities tested.

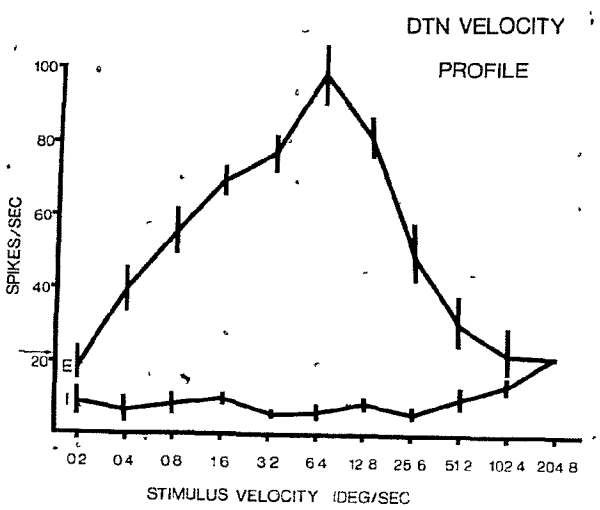
Figure 6D'

Excitatory and inhibitory velocity tuning for the DTN unit population. The abscissa of figure 6D (upper panel) plots the distribution of stimulus velocities at which greatest excitation was elicited against the number of cells on the ordinate. Most DTN units prefer velocities of 6.4 and 12.8 deg/sec. However, there is a substantial contingent of DTN cells displaying maximal excitation at relatively fast (51.2 and

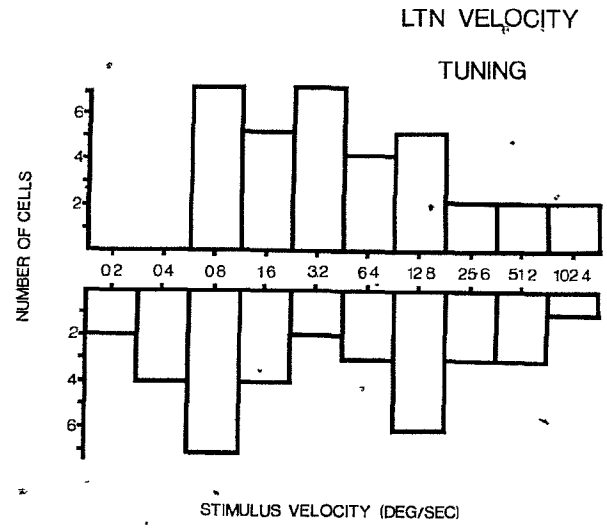
102.4 deg/sec) stimulus velocities. When compared to the LTN distribution (fig. 6B, upper panel), there are fewer cells preferring extremely slow stimulus velocities (i.e., < 0.2 deg/sec). The distribution of stimulus velocities which evoked deepest inhibition in DTN units is shown in the lower panel of fig. 6D. A clear peak in this distribution is evident at 25.6 deg/sec.


LTN VELOCITY
PROFILE
SPIKES/SEC
100
80
60
40
20
E
I
02 04 08 16 32 64 128 256 512 1024 2048
STIMULUS VELOCITY (DEG/SEC)

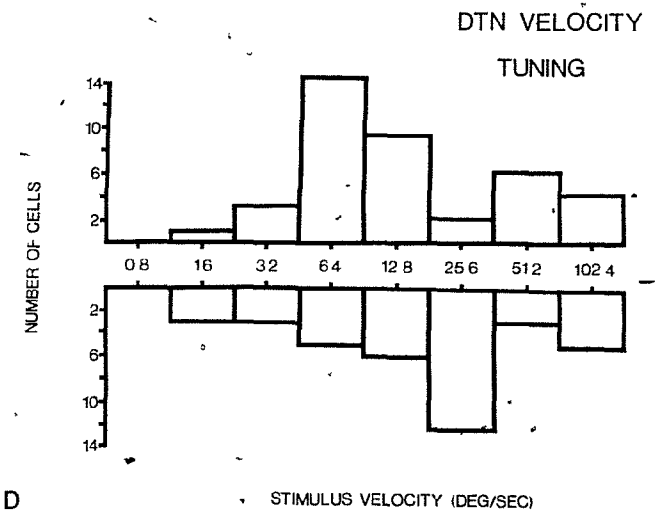
A


DTN VELOCITY
PROFILE
SPIKES/SEC
100
80
60
40
20
E
I
02 04 08 16 32 64 128 256 512 1024 2048
STIMULUS VELOCITY (DEG/SEC)

C


LTN VELOCITY
TUNING
NUMBER OF CELLS
6
4
2
02 04 08 16 32 64 128 256 512 1024
STIMULUS VELOCITY (DEG/SEC)

B


DTN VELOCITY
TUNING
NUMBER OF CELLS
14
10
6
2
08 16 32 64 128 256 512 1024
STIMULUS VELOCITY (DEG/SEC)

D

cities of 0.8 and 12.8 deg/sec, suggesting a bimodal, rather than a unimodal distribution of inhibitory response types. The overall range of inhibitory velocity tuning is somewhat greater than the excitatory velocity tuning. Some LTN units showed deepest inhibition in response to very low velocities of either 0.2 (2 cells) or 0.4 (4 cells) deg/sec.

Figure 6C shows a velocity tuning profile for a typical DTN unit. This response profile illustrates a DTN cell with dissimilar excitatory and inhibitory velocity specificity: while maximal excitation occurs with a pronounced peak at 6.4 deg/sec, deepest inhibition is evident in response to a relatively large range of velocities between 0.4 and 25.6 deg/sec. In addition, the resting discharge rate (indicated by an arrow on the ordinate) for this DTN cell is significantly lower than for most LTN cells. On average, the mean resting discharge rate for LTN units examined in the present study was 21 spikes/sec, whereas the average resting discharge for DTN cells was 11 spikes/sec.

Figure 6D upper panel illustrates the distribution of preferred velocities for all DTN units. Most DTN cells showed maximal excitation for stimulus velocities near 6.4 and 12.8 deg/sec. The lower panel of fig. 6D displays the distribution of velocities which elicited the deepest inhibition. In contrast to the inhibitory velocity tuning observed in the LTN (compare with fig. 6B, lower panel), there is a single predominant peak in this distribution for DTN cells occurring at 25.6 deg/sec. Note that the inhibitory-velocity response function for individual DTN cells was often quite broad (e.g., see fig. 6C), spanning a relatively greater range of velocities than the same function in LTN units. Thus, in order to generate the distribution shown

in fig. 6D lower panel, it was sometimes necessary to take the mid-point of the total range over which the deepest inhibition was evoked in DTN cells and define this as the "peak" inhibitory velocity.

Ocular dominance in the LTN and DTN

Anatomical studies of the cat AOS (Farmer and Rodieck 1982, Feran and Grasse 1982, Hayhow 1959, Laties and Sprague 1966, Lin and Ingram 1974, and Marcotte and Updyke 1982) have consistently demonstrated that virtually all retinal axons projecting into the accessory optic tract cross at the optic chiasm prior to synaptic termination in the DTN, LTN and MTN. The ocular dominance distribution for the LTN is shown in fig. 7A. This figure utilizes an abbreviated version of the Hubel and Wiesel (1962) method for characterizing ocular dominance, in which there are only 5, as opposed to 7 categories. Otherwise, the ocular dominance group numbers convey similar meaning: OD group 1 denotes cells driven by the contralateral eye only (with respect to the recording site), OD group 5 ipsilateral eye only, and OD group 3 both eyes equally. OD groups 2 and 4 denote binocular cells driven more effectively by the contralateral and ipsilateral eye respectively. There is a heavy contralateral bias in the distribution of fig. 7A, yet the number of binocular cells (especially OD 2 and 3) is quite large. Despite the clear ipsilateral input evident in fig. 7A, no LTN units were encountered which were driven solely through the ipsilateral eye (OD 5).

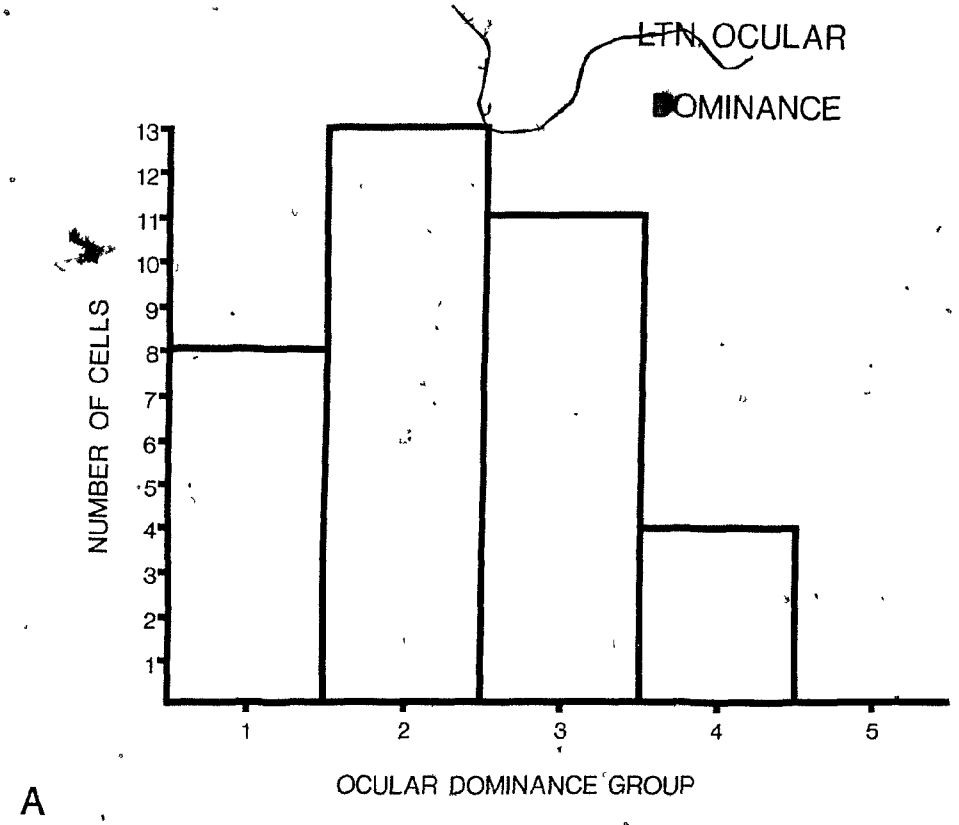
Figure 7B illustrates the ocular dominance distribution for the DTN. This distribution also discloses a significant ipsilateral input

Figure 7A

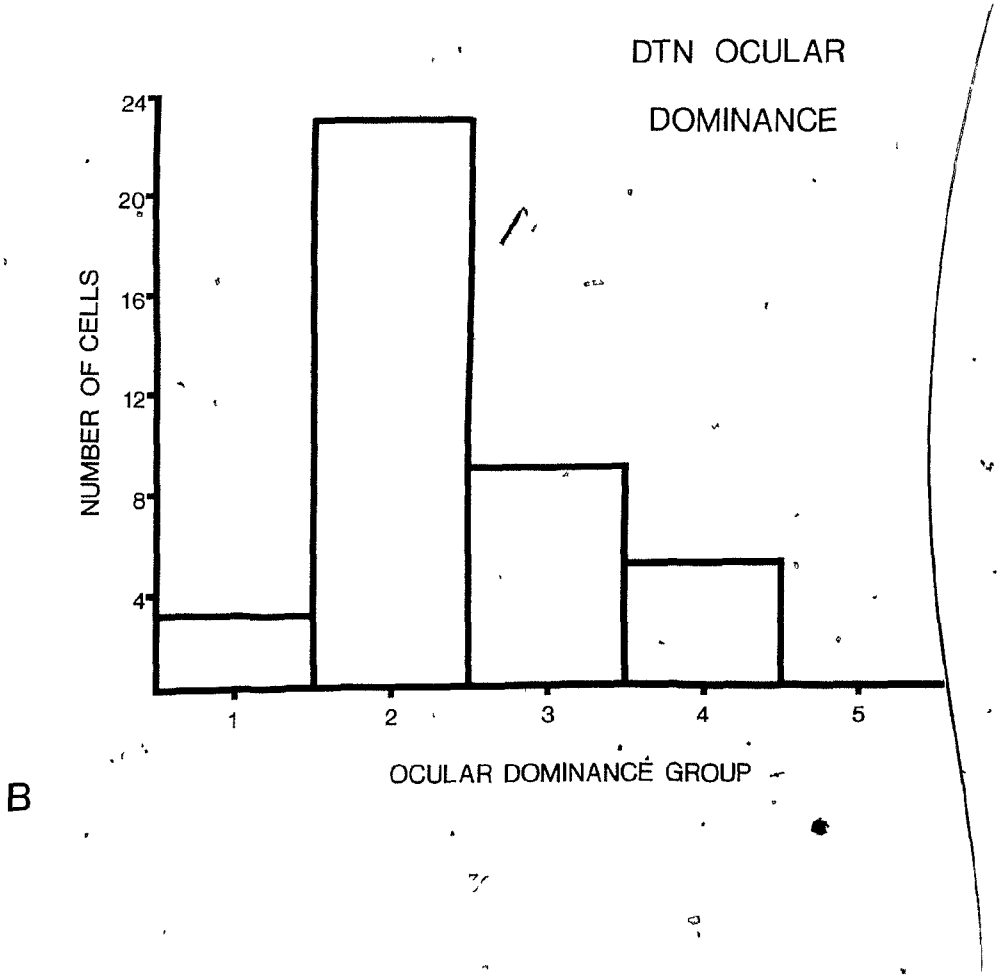
LTN ocular dominance distribution. Ocular dominance was determined through independent monocular testing. The histogram in fig. 7A shows the ocular dominance (OD) group versus the number of LTN units. Units in OD groups 1 and 5 are driven only through the contralateral and ipsilateral eye respectively (in relation to the recording site). OD group 3 denotes cells driven equally well through both eyes. There is significant ipsilateral input to LTN cells evident in this distribution, with the majority (78%) falling into OD groups 2-4. No LTN units were found, however, which were driven solely through the ipsilateral eye (OD 5).

Figure 7B

DTN ocular dominance distribution. Conventions for this figure are identical to those for fig. 7A. As in the LTN, the ocular dominance distribution for the DTN displays a high incidence (93%) of cells with ipsilateral eye input (OD groups 2-4). Most DTN cells fall into OD group 2, indicating a predominant contralateral eye input together with a relatively weaker input from the ipsilateral eye. Note how few DTN cells were driven through the contralateral eye alone (OD 1).


LTN OCULAR
DOMINANCE
NUMBER OF CELLS
13
12
11
10
9
8
7
6
5
4
3
2
1
1
2
3
4
5
OCULAR DOMINANCE GROUP

A


DTN OCULAR
DOMINANCE
NUMBER OF CELLS
24
20
16
12
8
4
1
2
3
4
5
OCULAR DOMINANCE GROUP

B

to DTN units. Most DTN cells fall into OD group 2. While there is a substantial contingent of binocular (OD 3) and ipsilateral dominant units (OD 4) in the DTN, there were fewer purely contralateral cells (OD 1) than in the DTN.

Conduction latency in the LTN and DTN

Routinely, bipolar stimulating electrodes were implanted in the optic chiasm (for details see Grasse and Cynader 1982). Whenever possible, isolated cells in the LTN and DTN were tested for orthodromic response to short pulses of electrical stimulation (ranging from 1-50 usec at 100-150 uA). The distribution of conduction latencies obtained from LTN units is shown in fig. 8A. The majority of LTN cells displayed conduction latencies of 4.5 to 5.0 msec, with a mean of 4.91 msec.

DTN conduction latencies, shown in fig. 8B, were similar to those observed in the LTN. The DTN latency distribution exhibits a peak at approximately 5.5 msec, with a mean of 5.75 msec.

General receptive field properties

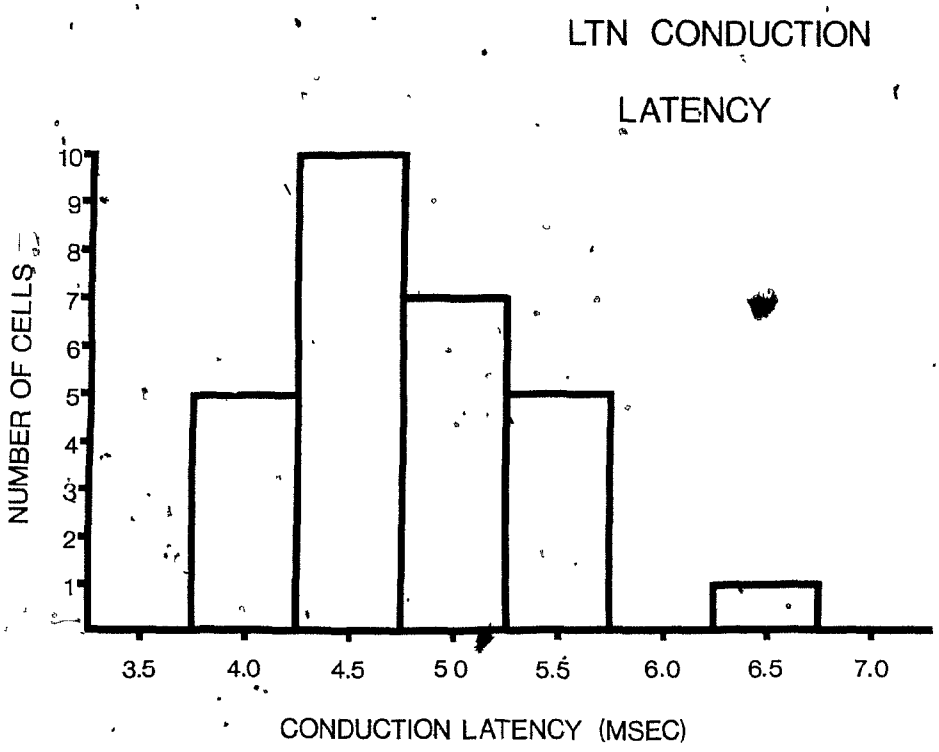
Similar to the cat MTN, and to the AOS of many other species, the receptive fields of LTN and DTN units were, on average, quite large, covering 60 deg or so in diameter when mapped with a large (i.e., 40 x 40 deg) manually projected random-dot pattern. The smallest receptive field encountered was that of a DTN cell which measured approximately 15 deg horizontally by 30 deg vertically. It was necessary to cover at least 2/3 of the total receptive field area with the stimulus target

Figure 8A

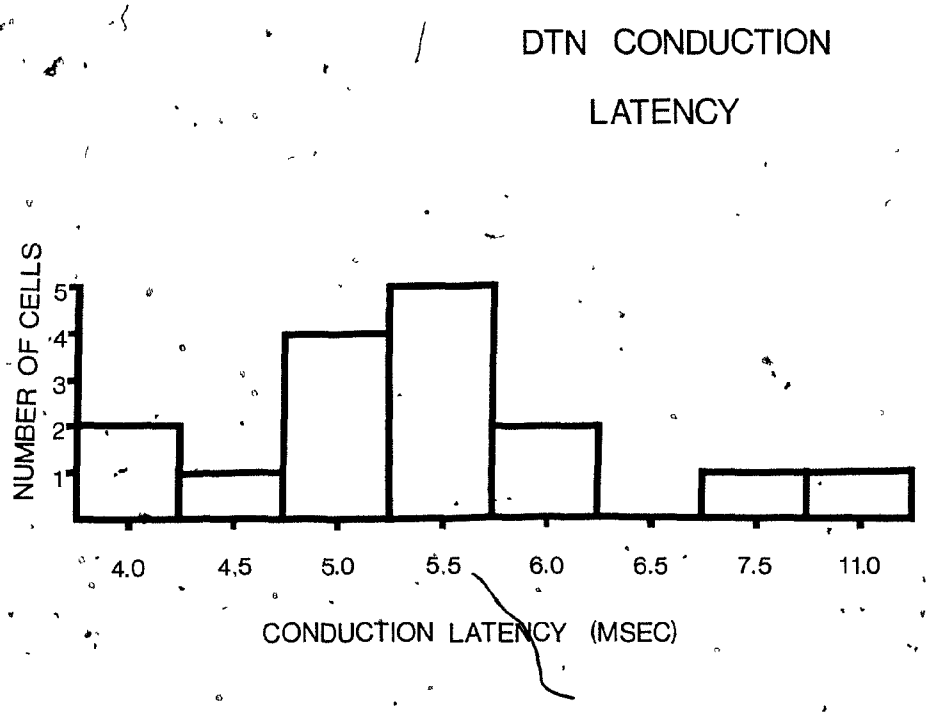
Distribution of conduction latencies for LTN input fibers. Figure 8A shows the conduction latency (in msec) versus the number of LTN cells. These latencies were obtained in response to a 100-150 uA stimulus pulse (1-50 usec in duration) delivered through bipolar stimulating electrodes placed in the optic chiasm. LTN latencies range from 4.0 to 6.5 msec, with a mean of 4.91 msec.

Figure 8B

Distribution of conduction latencies for DTN input fibers. There is an even broader range of conduction latencies for DTN units than was observed in the LTN, extending from 4.0 to 11.0 msec with a mean latency of 5.73 msec.


LTN CONDUCTION
LATENCY
NUMBER OF CELLS
10
9
8
7
6
5
4
3
2
1
3.5
4.0
4.5
5 0
5.5
6.0
6.5
7.0
CONDUCTION LATENCY (MSEC)

A


DTN CONDUCTION
LATENCY
NUMBER OF CELLS
5
4
3
2
1
4.0
4.5
5.0
5.5
6.0
6.5
7.5
11.0
CONDUCTION LATENCY (MSEC)

B

to produce optimal modulation. We have not observed surround inhibition in LTN and DTN cells. Stimuli which extend well beyond the borders of the receptive field continue to evoke vigorous responses from these units. Moreover, textured patterns proved to be more effective stimuli than low frequency square-wave gratings of equal areal extent.

Frequently more than one unit was recorded in succession during a single penetration. Whenever this occurred there were no obvious systematic changes in receptive field position, ocular dominance, velocity tuning, or direction selectivity. On some occasions, both upward and downward direction selective LTN cells were recorded in the same electrode track.

Finally, a variety of diffuse light responses was observed in the LTN and DTN. Units responsive only to changes in total luminance flux (and, therefore, not displaying direction selectivity) were encountered rarely.

DISCUSSION

Functional differentiation within the cat AOS

Some of the more striking response features of cells in the cat AOS are the very large receptive field dimensions, direction selectivity, and velocity specificity. In the following discussion, the characteristics of these properties will be compared to functional descriptions of AOS neurons of other species. The results of the present analysis suggest that units in the AOS may be involved in several different oculomotor contexts, including the monitoring of self-motion, the control of optokinetic nystagmus and/or smooth pursuit eye movements, as well as visual-canal and visual-otolith interactions.

Receptive field properties of cat AOS units

The response properties of AOS units have been examined in many different animals and, without exception, the receptive field dimensions are much larger on average than those of, for example, the geniculo-striate system. In the cat AOS, the largest receptive fields we encountered were approximately 100 deg in diameter. In addition, cat AOS units are modulated best by motion of extremely large textured stimuli. Among others, Gibson (1966 and 1981) has pointed out that movement of large parts of the visual field under normal circumstances arises from the organism's own motion, rather than from movement of external objects in the world. Based upon these and other considerations, Simpson et al. (1979) have proposed "that the AOS serves to

signal self-motion, a function similar to that of the vestibular system". In our experience, the receptive fields of cat AOS units average 60 deg in diameter and are driven best by large stimulus targets which encroach upon 2/3 or more of the total area. Thus, cat AOS cells exhibit area-response functions which are appropriate for the detection of whole-field motion.

Direction selectivity is a characteristic property of most cells in the cat AOS (see also Grasse and Cynader 1982). The ubiquity of this response feature suggests that the analysis of movement information is an important function performed by the AOS. There are noteworthy differences in the manner in which direction selectivity is expressed within the sub-nuclei of the AOS. For example, the distribution of preferred directions in the LTN is quite different from the distribution observed in the DTN (see figs. 4A and 5A). Conversely, there are also clear similarities in component groups of responses: e.g., the downward direction selective responses of LTN cells are virtually the vector equivalent of the downward directional responses of MTN units (see fig. 6B, and Grasse and Cynader 1982, fig. 3).

The pronounced anisotropy in the distribution of direction selectivity among units examined in our investigations can best be summarized by the statement that cat AOS units respond best for either vertically or horizontally-directed stimulus motion. Figure 4 shows that LTN cells respond best to either upward or downward vertical motion, while DTN cells are optimally modulated by horizontal motion.

Some investigators (Burns and Wallman 1980, Simpson et al. 1979) have drawn attention to the degree of angular separation between the major excitatory and inhibitory axes of direction selective units in

the AOS. These reports claim that the excitatory and inhibitory axes of AOS cells are not separated by 180 deg (non-colinear). In the cat AOS, on average, the E- and I-vectors of direction selective cells in the LTN and DTN are separated by approximately 180 deg (see fig. 7A & B). E- and I-vector separation in the cat MTN averaged 190 deg (Grasse and Cynader 1982). Because of the limited number of directions of motion sampled in our testing procedure, the mean angular separation of cat MTN units (190 deg) may not be significantly different from that of LTN and DTN units (180 deg). Thus, the cat AOS lacks the high incidence of direction selective cells with non-colinear excitatory and inhibitory axes which have been observed in the rabbit (Simpson et al. 1979) and chicken (Burns and Wallman 1980) AOS.

The velocity tuning of cat AOS cells displays significant differences when, e.g., the distribution of excitatory velocity tuning in MTN units is compared with tuning distributions obtained from LTN and DTN cells. Excitatory velocity tuning in the cat MTN is uniformly slow (i.e., near 1.0 deg/sec), while in LTN and DTN units the distribution is much more heterogeneous (see fig. 6B and 6D), showing a greater incidence of high velocity responses. In all three nuclei, units were observed whose excitatory and inhibitory velocity tuning displayed interesting dichotomies: some cat AOS cells showed greatest excitation to slow velocities (e.g., 1.0 deg/sec), while the deepest inhibition in the same cell was obtained in response to much faster stimulus velocities (e.g., 100 deg/sec).

Ocular dominance

On the basis of anatomical investigations (Farmer and Rodieck 1982, Feran and Grasse 1982, Hayhow 1959, Laties and Sprague 1966, Lin and Ingram 1974, and Marcotte and Updyke 1982), one might expect the eye contralateral to the recorded nucleus to drive units more effectively than the ipsilateral eye. Considering the small number of cells in the MTN (Grasse and Cynader 1982) which displayed significant ipsilateral input, it was surprising to observe such strong ipsilateral eye influence in the LTN and DTN (see figs. 7A and B). The NOT of the pretectum has been shown physiologically to possess a substantial proportion of binocularly-driven cells (Hoffmann and Schoppmann 1975, 1981). When the ipsilateral visual cortex is removed, NOT cells are driven almost exclusively by the contralateral eye (Hoffmann 1982). It is possible that the visual cortex provides the ipsilateral eye input to the LTN and DTN in an analogous fashion (Marcotte and Updyke 1982). However, it is still puzzling that the cat MTN, which appears to receive as much cortical input as the other AOS nuclei (Marcotte and Updyke 1982), displays so much less ipsilateral eye input. Experiments are presently underway to delineate sources of ipsilateral eye influence in the cat AOS.

Relationship between DTN and NOT

The direction selective responses recorded in the DTN closely resemble those described for units in the nucleus of the optic tract (NOT) of the pretectum (Hoffmann and Schoppmann 1975, 1981). The physiological landmarks used by Hoffmann and Schoppmann to locate the

NOT are very similar to those used to find the DTN in the present study. However, the location of the DTN as described in this report (see Fig. 1) is not the position of the NOT as indicated by Berman (1968), who places the NOT more anterior and medial near the fibers of the optic tract (compare fig. 1 with Berman 1968, plate 28, p. 56). Descriptions of the response properties in the DTN and NOT are almost identical. It is possible that the DTN and the NOT are two aspects of one continuous anatomical structure, although there presently is no anatomical evidence for this in the cat. Alternatively, there may be a dual representation of horizontal direction selectivity in the DTN and NOT, similar to the vertical direction selectivity in the LTN and MTN. This may reflect the presence of two parallel pathways carrying a similar type of whole-field motion information to different regions of the brain stem. Support for the parallel pathway hypothesis derives from anatomical findings which indicate that the NOT and MTN, but not the LTN and DTN, project to the cat inferior olivary complex (Feran and Grasse 1982, Walberg et al. 1981).

Efferent connections of the cat AOS

A number of anatomical and physiological studies have demonstrated that various anterior midbrain visual structures project to the inferior olivary complex (IOC) (Feran and Grasse 1982, Hoffmann et al. 1976, Maekawa and Simpson 1973, Maekawa and Takeda 1977, 1979, Simpson 1984, Takeda and Maekawa 1976, and Walberg et al. 1981). Some studies involving HRP injections into and around the dorsal cap (of Kooy) of the IOC, have purported to show that all three of the AOS nuclei in the rabbit send axons to this area (Maekawa and Takeda 1977, 1979 and

Takeda and Maekawa 1976). The dorsal cap provides a significant input to the cerebellar flocculus which projects to the vestibular nuclei. The vestibular nuclei, in turn, project to the oculomotor nuclei. However, there is some controversy concerning the efferent projections from the AOS in the rabbit. In a recent review of the AOS literature, Simpson (1984) states that the HRP-filled cells which Maekawa and Takeda claimed were in the LTN were actually in the posterior fiber bundle of the superior fasiculus of the accessory optic tract. It would appear that only the rabbit MTN and a small part of the DTN project to the dorsal cap of the inferior olive. Yet, even the observation that the DTN output fibers terminate in the olive is not firmly established. With regard to this issue, Simpson remarks that the accessory optic cells "that project to the caudal half of the dorsal cap are presumably part of the dorsal terminal nucleus." "An ipsilateral projection from the nucleus of the optic tract (NOT) to the dorsal cap has been reported in other mammals, but the likely contribution from the DTN has not been explicitly distinguished."

Walberg et al. (1981) injected HRP into the IOC of the cat and found that most back-filled cells were located in the posterior pretectal nucleus (PPN), and to a lesser extent in the NOT. Feran and Grasse (1982) also injected HRP into the cat IOC and, similar to the results of Walberg et al., a very small NOT projection was revealed. While Feran and Grasse reported a projection from the dorsal aspect of the MTN to the IOC, labelled cells were never observed in the DTN or the LTN of the cat AOS following these HRP injections.

Thus, at least for the cat MTN, there is one possible route by

which the visual information transferred through the AOS may influence neural structures involved in eye movement control. At the present time, however, the destination of the efferent axons of the cat LTN and DTN is not known.

Functional considerations

The predilection of cat AOS units for horizontal and vertical motion selectivity of large textured stimuli may be useful in several different contexts. These include visual-canal interactions, visual-otolith interactions, the control of optokinetic nystagmus and smooth pursuit eye movements, and in the sensation of self-motion. Before considering the possible theoretical significance of the present results, we shall consider structural and functional properties that distinguish the cat from the majority of animals in which the AOS has been examined thus far.

One important factor is the frontal position of the cat's eyes in the head. The forward migration of the eyes in the head throughout evolution has been accompanied by a parallel specialization within the central retina (i.e., the gradual development of a fovea or area centralis), which is only weakly approximated in a lateral-eyed animal such as the rabbit. The distribution of retinal ganglion cells projecting to the cat AOS displays a marked tendency toward central specialization, in that these cells are concentrated in the area centralis (Farmer and Rodieck 1982), to a greater extent than has been observed in the pigeon (Fite et al. 1981 and Karten et al. 1977) and rabbit (Oyster et al. 1980).

In the rabbit AOS Simpson et al. (1979) suggest that the direction

selectivity of the DTN, LTN, and MTN is organized around the planes of rotation of the semicircular canal planes of the vestibular system. The velocity tuning of rabbit MTN cells (from which the majority of Simpson's data were obtained) is uniformly slow (i.e., 0.1-1.0 deg/sec). In a frontal-eyed animal, the visual consequences of stimulation in the planes of rotation of the anterior and posterior semicircular canals, are very different than those for a lateral-eyed animal like the rabbit. For the purposes of this discussion we will assume that position of the eyes under paralysis is a reasonable approximation of the normal orbital position of the cat's eyes, and that the receptive field locations of cat LTN units are centered about a point 10 deg contralateral to the area centralis close to the horizontal meridian. Given these assumptions, vestibular stimulation in the plane of rotation of the anterior semicircular canal on the ipsilateral side, would produce motion across the center of a receptive field of a typical LTN cell with primarily an upward vertical component. In addition, the velocity and direction of visual stimulation resulting from head movement in a single canal plane, will vary as a function of both the position of the eye in the orbit and the locus of stimulation upon the retina. Rotation in the plane of the posterior semicircular canal would result in a similar direction of visual stimulation, but with a stronger horizontal component. While the characteristics of direction selectivity of LTN cells described in this report are not inconsistent with the notion that the major movement axes of LTN units may be aligned with the planes of rotation of one of the vertical semicircular canal planes, it cannot be uniquely

determined from the data obtained in the present study which vertical canal plane the direction selectivity of LTN cells may be aligned with. Moreover, it has not been determined in the cat or in any other species, whether AOS cells are more sensitive to rotatory as opposed to rectilinear stimulus motion.

An equally likely possibility, is that the conspicuous selectivity for upward and downward motion exhibited by LTN and MTN units could be used to signal the visual consequences of stimulation of the otolith organs. The otoliths respond, among other things, to linear accelerations which occur as a consequence of translatory motion of the head, and also to the effects of gravitational forces. This latter component is, of course, characterised by a substantial asymmetry in favor of vertical rather than horizontal forces. Therefore, in addition to visual-canal interactions, the marked selectivity for vertical motion shown by LTN cells also suggests that this nucleus may be involved in visual-otolith interactions.

A similar argument holds for the direction selectivity of DTN cells in which a marked trend toward horizontal direction selectivity was evident (see fig. 4D and F). To this extent, these data are not inconsistent with the notion that the direction selectivity of DTN cells may be aligned with the horizontal semicircular canal plane. Yet DTN cells may also provide information concerning the visual effects of horizontal translations of the head.

Two important types of self-motion which produce whole-field image displacements on the retinal surface are eye and head movements. There are two well known ocular stabilization reflexes (e.g., the vestibulo-ocular reflex and optokinetic nystagmus, or the VOR and OKN), which

serve to maintain the stability of the entire visual scene upon the retina. These reflexes have very specific requirements in terms of velocity. At low frequencies of stimulation, however, the gain of the VOR (eye velocity/head velocity) is reduced. Thus, visual input is required to assist in the control of stabilization at low frequencies or velocities of stimulation where the response of the vestibular system is the weakest (Melvill Jones and Milsum 1971). The slow velocity tuning exhibited by some AOS neurons (between about 1 and 13 deg/sec), suggests that these cells may comprise a possible source of visual input to VOR subsystems.

With regard to optokinetic eye movements, Colliwijn (1969) has shown that the optimal range over which horizontal OKN is driven in the rabbit occurs with visual stimulation below and up to 1.0 deg/sec. The bimodal velocity sensitivity observed in some cat AOS cells (e.g., fig. 6A) would be very useful for detecting the visual consequences of nystagmoid eye movements with reciprocally directed slow and fast components. The excitatory and inhibitory modulation observed in cat AOS units at high velocities also argues that this system may be sensitive to the visual consequences of saccadic eye movements, in addition to the quick phases of nystagmus.

Another type of oculomotor behavior which may generate whole-field motion is smooth pursuit. Smooth pursuit eye movements maintain the image of a small moving target on the fovea. During pursuit, ocular reflexes driven by whole-field motion must be entirely suppressed in favor of the relative stability of a small portion of the central visual field. In the cat, Evinger and Fuchs (1978) found that with and

without an optokinetic background, the cat accurately tracks moving targets up to velocities of less than 8.5 and 0.6 deg/sec respectively. The large receptive fields and velocity specificity observed in AOS units are, therefore, consistent with the notion that this system may also be involved in the control of smooth pursuit eye movements.

Alternatively, the influence of the whole-field motion information supplied by the cat AOS may be used as an inhibitory drive for the active suppression of compensatory eye movements which would otherwise interfere with the proper action of smooth pursuit control. Information supplied by the AOS may be used to suppress compensatory eye movements such as OKN while the animal is tracking small moving objects. For the unique specification of the direction and velocity of whole-field motion produced during eye and head movement, it is required that the monitoring system possess visual sensitivity to large field movement encompassing a relatively broad range of directions and velocities. This, of course, is an apt description of the properties found in the AOS. Westheimer and Blair (1974) were the first to propose that the AOS may be involved in smooth pursuit eye movements.

It should be kept in mind that both in the case of OKN and smooth pursuit, the spatial framework, if any, within which such eye movements may be "organized," will not necessarily be that of the semicircular canals of the vestibular system.

Concluding remarks

Throughout the life of an organism there will be many types of eye, head, and body movement in which whole-field motion information will be generated in the visual system. The direction and velocity selec-

tivity of cells in the cat AOS, along with their large receptive fields, make these units well suited to detect the visual consequences of some of these movements. In the face of so large an anatomical ignorance as that which presently surrounds the efferent connections of the LTN and DTN in the cat, support for this interpretation is based largely upon the physiological response properties exhibited by AOS units. At the present time it is not possible to constrain the cat AOS to a more specific functional role. This study and similar investigations in other species, have only shown that the direction and velocity of whole-field motion is signaled unambiguously by AOS neurons. Thus, in theory at least, there is no reason why this particular source of whole-field information could not be used in any oculomotor context where it has obvious utility.

PART II

ALTERATIONS IN RESPONSE PROPERTIES IN THE LATERAL AND DORSAL TERMINAL NUCLEI OF THE CAT ACCESSORY OPTIC SYSTEM FOLLOWING VISUAL CORTEX LESIONS

INTRODUCTION

The medial (MTN), lateral (LTN), and dorsal (DTN) terminal nuclei of the accessory optic system represent a phylogenetically ancient branch of the primary visual system which has recently been implicated in the control of optokinetic nystagmus, and visual-vestibular interactions. In the cat, retinal input to these nuclei originates primarily from slowly conducting afferent fibers of the contralateral eye (Hayhow 1959, Laties and Sprague 1966, Grasse and Cynader 1982, 1983, Farmer and Rodieck 1982, Feran and Grasse 1982, and Marcotte and Updyke 1982). However, a large proportion of single units in the cat LTN and DTN may be driven through both eyes (Grasse and Cynader 1984). Recent autoradiographic investigations by Berson and Graybiel (1980) and Marcotte and Updyke (1982) have demonstrated a large and diffuse afferent projection to the cat AOS from the ipsilateral visual cortex. These results raise the possibility that the ipsilateral eye input observed in the responses of LTN and DTN cells may arise by way of the cortical projection upon these nuclei. Further support for this hypothetical interaction is obtained by analogy with findings in other midbrain nuclei such as the superior colliculus and the nucleus of the optic tract (of the pretectum), in which decortication results in reduction or abolition of ipsilateral eye responses (Wickelgren and Sterling 1969, Berman and Cynader 1972, and Hoffmann 1982).

To investigate this possibility, a series of experiments was performed in which the visual cortex was removed unilaterally in normal adult cats. Single unit responses were then examined in the LTN and DTN ipsilateral to the decortication. In an earlier investigation

of the cat MTN (Grasse 1981 and Grasse and Cynader 1982), it was found that very few MTN cells exhibited binocular responses, and, therefore, in the present experiments attention was confined to the LTN and DTN. AOS units in the decorticate animal were tested quantitatively for direction selectivity, ocular dominance, and velocity specificity in the same manner as Part I.

METHODS

Recording Preparation

Most aspects of the recording preparation employed in this study have been described previously (see Part I and Grasse and Cynader 1982). Briefly, cats were anesthetized with intravenous (i.v.) sodium thiopental (2.5mg/kg) as required, the trachea was intubated, and the animal was placed in a modified stereotaxic frame which minimally obstructed the field of view. Paralysis was induced and maintained throughout the experimental session with i.v. administration of gallamine triethiodide (10mg/kg/hr) during which time animals were artificially respired with a 70:30 mixture of N_2O and O_2. Halothane (1.5%) was introduced into the gas mixture for the entire duration of surgery and discontinued thereafter. Monitoring of EEG activity under these conditions reveals a preponderance of slow-wave activity (see also Cynader and Berman 1972). End-tidal CO_2 was monitored and maintained near 4.0%. Wound margins were generously infiltrated with a long lasting local anesthetic (Bupivacaine hydrochloride 0.25%). Body temperature was kept near 37.5 C and controlled by a thermostatic heating pad. Pupils were dilated with atropine (1%) and nictitating membranes retracted with neosynephrine (10%). Contact lenses containing 4mm artificial pupils were selected by retinoscopy to focus images projected onto a tangent screen 46 inches from the eye. The locations of optic discs and areae centrales on the tangent screen were determined by the reversing ophthalmoscope technique.

The visual cortex was exposed by removing an 8mm by 16 mm bone flap

over one hemisphere, sparing the mid-sagittal sinus and overlying bone. The dura was opened and retracted, and cortical tissue was removed by subpial suction. The bottom of figure 9 shows a schematic drawing of the dorsal surface of the cat brain (shaded region shows the anterior-posterior and medio-lateral extent of the cortical lesion). Representative coronal sections illustrating the dorso-ventral extent of the lesion (blackened area) at various anterior-posterior levels are drawn above. The illustration in fig. 9 is a conservative estimate of the damage to the visual cortex. Lesions which spared the most ventral-lateral parts of visual cortex (i.e., parts of area 18 and 20), gave rise to similar results in the LTN and DTN. After surgery was completed, the brain cavity was filled with warm 0.5% agar gel. The animal was allowed to recover for a period of at least 3 hours before electrical recording began.

Electrical Recording

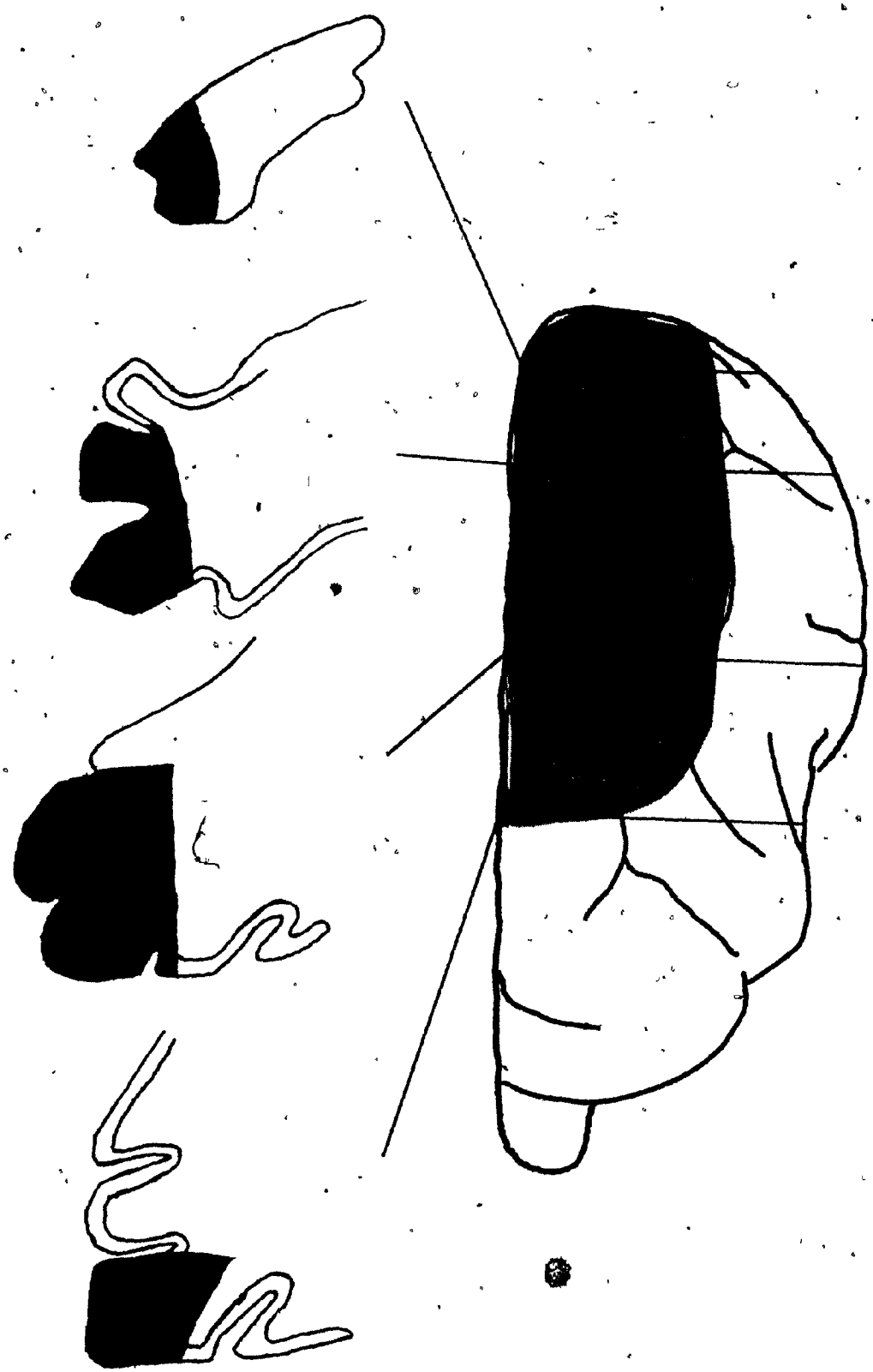
Single-unit recording methods were conventional and as described previously (Grasse and Cynader 1982). For details of the procedure used to locate the LTN and DTN see Part I. In all cases, single-unit recordings were made in the LTN and DTN ipsilateral to the cortical ablation.

Visual Stimulation And Data Collection/Analysis

As in Part I, a random-dot pattern (Julesz 1964, fig. 1) was employed as a stimulus target which extended approximately 100 deg vertically by 80 deg horizontally. Once the preferred and non-

Figure 9

Schematic drawing of frontal sections representing various anterior-posterior levels lying perpendicular to the dorsal aspect of the cat brain (shaded area at the bottom). The frontal sections of lesioned areas of the visual cortex (shown in black) are referred to the shaded region on the dorsal surface.



preferred directions were determined quantitatively, the following procedure was employed to assess ocular dominance: the stimulus moved along the preferred and non-preferred directions 8 times each at a constant velocity, first, with binocular viewing, second, each eye separately, and third, the binocular condition was repeated. The resting discharge was sampled in each of the three separate viewing conditions. The response to binocular stimulation served as a control condition against which any non-specific changes in cellular response characteristics (such as habituation) could be evaluated.

RESULTS

The data presented in Part II were obtained from 14 cats which underwent acute unilateral decortication. Of the 77 AOS units which were examined, 39 were in the LTN and 38 in the DTN. Under the conditions of these experiments, LTN and DTN units did not show any apparent signs of trauma due to the surgical removal of the visual cortex. For example, the average resting discharge sampled in the absence of moving stimuli for both the LTN and DTN of the visual cortex lesioned (VCL) animals was not significantly different from that of normal cats (average resting discharge for normal LTN was 21 spikes/sec versus 17 spikes/sec for VCL; average resting discharge for normal DTN was 11 spikes/sec versus 15 spikes/sec for VCL). In addition, overall responsivity was not depressed in either the AOS nuclei or in the superior colliculus. AOS units were located using the same physiological landmarks which were described in Part I.

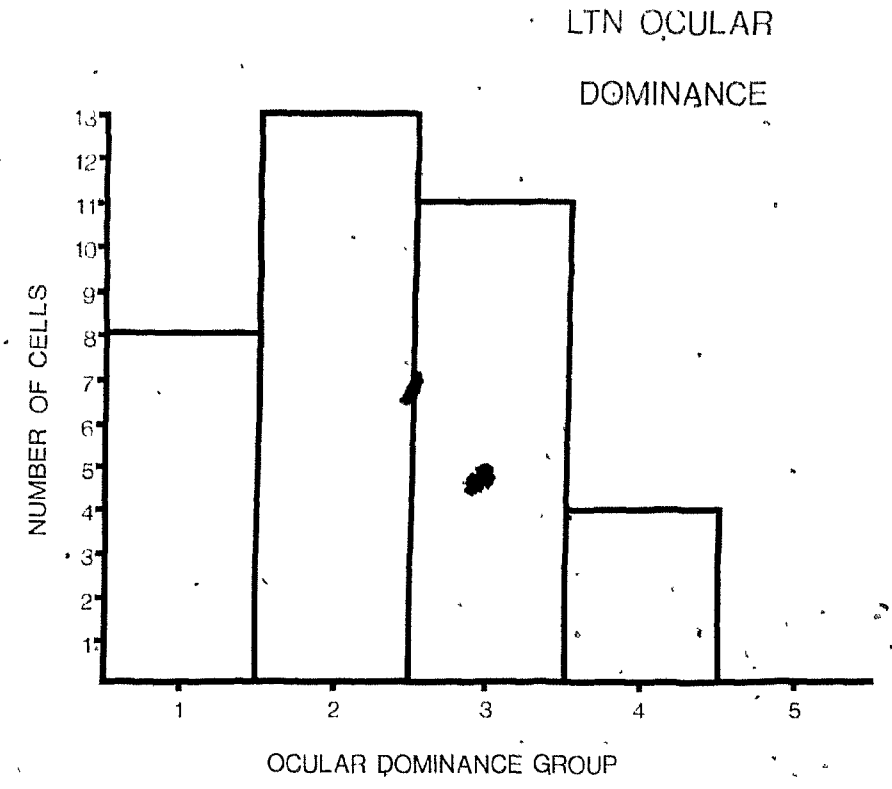
Ocular Dominance

The ocular dominance distribution for the normal LTN is shown in figure 10A (upper panel). In this and the following illustrations, the data from the normal LTN and DTN were obtained from Part I. Units in ocular dominance (OD) group 1 and 5 are driven best via the contralateral and ipsilateral eye respectively. Group 3 units are driven equally well through each eye. LTN cells of normal cats prefer input from the contralateral eye. Yet many LTN cells display a pronounced influence from the ipsilateral eye (groups 2 and 3). In contrast, figure 10B (lower panel) shows the ocular dominance

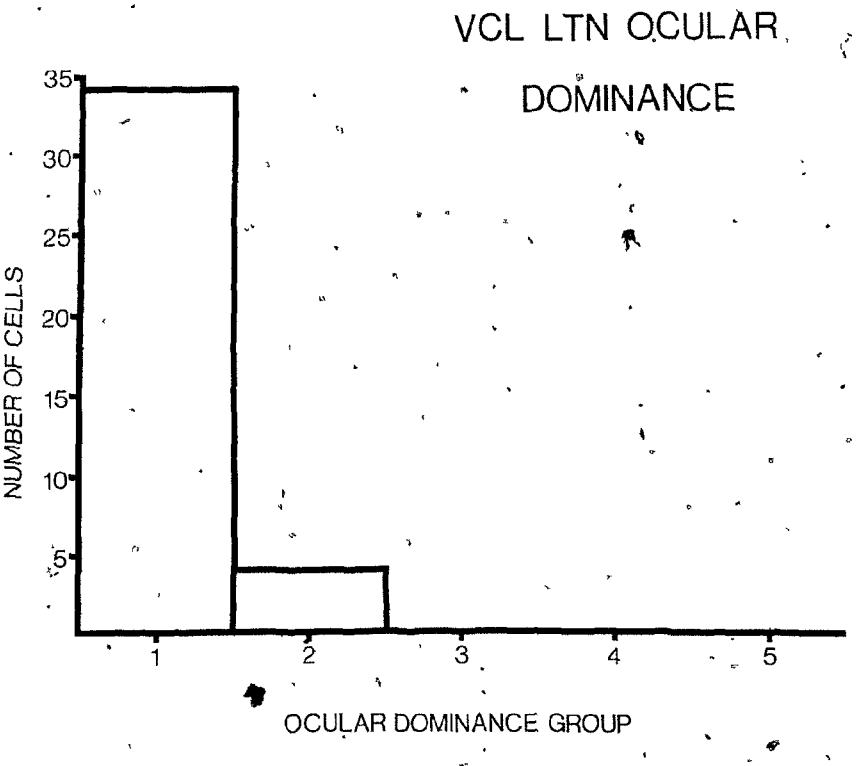
Figure 10

A) Normal cat LTN ocular dominance distribution. This histogram displays the ocular dominance group versus the number of LTN cells encountered. OD groups 1 and 5 denote units driven exclusively via the contralateral and ipsilateral eye respectively (with respect to the recording site). LTN cells driven equally well through both eyes are classified as OD group 3. The majority of LTN units (78%) fall into OD groups 2-4, indicating a significant input from the ipsilateral eye.

B) LTN ocular dominance distribution in visual cortex lesioned (VCL) cats. Conventions for this figure are identical to those for fig. 10A. The major effect of decortication upon ocular dominance is a severe reduction in the ipsilateral eye influence observed in the normal LTN unit population (see fig. 10A). Virtually all LTN units in the VCL cats are entirely dominated by the contralateral eye (OD group 1).


LTN OCULAR
DOMINANCE
NUMBER OF CELLS
13
12
11
10
9
8
7
6
5
4
3
2
1
1
2
3
4
5
OCULAR DOMINANCE GROUP

A


VCL LTN OCULAR
DOMINANCE
NUMBER OF CELLS
35
30
25
20
15
10
5
1
2
3
4
5
OCULAR DOMINANCE GROUP

B

distribution obtained from the decorticate LTN. This histogram shows that the purely contralaterally driven LTN units (group 1) were the most prominent class encountered, while the binocularly driven cells of groups 2 and 3 which were so common in the normal LTN (see fig. 10A), are encountered rarely (4 OD group 2 cells out of 39), or not at all (0 OD group 3 cells out of 39).

An equally striking effect was observed in the DTN ocular dominance of decorticate cats. Figure 11A (upper panel) shows the ocular dominance distribution for the normal DTN cell population. As in the normal LTN, the distribution of fig. 11A discloses a large proportion of binocularly driven neurons (OD groups 2-4) in the normal DTN population with an overall contralateral preference. However, following cortical ablation, the presence of ipsilateral eye input in the responses of DTN almost completely vanishes (see fig. 11B, lower panel). Thus, one very pronounced effect of the cortical lesion is to render most DTN cells monocularly driven through the contralateral eye. The magnitude of this effect is even more striking in view of the small number (3 of 41) of purely contralaterally driven cells (i.e., OD group 1) which were encountered in the normal DTN (see fig. 11A, upper panel).

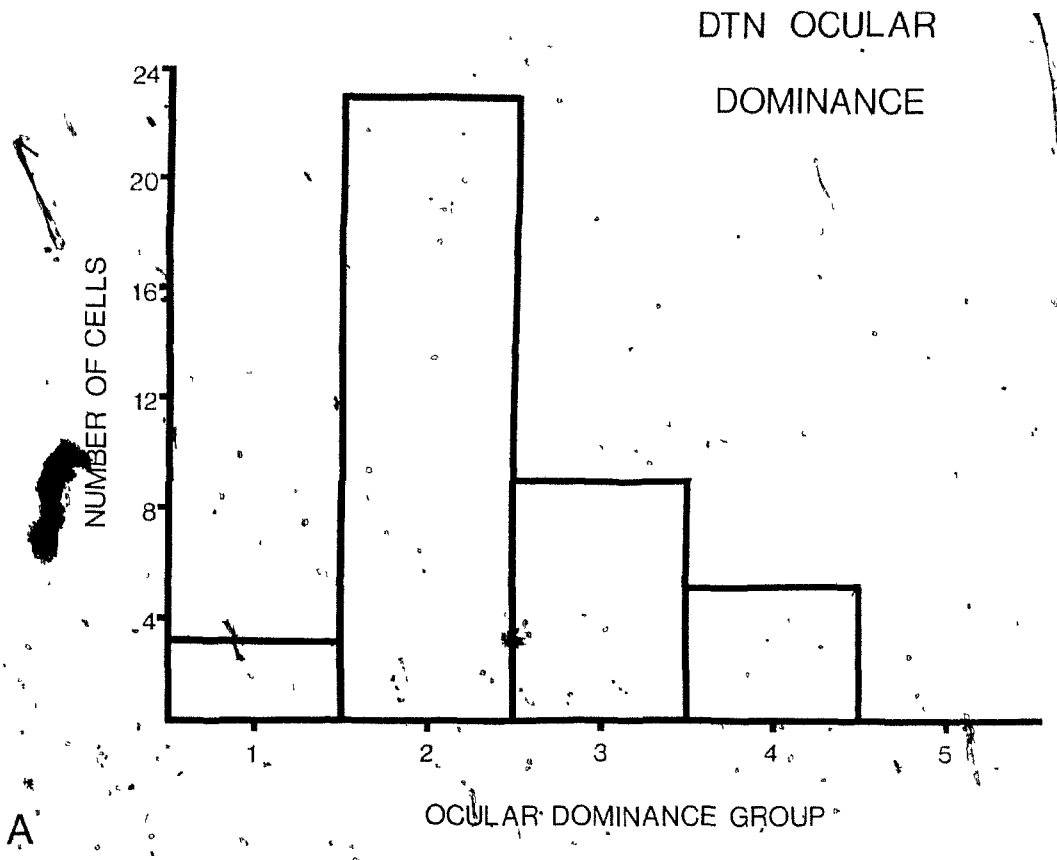
Direction Selectivity

Unlike the effects of decortication on the response properties of cells in the superior colliculus (Wickelgren and Sterling 1969, Berman and Cynader 1972, 1975), direction selectivity is not abolished in the cat LTN and DTN following removal of the visual cortex. There are, however, notable changes in the distribution of preferred and non-

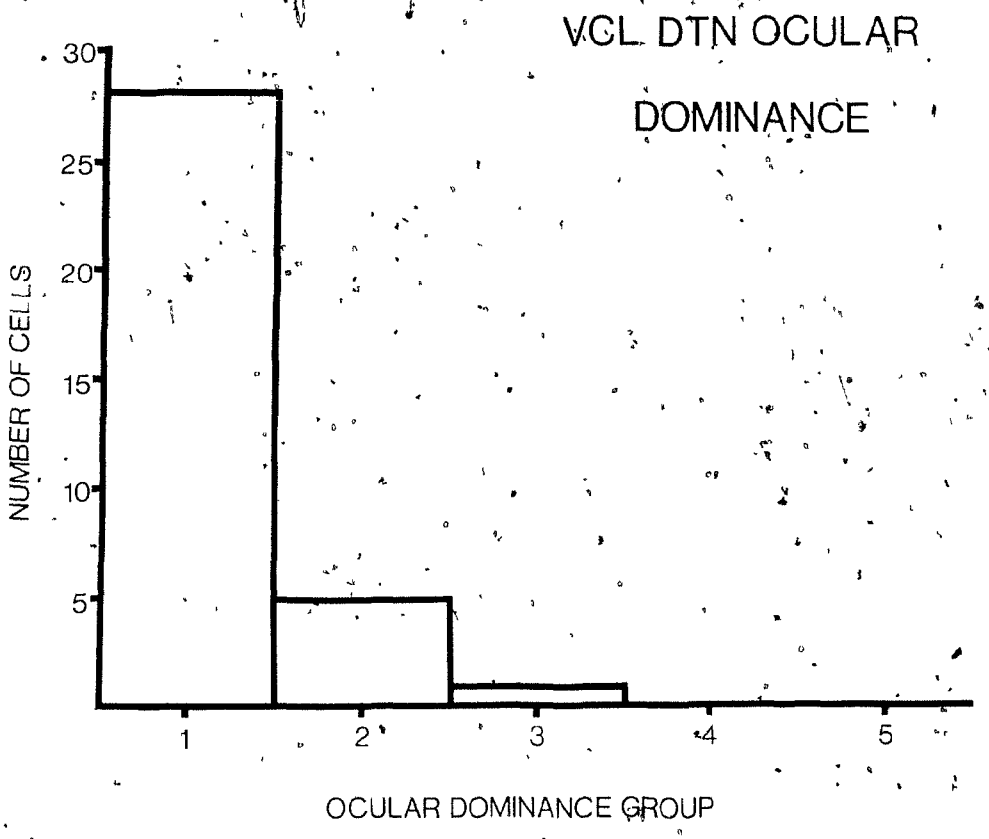
Figure 11

A) Normal cat DTN ocular dominance distribution. Similar to the normal LTN ocular dominance distribution (fig. 10A) the normal cat DTN unit population contains a high incidence (93%) of cells with some form of ipsilateral eye input (OD groups 2-4). Most DTN cells fall into OD group 2, indicating a predominant contralateral eye input together with a relatively weaker input from the ipsilateral eye. Only 3 DTN units are completely dominated by the contralateral eye.

B) DTN ocular dominance distribution in decorticate cats. Figure 11B shows the marked effects of decortication on the DTN ocular dominance distribution. In contrast to the normal DTN unit population (see fig. 11A, above), decorticate cat DTN cells are driven primarily through the contralateral eye only (OD group 1). As in the VCL cat LTN (see fig. 10B), the DTN unit population in decorticate cats shows a sizable reduction in the incidence of binocularly-driven neurons (OD groups 2-4). Conventions in fig. 11A and B are identical to fig. 10.


DTN OCULAR
DOMINANCE
NUMBER OF CELLS
24
20
16
12
8
4
1
2
3
4
5
OCULAR DOMINANCE GROUP

A


VCL DTN OCULAR
DOMINANCE
NUMBER OF CELLS
30
25
20
15
10
5
1
2
3
4
5
OCULAR DOMINANCE GROUP

B

preferred directions in both the LTN and DTN as a result of cortical lesions. The left hand side of fig. 12A shows the distribution of preferred directions (E-vectors), and the right hand side of fig. 12A the distribution of non-preferred directions (I-vectors), for the normal cat LTN. The overwhelming trend in both the E- and I-vector distributions obtained in the normal LTN is for approximately equal numbers of vertically up and down direction selective units. The distributions obtained from decorticate cat LTN are shown in fig. 12B. After cortical ablation the number of LTN cells displaying maximal excitation for upward stimulus motion is severely reduced. Only 25% of the cells encountered prefer upward stimulus motion, compared with approximately 50% in normal cats.

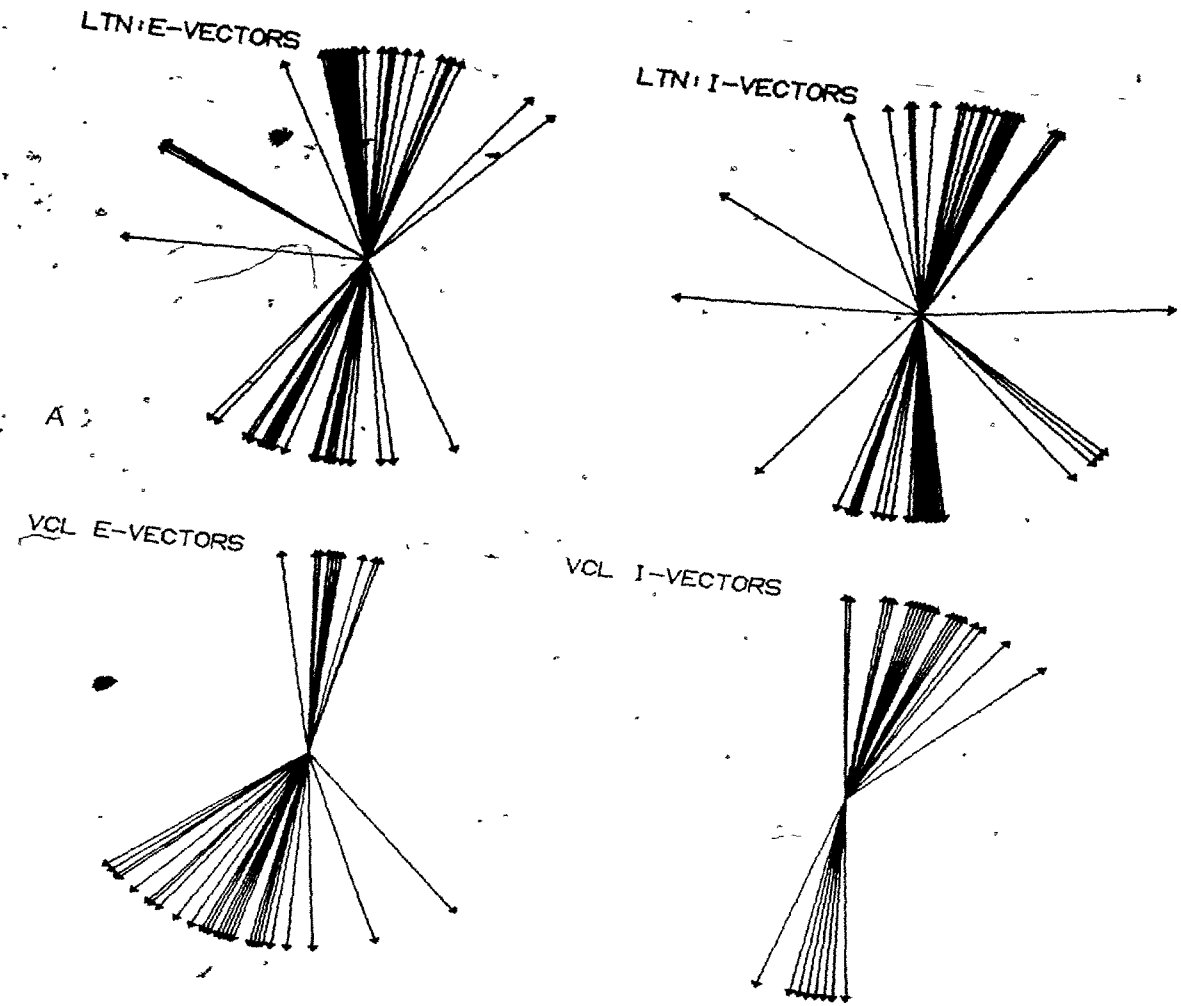
The effect of decortication on the distribution of preferred and non-preferred directions found in the DTN was not as pronounced as that observed in the LTN. The distribution of E- and I-vectors for the normal cat DTN is shown in fig. 13A. Fig. 13B shows the comparable distribution of E- and I-vectors obtained from the decorticate DTN. From a comparison of these two sets of distributions, it is evident that cortical ablation has not substantially altered the character of the E- and I-vector distributions for the DTN. There appear to be a few more DTN cells preferring vertically downward stimulus motion, and a few less preferring vertically upward stimulus motion. But, overall, the majority of DTN cells display maximal excitation for stimulus motion in the horizontal-nasal (medial) direction whether the visual cortex is present or not.

In previous studies of the cat AOS (Grasse 1981 and Grasse and Cynader 1982, 1983) an overall measure of direction selectivity was

Figure 12

A) Total distribution of E- and I-vectors for the normal cat LTN. From the vector analysis of individual cells, LTN E- and I-vectors have been collected and plotted together into a single circular distribution. All vectors have been given unit-lengths to emphasize dispersion. Two major groups approximately equal in number are apparent, showing an upward and downward directional preference respectively. All vector distributions in this and the following 4 figures (i.e., figs. 13-16) have been drawn to represent the visual field perspective of the animal's left eye. Thus, the left hand side of each vector plot represents the lateral visual field, and the right represents the medial visual field.

B) Total distribution of E- and I-vectors for the LTN of decorticate cats. Unlike the distributions obtained from the normal cat, the E- and I-vector distributions from the decorticate LTN show a clear inequality in the number of upward- versus downward-directed vectors. Approximately 3 times as many LTN units prefer downward (27 cells) as opposed to upward (10 cells) stimulus motion.


LTN: E-VECTORS
LTN: I-VECTORS
A
VCL E-VECTORS
VCL I-VECTORS
B

provided for entire groups or sub-groups of AOS cells by taking the vector analysis applied to individual response profiles, and re-applying it to larger ensembles of vectors. The "hyper vectors" which are generated in this fashion, possess a certain utility in the present context where we are interested in comparing AOS directional properties en masse in the normal and decorticate animal.

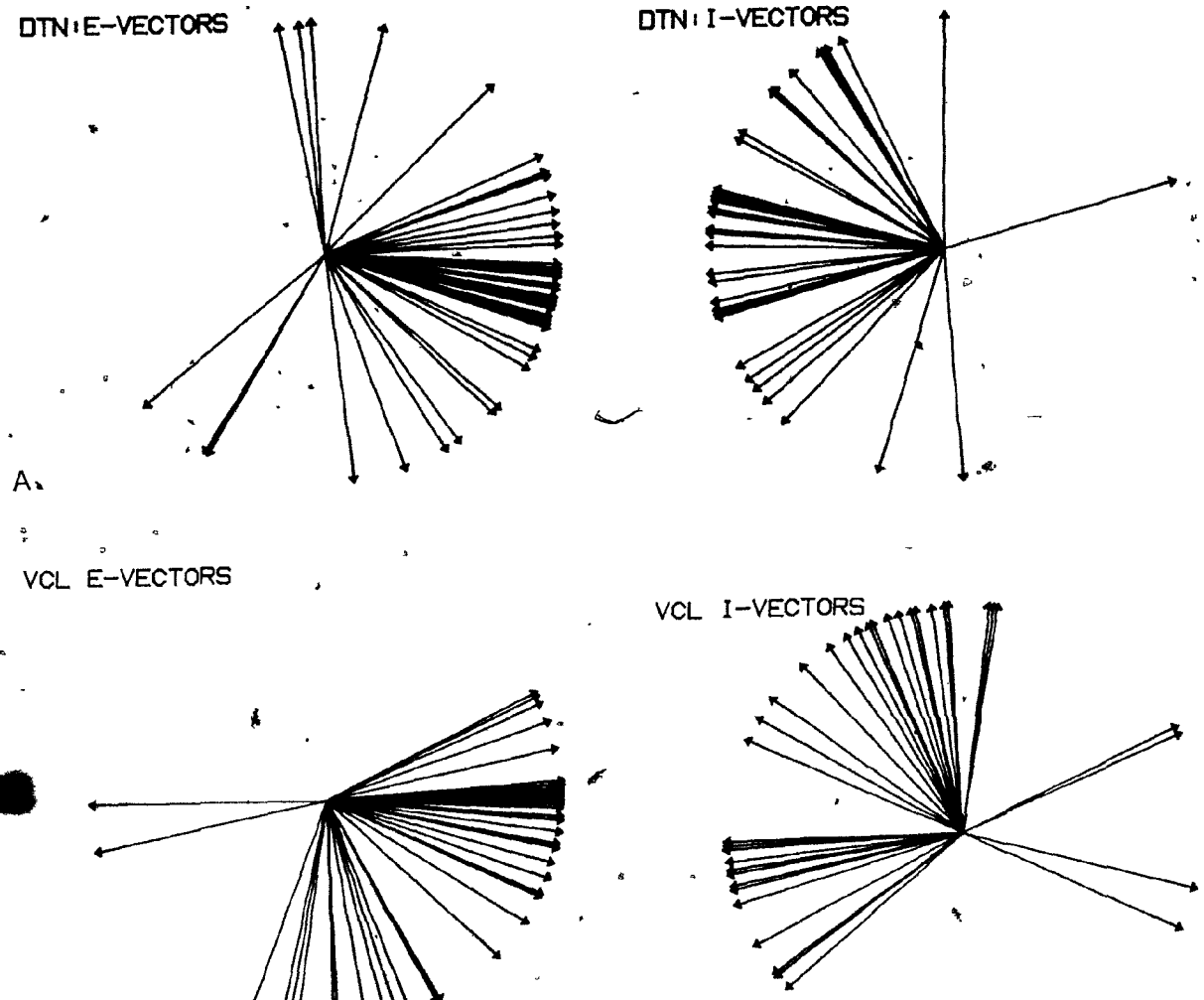
When the vector analysis is applied to the upward directed E-vectors of fig. 12A (left panel) and to the downward directed I-vectors (right panel fig. 12A) of the normal LTN, two hyper-vectors may be derived which are illustrated in the left hand side of fig. 14A. The most noteworthy features of these two vectors are that they point almost straight up and down, they are separated by approximately 180 deg. The hyper-vectors generated from the corresponding group of upward E-vectors (fig. 12B, left panel) and downward I-vectors (fig. 12B, right panel) of the decorticate LTN are shown in the left hand sample are skewed off vertical by equal amounts (approximately 10 deg) in opposite directions. The angular separation between the E- and I-vectors of fig. 14B, like those of fig. 14A, is approximately 180 deg.

The hyper-E- and I-vectors for the downward group of LTN cells derived from the normal and decorticate cat are shown in the right hand side of fig. 14A and B respectively. The E-vector (solid arrow) for the right hand pair of vectors in fig. 14A was generated from the downward directed vectors of fig. 12A, left panel, while the I-vector (broken arrow) of fig. 14A was generated from the upward directed I-vectors of fig. 12A, right panel. These vectors point almost straight up and down, and are separated by 180 deg. The hyper-E- and I-vectors for the downward group of decorticate LTN cells are shown in the right

Figure 13

A) Total distribution of E- and I-vectors for the normal DTN. Most DTN units display greatest excitation for horizontal stimulus motion toward the medial hemifield (left hand side of fig. 13A), and deepest inhibition for motion in the opposite direction (right hand side of fig. 13A). A few DTN cells exhibit preferred and non-preferred directions for vertical stimulus motion.

B) Total distribution of E- and I-vectors for the DTN of decorticate cats. While the predominant trend for horizontal direction selectivity is still clear in the decorticate DTN unit population, there is an increase in the number of cells preferring downward stimulus motion, and a decrease in the number of units preferring upward motion (left hand side of fig. 13B).


DTN: E-VECTORS
DTN: I-VECTORS
A.
VCL E-VECTORS
VCL I-VECTORS
B

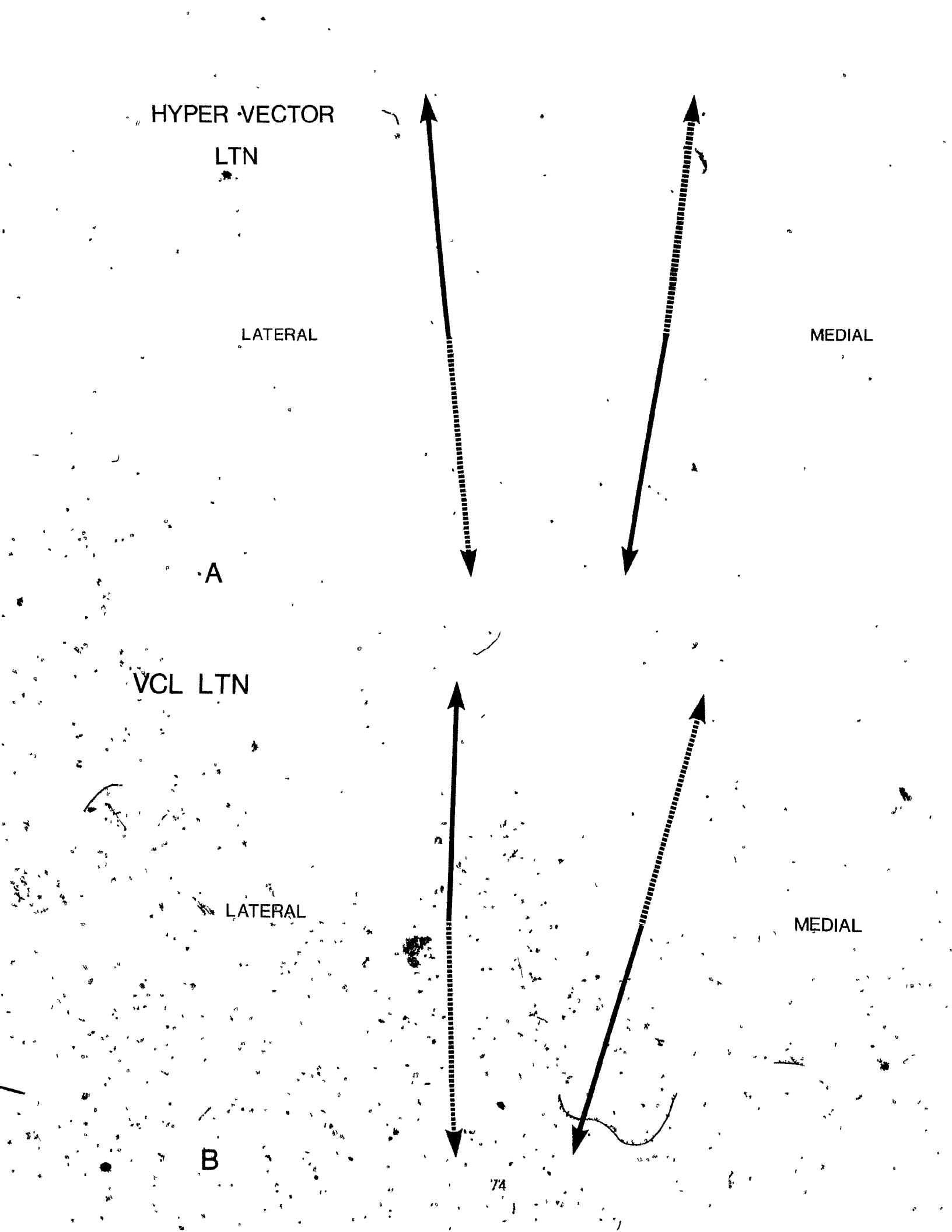
hand side of fig. 14B. In most respects the hyper-vectors shown in fig. 14A and B are very similar. Thus, while LTN units preferring upward stimulus motion are found less frequently in the decorticate LTN, when encountered, these neurons exhibit direction selective properties which are virtually identical to those exhibited by normal LTN cells despite the lack of cortical input.

Hyper-vectors were also generated for the population of DTN cells in normal and decorticate animals. Figure 15A shows the hyper-E- (solid arrow) and I-vector (broken arrow) derived from the E- and I-vectors of fig. 13A. A preponderance of cells exhibiting maximal excitation for horizontal motion from lateral to medial (temporal to nasal) is evident from either the total vector plot of individual DTN units (fig. 13A, left panel), or from the hyper-E-vector (solid arrow) of fig. 15A. To a large extent, this selectivity for horizontal motion persists in the decorticate DTN, but with some modification. It has already been pointed out that in decorticate cats, the distribution of E-vectors (fig. 13B, left panel) consists of more units with a strong vertical, downward component, and fewer units with a strong vertical, upward component (compare fig. 13B, left panel, with fig. 13A, left panel). These differences in component directions (i.e., vectors) lead to the shift away from horizontal observed in the hyper-vectors of fig. 15B. If the hyper-vectors in each case are calculated only from those DTN vectors in both the normal and the decorticate sample which possessed a greater horizontal than vertical vector component, then the resulting hyper-vectors would be indistinguishable. Thus, the difference in overall directional bias exhibited by DTN cells in the lesioned animals seems to be due to differences in the relative con-

Figure 14

A) Hyper-E- and I-vectors for normal cat LTN cells. Hyper-vectors are derived by repeating the vector analysis on each group of individual cell response vectors. The left hand side of fig. 14A illustrates 2 hyper-vectors representing the overall directional bias of upward-preferring (solid arrow) and downward-non-preferring (broken arrow) LTN cells. The right hand side of fig. 14A shows the downward-preferring (solid-arrow) and upward-non-preferring (broken arrow) hyper-vectors derived from the remaining unit population of normal LTN cells. Note that these vectors deviate only slightly from pure vertical.

B) Hyper-E- and I-vectors for LTN cells in decorticate cats. Fig. 14B shows the 2 sets of hyper-vectors derived from the 2 groups of LTN cells encountered in the decorticate cat. Except for the fact that the vectors on the left hand side of fig. 14B were generated from many fewer cells (10 cells for the VCL cats, as opposed to 25 for normal cats), the directions are very similar. The downward-preferring and the upward-non-preferring hyper-vectors (right hand side of fig. 14B) are also very similar to the corresponding hyper-vectors obtained from the normal LTN unit population. Thus, whereas the incidence of directional response types may change in the decorticate cat LTN, the overall directional bias of existing sub-groups is not significantly different from normal.


HYPER VECTOR
LTN
LATERAL
MEDIAL
A
VCL LTN
LATERAL
MEDIAL
B

tributions made by DTN units with greater vertical rather than horizontal direction selective component.

Velocity Tuning

In addition to the marked effects of decortication upon the ocular dominance distribution and direction selectivity of LTN and DTN cells, a large change in the distribution of excitatory and inhibitory velocity specificity was also observed in the responses of cells in these nuclei. The distribution of velocity tuning for the normal LTN is shown in fig. 16A and B. LTN response profiles have been segregated into those displaying upward (fig. 16A) versus downward (fig. 16B) direction selectivity (DS). It is evident from the histograms of figs. 16A and B that most of the high velocity tuned cells in the normal LTN are also sensitive to upward stimulus motion, while the majority of the low velocity tuned cells prefer downward directed motion.

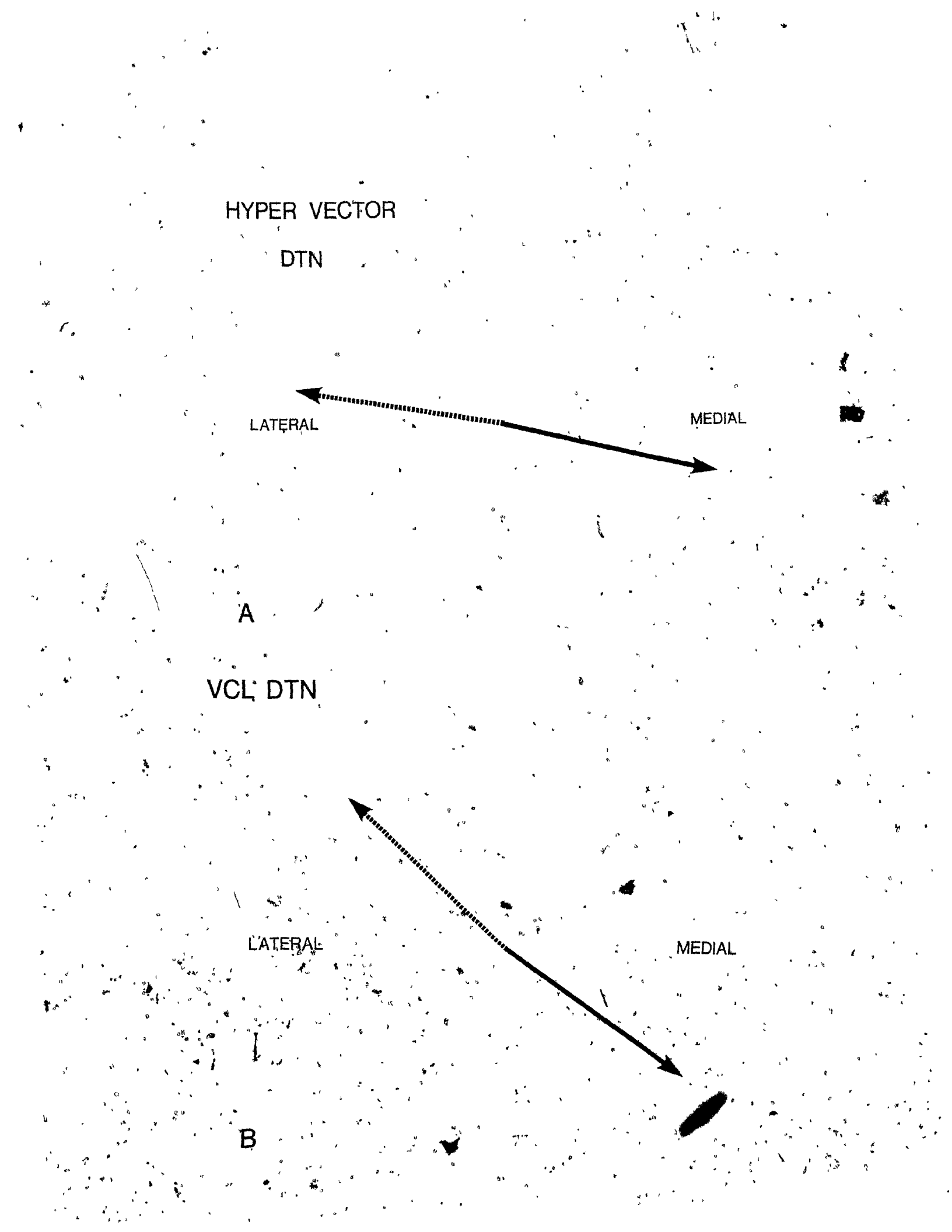
Figure 16C and D illustrates the velocity tuning distributions obtained from the visual cortex lesion (VCL) animals. These histograms show that in the decorticate LTN, the velocity tuning is relatively low regardless of the preferred direction.

The shift toward lower stimulus velocities was also observed in the inhibitory component of the velocity response. The lower inverted portion of fig. 16A-D illustrates the distribution of stimulus velocities which evoked the deepest inhibition in the normal and decorticate cat LTN. For upward preferring cells in the normal LTN, one observes a bimodal distribution with cells displaying deepest inhibition at either 0.8 or 12.8 deg/sec. For downward preferring units, deepest inhibition is found near 1 deg/sec. The inhibitory

Figure 15

A) Hyper-E- and I-vectors for normal cat DTN cells. Re-application of the vector analysis to the total distribution of E- and I-vectors for the DTN unit population yields the 2 hyper-vectors shown in fig. 15A. Conventions for this figure are identical to fig. 14. While the hyper-E-vector (solid arrow) points into the horizontal-medial visual field, the hyper-I-vector (broken arrow) points into the horizontal-lateral visual hemi-field.

B) Hyper-E- and I-vectors for DTN cells in decorticate cats. The overall bias for horizontal stimulus motion is still clear in the hyper-vectors shown in fig. 15B which were derived from the VCL unit population. However, the hyper-E-vector points down into the inferior-medial quadrant, and the hyper-I-vector points upward into the superior-lateral visual field. There is a much greater difference between the normal and decorticate cat hyper-vectors for the DTN than for the LTN unit populations.


HYPER VECTOR
DTN
LATERAL
MEDIAL
A
VCL DTN
LATERAL
MEDIAL
B

velocity tuning of decorticate cat LTN cells lacks the high velocity tuning observed in the intact cat. Instead, the lower portion of fig. 16C and D shows a marked shift toward low velocities. This shift is very pronounced in the small LTN unit population which prefers upward motion, but can also be observed in the downward-preferring group.

The alterations in velocity tuning observed in LTN units following cortical ablation were mirrored to some extent in DTN velocity tuning profiles obtained under similar conditions. Fig. 17A shows the normal distribution of excitatory and inhibitory velocity tuning for the DTN of intact animals. While the peak in the distribution of normal DTN velocity responses occurs at 6.4 deg/sec, with a healthy proportion of cells displaying maximal excitation for even higher stimulus velocities, the excitatory velocity tuning of DTN cells in the decorticate cat is concentrated near the low velocities with a peak at 0.8 deg/sec.

In a similar fashion the inhibitory velocity tuning of the DTN is shifted to lower velocities as a result of decortication. The lower portion of fig. 17A shows that the stimulus velocity at which most DTN units displayed deepest inhibition was 25.6 deg/sec. Brief inspection of fig. 17A, shows that not a single DTN cell in the intact animal displays deepest inhibition at stimulus velocities less than 1.6 deg/sec. Following these cortical lesions, a drastically different picture emerges (see fig. 17B), in which the inhibitory velocity tuning is concentrated at low velocities between 0.2 and 6.4 deg/sec, with a peak at 0.4 deg/sec.

Figure 16

A) Normal cat LTN excitatory and inhibitory velocity tuning for cells displaying direction selectivity for upward stimulus motion (upward DS). The conventions of this and the following figure (fig. 17) are identical. Along two directions of stimulus motion aligned with the two directions of maximal and minimal firing for individual LTN cells, units were tested for response to a wide range of stimulus velocities (from 0.2 to 204.8 deg/sec). Each velocity was presented 8 times in a randomized sequence. The upward- and downward-directed bar graphs of fig. 16A show the velocity at which maximal excitation (upward) and the deepest inhibition (downward) were obtained versus the number of LTN cells preferring upward stimulus motion. Most units in this group achieve greatest excitation between 3.2 and 12.8 deg/sec. Some of the remaining units show preferences for faster velocities (25.6 to 102.4 deg/sec). The downward-directed bar histogram illustrates the distribution of stimulus velocities which evoked deepest inhibition. For inhibitory velocity tuning, the range of non-preferred velocities shown in fig. 16A suggests a bimodal rather than a continuous distribution, with peaks at 0.8 and 12.8 deg/sec.

B) Normal cat LTN velocity tuning for cells displaying direction selectivity for downward stimulus motion (downward DS). Unlike the upward group of LTN cells shown in fig. 16A, most downward direction selective LTN units are sensitive to relatively slow stimulus velocities around 0.8 to 1.6 deg/sec.

C) LTN velocity tuning for upward direction selective cells in decorticate (VCL) cats. In contrast to the distribution of

excitatory and inhibitory velocity tuning for the normal cat LTN, fig. 16G shows that the the majority of upward DS LTN units in the VCL cats display maximal excitation for 0.8 deg/sec, while the deepest inhibition is obtained at velocities less than or equal to 3.2 deg/sec. Thus, the high velocity tuning observed in the normal LTN unit population of upward direction selective cells (see fig. 16A) is no longer evident in the VCL velocity response profile. Instead, the decorticate animals display relatively slow excitatory and inhibitory velocity specificity.

D) LTN velocity tuning for downward direction selective cells in decorticate (VCL) cats. Similar to the upward group of direction selective cells, the downward DS units encountered in the VCL cats displayed uniformly slow velocity tuning (around 0.8 deg/sec). Note that the distribution shown in fig. 16D is very similar to that of fig. 16B.

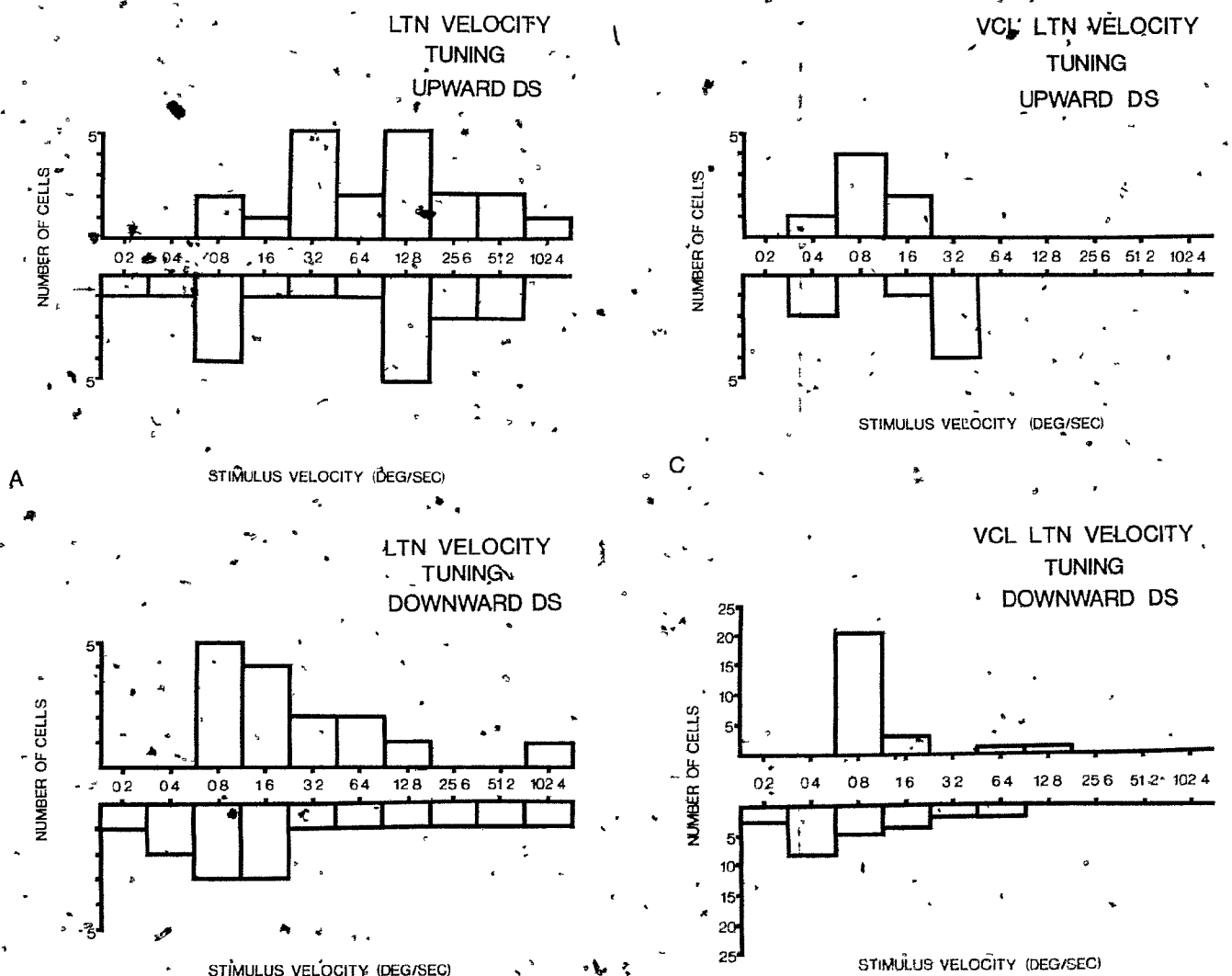
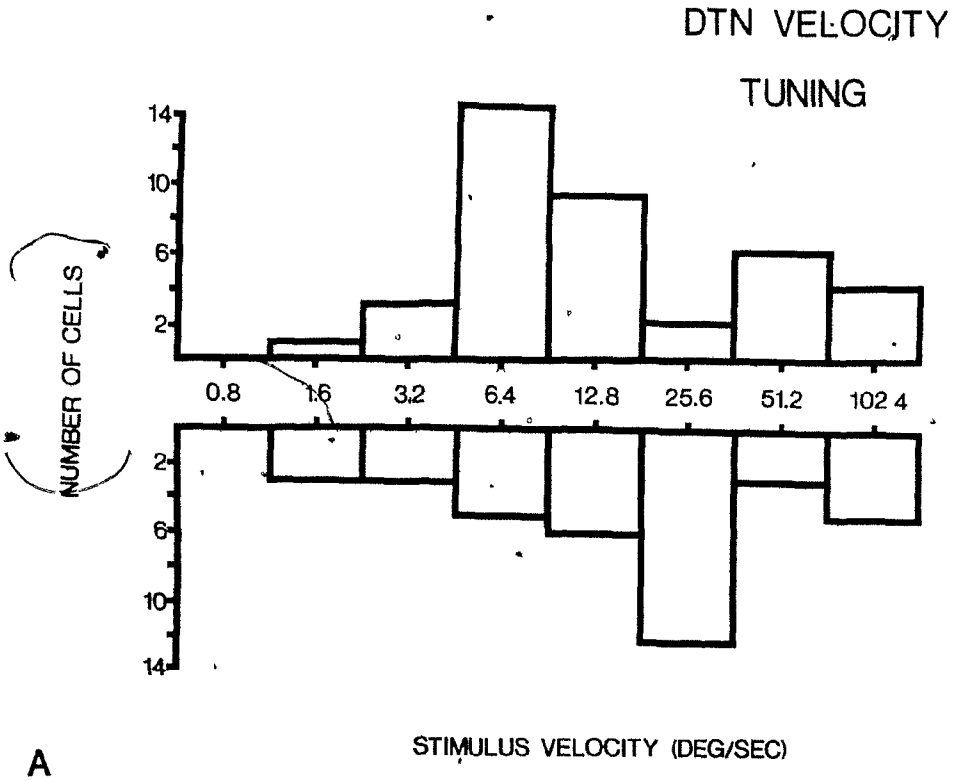

LTN VELOCITY
TUNING
UPWARD DS
NUMBER OF CELLS
5
02 04 08 16 32 64 128 256 512 1024
5
STIMULUS VELOCITY (DEG/SEC)
A
VCL LTN VELOCITY
TUNING
UPWARD DS
NUMBER OF CELLS
5
02 04 08 16 32 64 128 256 512 1024
5
STIMULUS VELOCITY (DEG/SEC)
C
LTN VELOCITY
TUNING
DOWNWARD DS
NUMBER OF CELLS
5
02 04 08 16 32 64 128 256 512 1024
5
STIMULUS VELOCITY (DEG/SEC)
B
VCL LTN VELOCITY
TUNING
DOWNWARD DS
NUMBER OF CELLS
25 20 15 10 5
02 04 08 16 32 64 128 256 512 1024
5 10 15 20 25
STIMULUS VELOCITY (DEG/SEC)
D

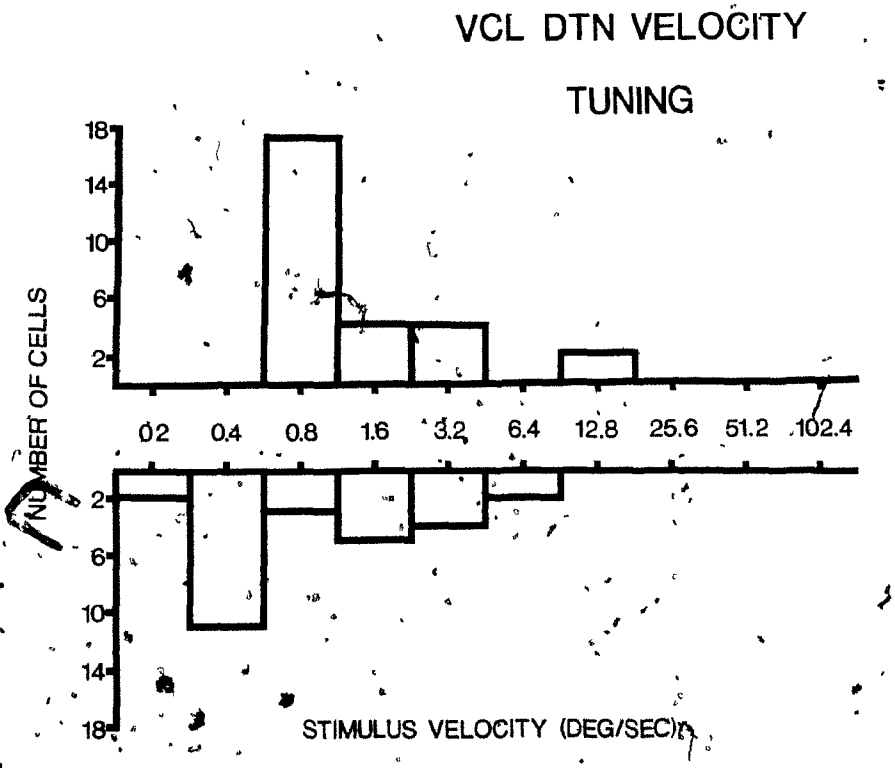
Figure 17

A) Normal cat DTN excitatory and inhibitory velocity tuning. The distribution of velocities eliciting maximal excitation in DTN cells is shown in the upward-directed histogram of fig. 17A. The majority of DTN units prefer stimulus velocities of 6.4 deg/sec. As in the normal cat LTN, there is a significant proportion of DTN cells preferring velocities greater than 25.6 deg/sec. The lower-inverted portion of fig. 17A displays the distribution of velocities at which deepest inhibition was evoked from DTN units. Unlike the distribution of preferred velocities, the majority of DTN units are most strongly inhibited by a stimulus velocity of 25.6 deg/sec.

B) DTN velocity tuning in decorticate cats. In contrast to the normal DTN, the distribution of preferred velocities obtained from the decorticate DTN (upward-directed histogram, fig. 17B) displays a marked shift toward lower velocities. In VCL cats, most DTN cells prefer a stimulus velocity of 0.8 deg/sec. A similar shift is seen in the inhibitory velocity tuning shown in the lower-inverted portion of fig. 17B, where the majority of DTN cells exhibit deepest inhibition for velocities of 0.4 deg/sec.


DTN VELOCITY
TUNING
NUMBER OF CELLS
14
10
6
2
0.8
1.6
3.2
6.4
12.8
25.6
51.2
102.4
STIMULUS VELOCITY (DEG/SEC)

A


VCL DTN VELOCITY
TUNING
NUMBER OF CELLS
18
14
10
6
2
0.2
0.4
0.8
1.6
3.2
6.4
12.8
25.6
51.2
102.4
STIMULUS VELOCITY (DEG/SEC)

B

DISCUSSION

Cortical-Subcortical Interactions

Along with the structural expansion and elaboration of neocortex throughout evolutionary development, has come the concomitant demand for increased functional coordination between phylogentically older neural networks in the midbrain and relatively more recent cortical systems. In the mammalian visual system, an extensive body of literature has emerged in the last decade concerning both anatomical and physiological studies which have helped to clarify the nature of the functional relationship between the visual cortex and, in particular, the superior colliculus, the pretectum, and the accessory optic nuclei. All of these structures have been suggested to play a role in eye movements.

Cortical Contributions to Subcortical Visual Function: Effects of Decortication on Ocular Dominance

In addition to the retinal projection, many subcortical regions receive afferents from a number of central visual structures which, in some cases, contribute to the observed binocular responses: e.g., the superior colliculus, pretectum, and accessory optic nuclei all receive input from the visual cortex and the lateral geniculate complex. In the decorticate cat, a severe reduction in the degree of binocularity has been observed in the superior colliculus (SC) (Wickelgren and Sterling 1969, Berman and Cynader 1972). Thus, the alterations in binocular function observed in the decorticate SC of the cat may be

accounted for by the elimination of input from the visual cortex.

The cortex also provides a large and diffuse afferent input to the nucleus of the optic tract (NOT) of the pretectum (Berson and Graybiel 1980, Marcotte and Updyke 1982, Schoppmann 1982, Hoffmann 1982). Similar to the cat SC, NOT cells of the intact animal display a substantial binocular input (Hoffmann and Schoppmann 1975, 1981). Following unilateral ablation of the visual cortex, NOT cells become almost exclusively dominated by the contralateral eye (Hoffmann 1982). This alteration in NOT ocular dominance is somewhat surprising in view of the fact that in an autoradiographic study of the pretectum, Berman (1977) has found that "The label in the NOT ipsilateral to the injected eye is ... in the form of oblique strips and is almost as dense as on the contralateral side." Thus, the cat NOT appears to receive approximately equal innervation from both eyes. Yet, for reasons which are not at all clear, cat NOT cells no longer display the normal degree of ipsilateral eye input following decortication, despite the fact that the uncrossed ipsilateral retinal projection should in no way be compromised by the cortical lesion.

When compared to the cat SC and NOT, the terminal nuclei of the cat AOS receive most of their retinal input from the contralateral eye and an extremely small uncrossed retinal projection from the ipsilateral eye (Farmer and Rodieck 1982, Feran and Grasse 1982, Hayhow 1959, Laties and Sprague 1966, Lin and Ingram 1974, Marcotte and Updyke 1982). In addition, anatomical investigations using autoradiographic methods have shown that all three accessory optic nuclei receive a diffuse but substantial projection from the ipsilateral visual cortex (Berson and Graybiel 1980, Marcotte and

Updyke 1982). The results of the present study show quite clearly that when the ipsilateral visual cortex is removed, the normally high incidence of binocular responses observed in units of the LTN and DTN is almost entirely eliminated (see figs. 10B and 11B). These results, obtained through independent monocular testing, suggest that the remaining afferent projection arising from the ipsilateral retina does not sustain a significant influence on LTN cells which have been deprived of cortical input.

A bilateral afferent projection to the cat LTN arising from the ventral lateral geniculate (LGN_V) has been reported by Swanson, Gowan and Jones (1974). The LGN_V projection to the LTN was not disrupted by the cortical lesions made in the present experiments. Nonetheless the ipsilateral eye input arriving via the LGN_V appears insufficient to drive LTN cells. Whatever contribution the LGN_V may be making to LTN responses, the results of the present experiments suggest that this residual input, like that coming directly from the ipsilateral retina, is not sufficient to provide a normal degree of ipsilateral eye response in the LTN when cortical input is removed. Therefore, within the limitations of these techniques, the visual cortex would appear to supply the major source of ipsilateral eye input to cat LTN cells. With regard to ocular dominance, decortication renders cells in the cat LTN and DTN almost completely monocular (i.e., contralaterally dominant), and, therefore, similar to normal cat MTN cells (Grasse and Cynader 1982). Decortication also renders LTN and DTN cells similar to AOS units in the normal frog (Gruberg and Grasse 1984), chicken (Burns and Wallman 1982), and rabbit (Simpson, Soodak and Hess 1979) which do

not receive a cortical projection. Thus, the increased ipsilateral eye input which has developed simultaneously with the frontal placement of the eyes, is clearly reflected even in a system as phylogenetically ancient as the AOS.

Decortication and Subcortical Direction Selectivity

In the cat, Wickelgren and Sterling (1969), Berman and Cynader (1972, 1975), and Mize and Murphy (1976) have shown that visual cortex lesions abolish direction selectivity in the superior colliculus, despite the fact that at least 2/3 of the cells in the normal cat colliculus are direction selective. From these considerations, one is encouraged to conclude that, in general, the corticotectal pathway in the cat confers both the properties of binocularity and direction selectivity onto cells in the SC.

In contrast to findings in the colliculus, the incidence of direction selectivity in cat NOT cells is not altered following decortication. Single units in the NOT of the normal cat most often display direction selectivity for temporo-nasal directed horizontal motion of large textured stimuli over a broad range of velocities (Hoffmann and Schoppmann 1975, 1981). Similarly, we have found that LTN and DTN units also remain direction selective after visual cortex lesions, though the number of LTN and DTN cells preferring upward-directed motion is drastically reduced. Thus, through a process of elimination, it would appear safe to say that the property of direction selectivity observed in the cat NOT and the cat LTN and DTN, is derived to a large extent from properties inherent in the retinal fibers which comprise a significant proportion of the afferent supply to these structures.

However, the dramatic alteration in the distribution of preferred and non-preferred directions for the LTN and DTN resulting from decortication implies that the overall distribution of preferred directions normally observed in these nuclei, is not solely derived from the intrinsic properties of the retinal axons of the accessory optic tract. On the contrary, the present results strongly suggest that a large proportion of the upward direction selectivity displayed by normal LTN and DTN cells in the cat arises from input from the visual cortex.

The exact mechanism underlying the reduced incidence of upward-preferring LTN neurons in the decorticate cat remains uncertain. Three possibilities exist: 1) upward preferring cells could be transformed into downward-preferring cells; 2) upward-preferring cells could be transformed into cells with no directional preference (by analogy with the superior colliculus (Wicklegren and Sterling 1969)); and 3) upward-preferring neurons could become visually unresponsive or unrecordable. Our data do not allow a firm conclusion, but it would require a quite unusual form of visual input to actually cause a neuron's preferred direction to reverse. In order for inhibition with downward motion to be transformed into excitation and vice versa, cortical input would have to effectively multiply a direction selective input by (-1). This is a possible mechanism, but hardly seems likely. Also, it seems unlikely that upward direction selective cells become non-direction selective upon decortication. As in normal animals, all LTN units encountered in decorticate cats retain some directional preference.

Therefore, it may be the case that the upward-preferring LTN cells become unresponsive or unrecordable as a result of decortication. According to this view, the formerly upward-preferring neurons would receive virtually all of their visual input from the cortex rather than from the retina. This possibility is testable, but would require a different series of experiments in which the visual cortex was reversibly inactivated while recording from LTN units.

Decortication and Subcortical Velocity Sensitivity

Hoffmann (1982) has shown that cat NOT cells no longer respond with increased excitation to stimulus velocities greater than 10 deg/sec when the ipsilateral visual cortex is removed. Normally, NOT units display a rather broad range of velocity sensitivity. This result is clearly very similar to the effects of decortication on the excitatory velocity tuning of LTN and DTN cells (see figs. 16A-D and 17A,B) described in the present study. In addition, we have observed alterations in the inhibitory velocity tuning of AOS units resulting from cortical lesions. In previous studies of the cat AOS (see Part I and Grasse and Cynader 82), single units were encountered which exhibited different velocity tuning for excitation and inhibition: e.g., cells were found which displayed maximal excitation for slow stimulus velocities and deepest inhibition for relatively fast velocities. This unusual form of velocity sensitivity was never observed in the decorticate preparation where the velocity tuning was equally slow for excitation and inhibition, suggesting that the visual cortex makes substantial contributions to both the excitatory and inhibitory components of the high velocity response of LTN and DTN

units.

Figure 16A and B shows that upward directional preferences and high velocity response are linked in units of the normal cat LTN. One interpretation of these data is that the retinal input provides the low velocity preferences and that cortical input is especially strong for upward preferring units. The finding that there is a reduction in both upward direction selectivity and high velocity response in the LTN of lesioned animals, is consistent with the results obtained in normal cats.

Subcortical Visual Pathways Involved in Oculomotor Control: Functional Consequences of Cortical Input

The preceding discussion presents many examples illustrating the influence the visual cortex exerts upon the superior colliculus, pretectum, and accessory optic nuclei. All three of these subcortical structures have, with descending degrees of confidence, been implicated in some form of oculomotor function. There is an extensive body of literature implicating the SC in eye movement control (e.g., the generation of saccadic eye movements and foveal acquisition of visual targets) which are too numerous to be reviewed here. For the purpose of this discussion, attention will be confined to the pretectal NOT and the AOS nuclei.

If electrical shocks are applied to the NOT, biphasic eye movements are evoked which closely resemble optokinetic nystagmus (OKN): the eyes move along a horizontal axis with a slow phase toward the site of stimulation followed by a fast phase in the opposite direction

(Colliwijn 1975A). These evoked eye movements are consistent with both behavioral evidence showing OKN deficits following NOT/pretectal lesions (Colliwijn 1975A and Precht and Strata 1979), and with the physiological response properties of NOT cells (Colliwijn (1975B) and Hoffmann and Schoppmann (1975, 1982, see above)). More recently, Hoffmann and Huber (29) have shown that single unit responses in the alert cat NOT during optokinetic eye movements are highly correlated with the slow and fast phases of OKN.

Wood, Spear, and Braun (1973) investigated the affects of visual cortex lesions on OKN. Normally, in afoveate animals under monocular conditions, horizontal OKN is more vigorous in response to whole-field motion in the temporo-nasal direction than in the nasal-temporal direction. In the cat, monocular OKN is only slightly weaker for nasal-temporal stimulus motion than for temporo-nasal motion (Honrubia et al 1967, Harris and Cynader 1981). However, when the visual cortex is removed, monocular OKN becomes much more asymetrical and is no longer driven well by nasal-temporal horizontal motion. Thus, the bidirectional nature of monocularly-evoked horizontal OKN in the cat appears to arise from the convergence of both retinal and cortical inputs on the NOT: the direct retinal input mediates OKN responses to temporo-nasal stimulus motion, while the indirect cortical input provides OKN responses to nasal-temporal motion. Superimposed upon this asymetry in the direction of OKN responses in decorticate animals, is a reduction in OKN responses to high velocity motion in both horizontal directions. This reduction in response to high velocity stimulation may reflect the abnormally low velocity preferences of NOT cells of decorticate animals.

As yet, the possible behavioral effects of microstimulation of the accessory optic nuclei have not been investigated in the cat. Nor have selective lesion studies been performed examining possible behavioral deficits which may result from localized damage to individual AOS nuclei. Because of the general similarity in response properties between cells in the NOT and cells in the AOS, it seems reasonable to postulate similar functions for these two networks. If this is assumed, one might expect that the DTN would be primarily involved in some form of horizontal eye movement control, perhaps very similar to the NOT, while the LTN would be involved in some form of vertical eye movement control.

Unlike horizontal OKN, which in the normal cat and monkey may be elicited in response to either stimulus rotation from right-to-left or from left-to-right, vertical OKN in both species displays a significant up-down asymetry: OKN in response to upward vertical motion is much more vigorous than in response to downward vertical motion (Cohen 1973, Harris and Cynader 1981). If one assumes that the excitatory preferred directions of AOS cells determine the strength of OKN in a particular direction, then one might anticipate that more upward than downward preferring AOS units would be encountered in the intact cat. Yet this is not the case for either the LTN, in which equal numbers of upward and downward cells are found, or for the MTN, in which more units prefer downward directed stimulus motion (Grasse and Cynader 1982). The up/down asymetry in normal cat OKN is most pronounced at high stimulus velocities (Cynader and Grasse, unpublished observations). If the LTN is involved in the generation of vertical

OKN, then the correlation between high velocity tuning and upward direction selectivity (fig. 16A and B) may account for the observed asymetry in OKN of the normal animal. Preliminary evidence (Cynader and Grasse, unpublished observations) suggests that the up-down asymetry of vertical OKN is still present in cats which have undergone visual cortex lesions. This finding is not easily reconciled with any simple-minded hypothesis linking AOS excitatory responses and OKN. More detailed investigations are required before the possible relationship, if any, between the reduced incidence of upward direction selective cells in the LTN of decorticate animals observed in the present study, and the oculomotor behavior of normal and decorticate cats, may be critically evaluated.

In a manner typical of most experimental results, the present findings pose as many questions as they provide answers. A more accurate notion of the functional relationship between the LTN and DTN and oculomotor behavior, requires both knowledge of the efferent connections of these nuclei, and also knowledge of the consequences of stimulation or removal of these structures on oculomotor performance. Experiments are in progress to address these issues.

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