BINOCULAR FACILITATION AND INHIBITION IN THE LATERAL GENICULATE NUCLEUS OF THE CAT

Thesis by

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Abstract

The lateral geniculate nucleus (LGN) relays visual information from the retinas to the cortex, segregating input from each eye into separate laminae. The LGN receives an equally large input back from the visual cortex, whose cells are driven from both eyes. Therefore, binocular interactions in the LGN were studied by systematically varying visual stimuli known to fire cortical neurons. Binocular to monocular responses were compared by interleaving them using computer driven shutters in order to eliminate errors due to LGN cell response variability. Full statistical analysis was used to identify significant binocular facilitation and inhibition.

Significantly more and stronger binocular feedback (BF) was seen with this approach than in previous studies. The vast majority of LGN cells showed both binocular facilitation and inhibition; as many as half showed BF amplitudes exceeding 50% of their typical monocular firing rate. Importantly, BF was found to be well tuned to velocity, relative retinal disparity, and sweep direction, parameters known to profoundly affect cortical firing. Multiple regions of BF were found for most cells, with the majority located near the monocular receptive fields in visual space. Regions of facilitation required zero retinal disparity twice as often as inhibition. Further, most BF reached maximum amplitudes at 6^{o}/sec to 12^{o}/sec. These results are a strong indication that the BF is cortical in origin.

It is likely that this BF has a role in highlighting visual features on the plane of fixation. Because BF is very sensitive to

parameters of motion, it is also conceivable that it is involved in interpreting the visual signals generated by eyes constantly in motion. This and other possible roles of BF are discussed.

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Table of Abbreviations

N^{o}	- N degrees
N^{o}/sec	- N degrees per second
s/s	- spikes per second
AC	- Area Centralis
BDH	- Binocular Difference Histogram
BF	- Binocular Feedback
CONTRA	- Contralateral
IPSI	- Ipsilateral
LGN	- Lateral Geniculate Nucleus
RF	- Receptive Field

1. INTRODUCTION

By studying the anatomy and physiology of the dorsal lateral geniculate nucleus (LGN), neurobiologists have gained an understanding of the role played by the LGN in transferring visual information from the retina to the cortex. In the cat and primate, this nucleus is strikingly divided into clear laminae, each lamina receiving direct input from one retina (Hubel and Wiesel, 1961; Kaas et al., 1972). Many properties of the relay cells in the LGN have been well studied and for the most part seem accounted for by a simple model consisting of each LGN cell being driven by one or a few retinal ganglion cells (Hubel and Wiesel, 1961; Bishop et al., 1962; Stevens and Gerstein, 1976). Recording simultaneously from pairs of retinal ganglion cells and LGN neurons, Cleland et al. (1971) showed that every spike from one LGN cell can be accounted for by the firing of a few ganglion cells from one retina. However, an LGN neuron produces fewer spikes than the retinal cells driving it and must by some mechanism select a subset of the spikes available to it.

The simple monocular model of LGN neurons is inadequate. Although the evidence in favor of complete segregation of the pathways from the two eyes in the LGN is strong, a number of studies have demonstrated binocular influences on LGN relay cells. Bishop and Davis (1953) first showed that a conditioning electric shock applied to one optic nerve depressed the post-synaptic field potential elicited by a test volley to the other nerve. Intracellular and single unit recording showed that electrical stimulation of the non-dominant

eye's optic nerve would inhibit the firing of an LGN cell that follows electric shocks to the dominant eye's nerve (Suzuki and Kato, 1966; Suzuki and Takahashi, 1970). The importance of binocular interactions in the functioning of the LGN was further supported by the discovery of inhibitory and excitatory fields from a cell's non-dominant eye (Singer, 1970; Sanderson et al., 1971). The fields were most often inhibitory and were discovered with flashing spots and moving lines instead of electric shocks. The presence of visually driven inhibition and occasionally facilitation of an LGN cell from the non-dominant eye has also been demonstrated in awake, chronically-implanted cats (Noda et al., 1972). There is evidence that some non-dominant LGN receptive fields (RFs) have a center-surround structure, with facilitation in the center and inhibition in the surround (Schmielau and Singer, 1977). All researchers agree that the fields in the non-dominant eye occupy approximately the same relative retinal position as the RF in the dominant eye and that the non-dominant responses are quite weak in comparison. To date, however, the functional significance of these interactions is unclear.

What could be responsible for binocular interactions in a structure that has such clear separation of the input from the two eyes? It is likely that the visual cortex is involved in these interactions in the LGN. The existence of a massive projection from the visual cortices to the LGN has been demonstrated repeatedly in both the cat and monkey. Lesions in areas 17, 18 and 19 of the cortex have been shown to result in synaptic degeneration in the LGN (Guillery, 1967; Kawamura et al., 1974). Retrograde transport and autoradiographic

techniques have shown that the projection is heaviest from the striate cortex and is topographically organized (Hollander, 1972; Gilbert and Kelly, 1975; Lund et al., 1975; Updyke, 1975). The projection is very large; more than half of the neurons in layer VI of the striate cortex send axons to the LGN (Gilbert and Kelly, 1975) and at least half of the synapses seen in the LGN are of the type that degenerate soon after the cortex is removed (Jones and Powell, 1969; Guillery, 1971). Clearly, this large feedback system from binocular cells in the visual cortex must profoundly affect LGN function.

A number of workers have demonstrated that the cortex has an influence on the activity of LGN relay cells. Widen and Marsan first showed in 1960 that an electric shock to the visual cortex can inhibit or facilitate the response of an LGN unit to visual or electrical stimulation. Others have shown in both the cat and monkey that cooling the cortex decreases the spontaneous firing and the responses to visual stimuli in about one third of the LGN cells and increases them in about half that number (Hull, 1968; Kalil and Chase, 1970). Tsumoto et al. (1978) excited cortical neurons in small areas of layer VI in area 17 with the application of glutamate; both facilitation and inhibition of firing to visual stimuli could be found in LGN cells. Schmielau and Singer (1977) found that cortical cooling sometimes altered the non-dominant LGN receptive fields; center facilitation was replaced by inhibition and surround inhibition was decremented. The implication that only some of the binocular inhibition in the LGN is mediated through the cortex is supported by the earlier studies of Singer (1970) and Sanderson et al. (1971) where it was

shown that the non-dominant inhibitory fields remained following cortical destruction or cooling. The functional significance of this feedback remains to be elucidated.

Because of the probable involvement of the visual cortex, a study designed to explore the nature and functional significance of binocular interactions in the LGN would best take into account the properties of cortical neurons. It is well established that cortical cells are binocular and respond best to moving oriented stimuli, with each cell expressing strong preferences for stimulus orientation, sweep velocity and direction, retinal disparity, as well as other parameters (Hubel and Wiesel, 1962; Barlow et al., 1967; Pettigrew et al., 1968a). It has already been shown that some LGN cells show weak preferences for orientation and it is possible that this is due to cortical influences (Daniels et al., 1977). It would be optimal to consider the specific properties of cortical cells that project to the LGN. To date, identification of these cells by antidromic firing from the LGN reveals only that they can be either simple or complex and are most often binocular (Gilbert, 1977; Harvey, 1978).

Another issue that such a study should handle is the problem of LGN unit response variability. The amplitude of the response of an LGN neuron to a visual stimulus often varies as much as two-fold or more with factors that are difficult to control (Malcolm et al., 1970; Coenen and Vendrik, 1972; Burke & Cole, 1978). The most common factor that varies is the animal's level of arousal which can shift often in several minutes. Any difference found between a binocular

response tested over a period of a few minutes and a monocular response taken a few minutes later could be due simply to changes in neuron responsivity (Figure 1).

In this work, a new strategy was used to study the binocular interactions in the LGN. First, control is exerted over parameters of visual stimuli that are known to profoundly influence the firing of cortical cells. Moving slits, edges, and gratings were used and tested with systematic changes in orientation, sweep velocity and direction, and relative retinal displacement. Second, binocular interactions were studied by comparing binocular and monocular responses taken in tandem. Computer operated shutters placed over the animal's eyes allowed continuous alternation between monocular and binocular tests. Histograms were constructed from the difference between each monocular and binocular paired sweep as recorded by computer. Third, complete statistical analysis was applied to all histograms so constructed to clearly identify real binocular interactions.

We have found that the great majority of LGN cells show both binocular inhibition and facilitation and that the polarity and amplitude of the binocular interaction is strongly a function of stimulus velocity, position, retinal disparity, and sweep direction. The functional significance of these interactions and the evidence that they are due to influences from the cortico-thalamic pathway is discussed.

Figure 1

This figure shows the responses of two cells each recorded over a period of about 28 minutes to stimuli sweeping over their dominant receptive field (RF). The top cell LA7-1A (CONTRA-Off) was stimulated with a slit and the bottom LA7-4 (CONTRA-On) with a 1.7^{o} grating at three different velocities. The left column for each shows a histogram for the first 14 minutes (50 trials) and the right column for the next 14 minutes. Notice that the amplitude of the response peaks has changed considerably. In comparing LGN monocular responses taken at one time with binocular responses taken at another, one cannot expect to get a good measure of the difference. Taking both binocular and monocular sweeps in alternating succession is the strategy used in this study.

LGN RESPONSE VARIABILITY

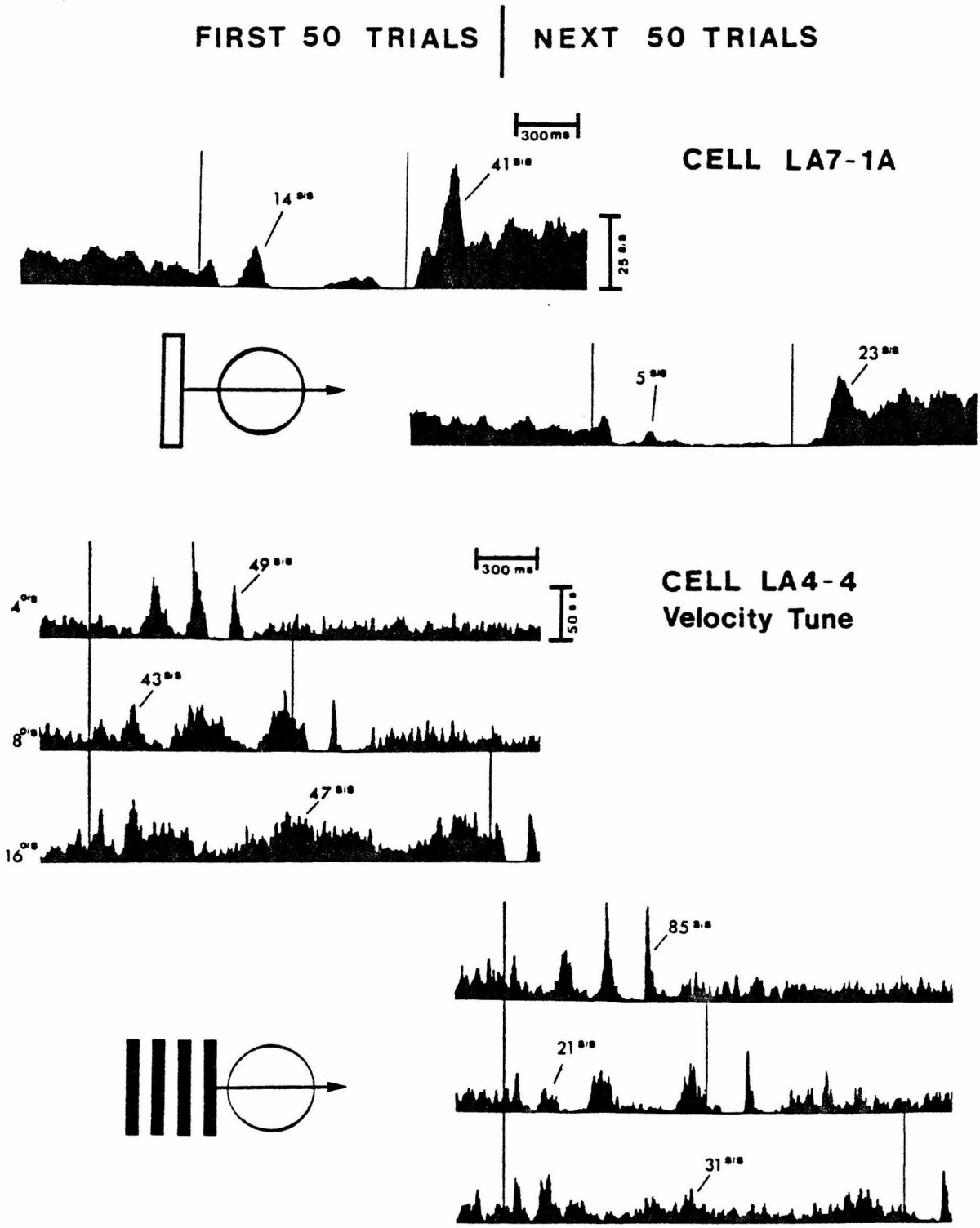

Figure 1

2. METHODS

2.1 Electrophysiology

Nine normal adult cats were prepared for single unit recording using standard methods (Barlow et al., 1967). Anaesthesia was induced with 4% halothane and then shifted to 0.5% to 2% in a 2:1 mixture of nitrous oxide and oxygen. After insertion of venous and tracheal cannulae (and in some cases a bilateral sympathectomy to reduce eye movements), the animal was transferred to a stereotaxic headholder and put on a continuous intravenous infusion of a paralytic mixture designed to minimize eye movements (Rodieck et al., 1967). The mixture delivered 5 mg/kg/hr Flaxedil, 0.5 mg/kg/hr d-tubocurarine and 0.1 to 0.4 mg/hr Dexamethasone in 5% dextrose and 0.25% saline at 5 ml/hr. The animal was artificially respired at 40 breaths/min with a 75% nitrous oxide, 22.5% oxygen, 2.5% carbon dioxide mixture at 30% hyperventilation relative to the Harvard respirator recommendations. Heart rate was monitored. A rectal thermometer and electric blanket circuit were used to keep body temperature at 37.5°C to 38°C.

The pupils were dilated with Cyclogyl, nictitating membranes retracted with neosynephrine, and the corneas protected with zero power contact lenses. An image of the retina was projected on a tangent screen 57 cm away using the fiber optic technique (Pettigrew et al., 1979), and the positions of the optic disks (and areae centrales when visible) were plotted. When not visible, the areae centrales (AC) were taken to lie 15.6° nasal and 6.8° down from the optic disks (Nikara et al., 1968).

Tungsten-in-glass electrodes (Levick, 1972) were lowered toward the LGN through a craniotomy located on or near 6 mm anterior and 8.5 mm lateral to Horsley-Clark zero; variations were used to sample different parts of the visual field. For some animals, a second electrode was placed into area 17 through another craniotomy near the midline of the skull at 1 mm posterior to AP zero. Cortical electrode guides were held in a chamber filled with agar and sealed with paraffin to maintain recording stability. LGN recordings were found to be stable without a chamber. Most often, electrodes were advanced into the brain with a custom-built stepping motor microdrive system (Central Engineering Services, Caltech). This system enabled precise positioning of electrode depth with minimum delay. Signals from the electrode were picked up by a high input impedance preamplifier and fed into an oscilloscope, audio amplifier, and spike discriminator. Output from the discriminator was fed into a Nova computer (also used for stimulus control and data analysis - see below). Recording sessions lasted up to 48 hours.

The LGN electrode was lowered to 11 mm from the surface automatically over a period of from 0.5 to 1 hour. It was then lowered under hand control until strong modulation of background activity by stroboscopic illumination and by shifting of a hand held grating (at all orientations) was obtained. Single units with isolated spikes capable of triggering the discriminator were then sought. An LGN unit was characterized by a clear center-surround RF with a crisp On or Off response to a spot flashed in the RF center in only one eye. LGN tracts always started with purely CONTRA cells and then showed a

clear transition to IPSI cells at a greater depth, followed again by CONTRA cells even deeper.

2.2 Visual Stimulation and Protocol

A visual stimulus was projected onto small mirrors mounted on computer controlled pen motors capable of placing an image anywhere on the tangent screen. The stimuli were most often slits of adjustable dimensions, but gratings on 35 mm slides were also used. The orientation of a stimulus could be controlled manually or by the computer. A plotting table received an image of the tangent screen reflected from a plexiglas sheet mounted appropriately between the screen and the projector.

Typically, an LGN unit was found with a hand held grating and then plotted in detail using a 0.25^{o} spot controlled manually with a joystick and an on/off switch. The following data were recorded for each unit before binocular interactions were studied: 1) electrode depth, 2) eye dominance (CONTRA or IPSI), 3) receptive field (RF) type (On or Off), 4) RF configuration, including diameter, boundaries, and annulus extent, and 5) position relative to the dominant eye's AC.

The study of binocular interactions was started for each cell by determining and correcting for the vergence of the two eyes. The vergence was estimated in one or more of three ways. The first was always employed and involved the above described plotting of the positions of the ACs. The second was used when cortical units were recorded (in about half of the animals); the average position of the RFs for each eye was determined from several strongly binocular cortical neurons. This yielded a physiologically accurate measure of

vergence. The third could be used only after crossing a laminar border in the LGN; vergence was taken as the shift in the position of two units' RFs when the units were driven from different eyes and thus were on opposite sides of the border. The vergence estimated by these techniques was eliminated by placing a prism in front of one of the eyes to shift its AC to the same position as the other on the tangent screen.

The apparatus used to study binocular interactions, as well as all of the equipment physically in contact with the animal, is shown in Figures 2 and 3. Figure 2 shows two 5 mm artificial pupils, one over each eye, each of which could be closed independently by a shutter driven a by small D.C. motor. The shutters could be controlled both by hand and from the computer. Figure 3 shows a variable prism over the right eye that is driven by a stepping motor, also controlled by hand or from the computer. This prism was used to vary binocular displacement and could be placed over either eye. It also provided a mounting for the vergence correcting prism described above. Over the left eye is a dove prism which was occasionally used to present different sweep directions to each eye. The variable prism, dove prism and other optical devices could be mounted in front of the shutters (as in the figure). A small laser was used to insure proper alignment of all optical devices. The reflective tapetum was visible through all optics when viewed through an ophthalmoscope held at the position of the tangent screen 57 cm away.

Figure 2

This figure shows the preparation from a the point of view of the tangent screen, with all correcting and modifying prisms moved to the side to show the artificial pupils and shutters. These shutters could be opened and closed independently under manual or computer control. Other visible items include 1) electrode microdrive pushing electrode into the brain, 2) preamplifier, 3) computer drivable variable prism (pulled aside), 4) tracheal tube with hoses leading to respirator, 5) cat, 6) artificial pupils with motor driven shutters, 7) dove prism (pulled aside) and 8) aluminum foil shielding to reduce electrical noise.

Figure 3

This is similar to Figure 2 but with the stepping motor variable prism and dove prism put in place. The variable prism also acted as a mounting for the vergence correcting prisms. Notice that the shutters and artificial pupils are still in place.

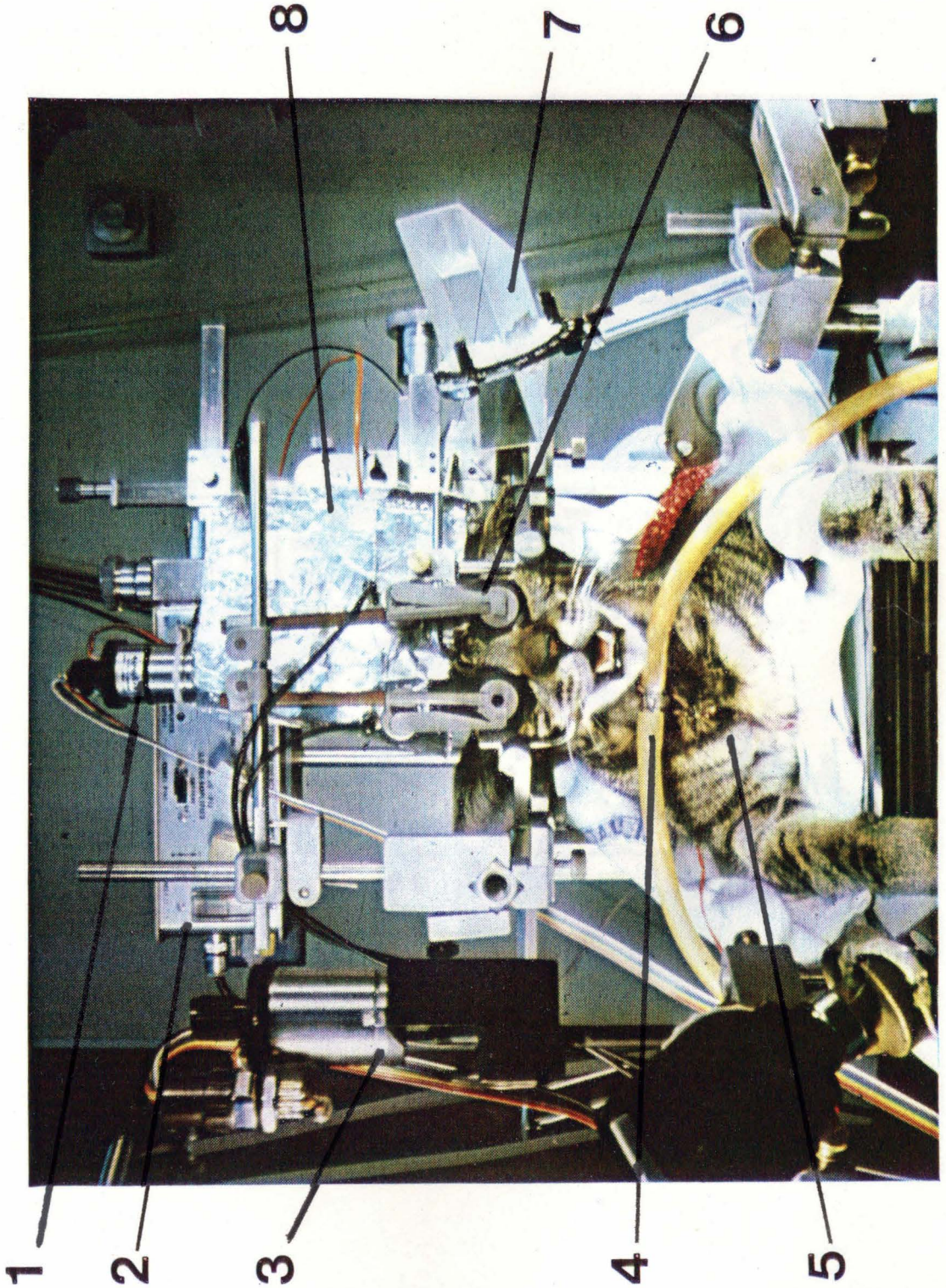

Figure 2

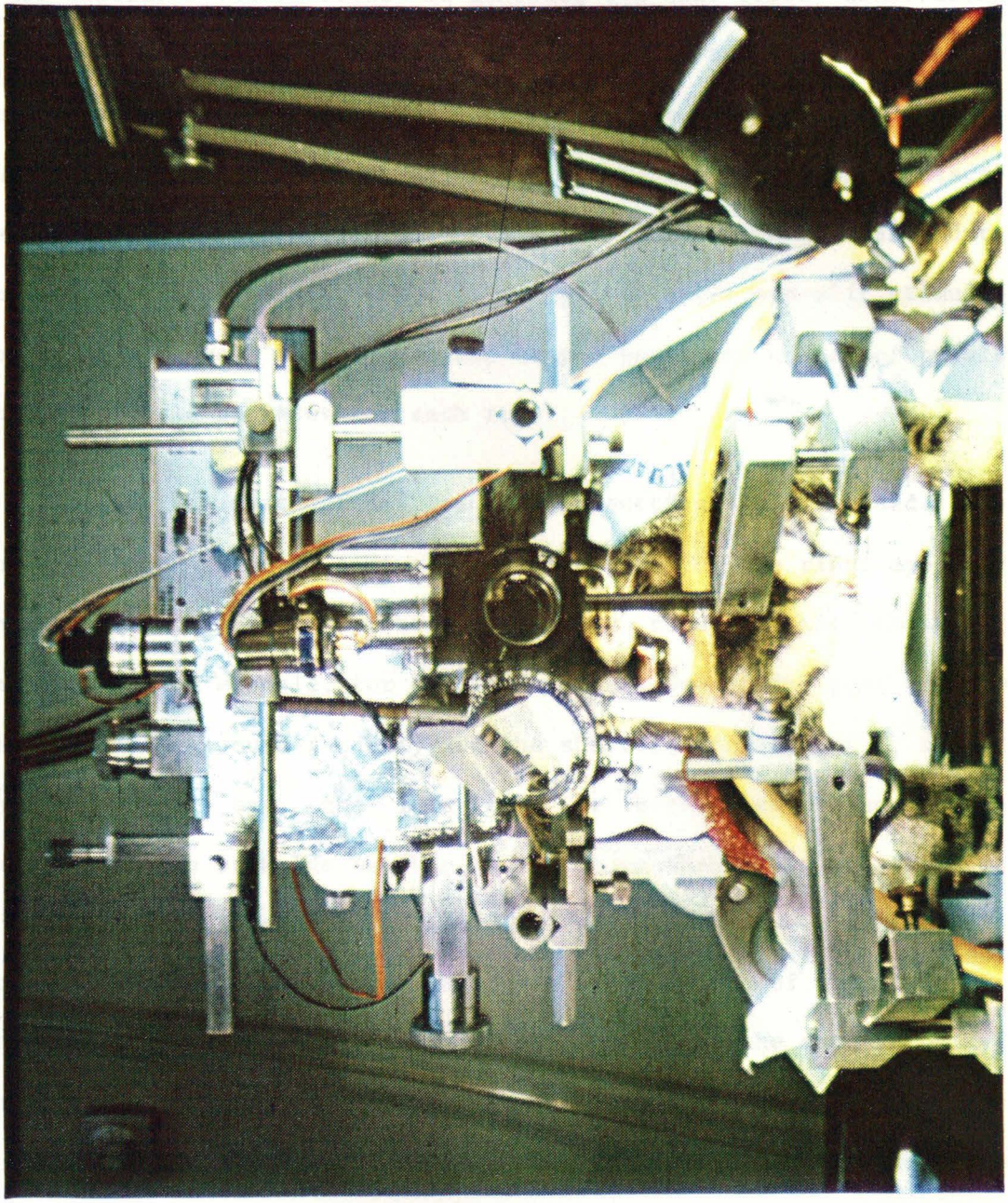

Figure 3

The NOVA computer was programmed to control the described apparatus and the visual stimulator in a coordinated fashion so as to study binocular interactions. In general, the user first constructed a "run" by describing to the controlling program the set of values to be tested for a particular visual parameter. In the present study, the orientation, direction, velocity or relative binocular displacement could be varied during a run. All parameters held constant during a run, such as slit size, illumination level, non-slit stimulus (on a slide), sweep duration, sweep center position, number of trials and so on could be reset for each run.

Second, the user defined the shutter settings to be used. The computer was asked to test the cell response for the right eye only and/or left eye only and/or both. It then runs in the following manner, as an example, for a velocity tune. One of the test velocities is chosen pseudo-randomly and the shutters are instantly opened for the right eye, the left eye, or both (also chosen pseudo-randomly). The stimulus is then swept across the screen and the time of occurrence of each spike with reference to the sweep is recorded by the computer. The shutters are then reset to one of the positions not yet tested and the stimulus swept again at the same velocity, continuing until all of the shutter positions are run. The process is then repeated with the next velocity. The entire set of velocities are tested in this manner for a preset number of trials.

The LGN shows large variations in response amplitudes over just a few minutes (INTRODUCTION). With the above interleaving technique,

the separation in time between each monocular and binocular sweep was never more than a few seconds. Accurate measurement of the differences between monocular and binocular responses could then be made independent of shifts in a cell's overall responsiveness. It became possible to construct "binocular difference histograms" by subtracting each dominant-eye sweep from the binocular sweep taken in tandem and then adding all of these "difference sweeps" together.

The general protocol was to find a cell, record all basic data (described earlier), eliminate vergence, and then to study binocular interactions as a function of velocity, binocular displacement, direction of sweep, and other parameters as time allowed. Most often horizontally moving vertical slits, edges and gratings were used. The computer displayed a wide-bin histogram for each shutter setting as the experiment was running and a crude visual estimate of the binocular differences were made. In general, two to four sets of three to seven velocities ranging from 0.5^{o}/sec to 40^{o}/sec were run first and an estimate made from the display as to the velocity producing maximal binocular interaction. That velocity was then used in a series of binocular displacement tests (using the computer driven variable prism), usually run at 1^{o} increments over of range of 8^{o}. Displacements appearing to show greater binocular interactions were often then studied with finer test increments. Occasionally, binocular displacement tunes were run at more than one velocity. Following this, direction tunes comparing responses of vertical stimuli moving toward versus away from the AC were done at various velocities and displacements. Occasionally full velocity tunes and/or displacement tunes

were done for both directions. At times, full orientation tunes were run. Other tests were run as time allowed. Cells were rarely held for more than five hours - enough time for all of the above tests and more. More often, a cell would be lost before all tests were completed. The described protocol was varied often to allow completion of a significant number of some of the latter tests.

2.3 Data Analysis

On the average, 40 runs of from 10 to 100 trials each over a range of from 2 to 10 parameter settings were obtained from one cat, with an average of five well tested cells per cat. This often resulted in more than 1.5 megabytes of information recorded per cat. The goal of the analysis was to produce clear, accurate, and reliable measures of monocular responses and binocular interactions from these data. The analysis involved putting the data file from each run through a series of programs which 1) extracted monocular histograms and binocular difference histograms (BDHs), 2) checked each BDH for intervals of statistically significant differences (between the monocular and binocular response), 3) extracted amplitudes of inhibition or facilitation for each of these intervals, and 4) displayed all of the data and analysis results in a variety of usable charts and plots. Each of these steps is defined more clearly below. The results were then collected together by hand to build up the final tuning curves and maps represented in the RESULTS section. It should be noted that simulations of a neuron with preset monocular responses, binocular interactions and statistical variability were programmed to create runs to test and debug these steps. The analysis programs were shown to accurately extract the data that had been set into the simulation.

BDHs were built up for each sweep by subtracting for each "moment" (in units of 3 msecs for technical reasons) the number of spikes in the dominant eye sweep from its paired binocular sweep. Each moment then had from -3 to 3 spikes as the difference between

the binocular and monocular response and a sweep typically consisted of 300 to more than 1000 such moments. A BDH could be built up by adding moment by moment all of the sweeps so generated. If four velocities were run, four BDHs would be built.

The binocular difference occurring during a time interval on a BDH was tested for statistical significance using the paired t-test (Duckworth, 1968). The computer scanned a BDH and for every moment calculated t-values for intervals of a large range of sizes. The interval size producing the maximum t-value for any one moment was noted when significance exceeded 99.5% on a double-sided test (most demanding criteria conventionally used). Overlapping intervals were joined together as one interval of real binocular difference. The maximum spikes/sec difference found in any twelve msecs interval was assigned as its amplitude. Twelve msecs was chosen because it was small enough not to dilute sharp peaks, large enough to produce a representative firing rate and technically convenient. Inhibition was represented by negative amplitudes and facilitation by positive.

A variety of plots and charts were produced from each run for examination and for construction of tuning curves: 1) monocular response histograms, 2) statistically filtered and unfiltered BDHs at various boxcar sizes (Figure 4 explains boxcar histograms and Figure 5 shows filtering), and 3) printed charts of all intervals near or exceeding statistical threshold, including for each a t-value, duration, amplitude, corresponding monocular amplitude, etc. The various tunes and maps described in RESULTS were then put together by hand by combining results from the appropriate runs.

Figure 4

This figure shows the use of the boxcar technique to visualize binocular difference histograms (BDHs). Normally histograms consist of neighboring bins that are much wider than the minimum measurement "grain", which is 1 msec for spikes. All monocular histograms in this paper are so built. If a peak response occurs over a duration less than or equal to the bin width, it does not show fully if it is out of phase with the bin construction, which is usually arbitrary. Boxcar histograms are constructed using bins of constant size built at every grain, as if each bin were a boxcar travelling along the time axis. Phase is never a variable in this type of histogram; the only variable is the width of the boxcar. Three widths are shown here. Each width is analagous to a band pass filter and, for example, boxcar histograms with narrow bins will optimally show short duration responses. A range of narrow and wide boxcar BDHs were prepared to scan binocular differences because no good information predated this study as to the timing of binocular difference responses in the LGN. Note that the amplitude decreases with larger boxcars because of the dampening that results from averaging peaks with neighboring lower response frequencies.

BOXCAR HISTOGRAMS

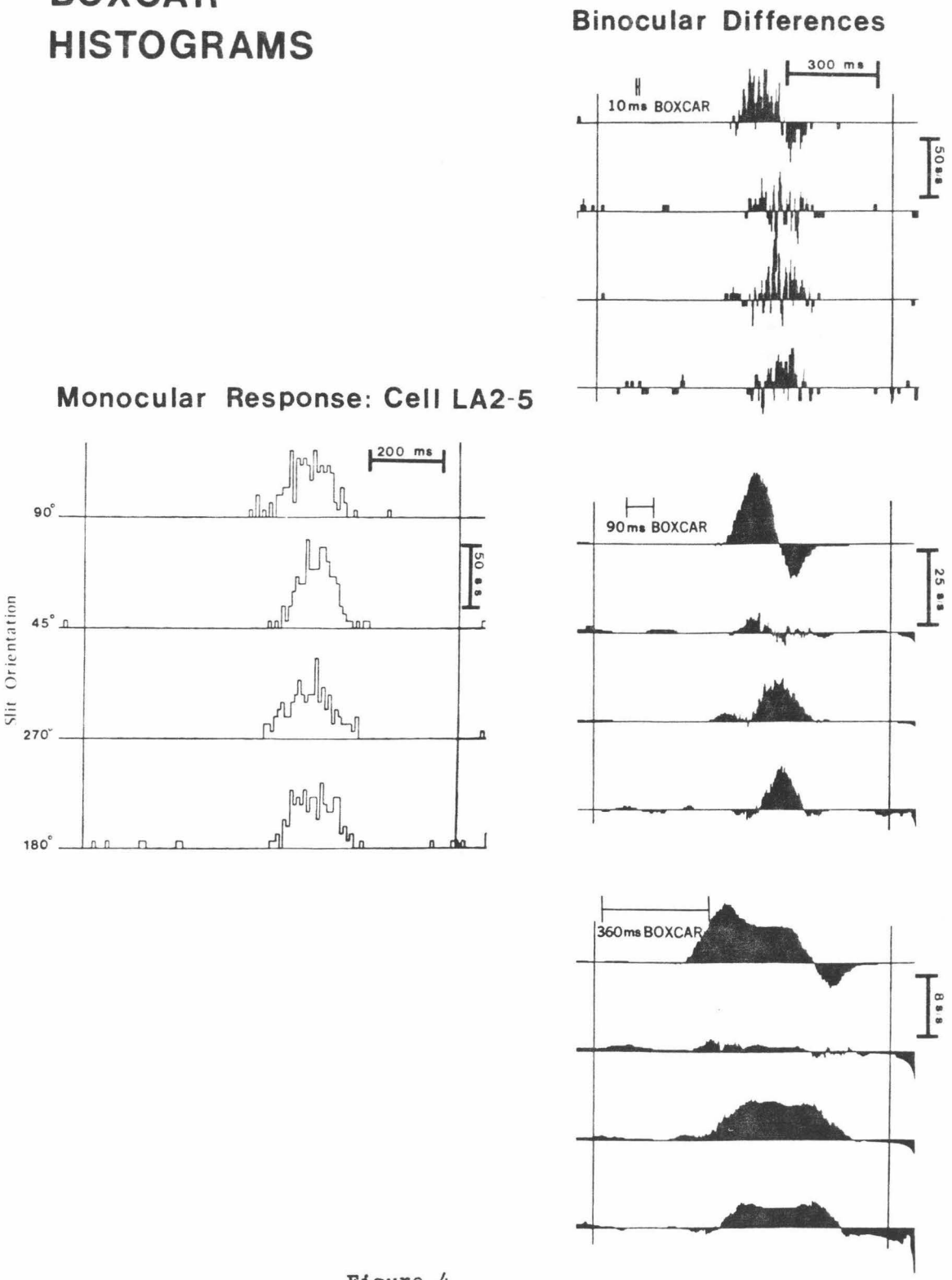

Figure 4

Figure 5

This figure shows the monocular response and BDHs for a partial displacement tune. In general, BDHs were prepared for viewing as collected from the cell. After t-values were calculated for all intervals along the BDHs, all parts that did not meet a chosen statistical threshold were eliminated, and parts that were near the threshold were scaled down. In this case, three peaks of similar amplitude show different levels of significance and thus the middle one is reduced by filtration at the 99.2% level. For the purpose of scanning BDHs, filtration was done to that level, but for the purposes of data presentation in this thesis, filtration is usually done to the 99.5% level, the chosen cutoff for defining a binocular difference as real.

STATISTICAL FILTERING: CELL LA2-5

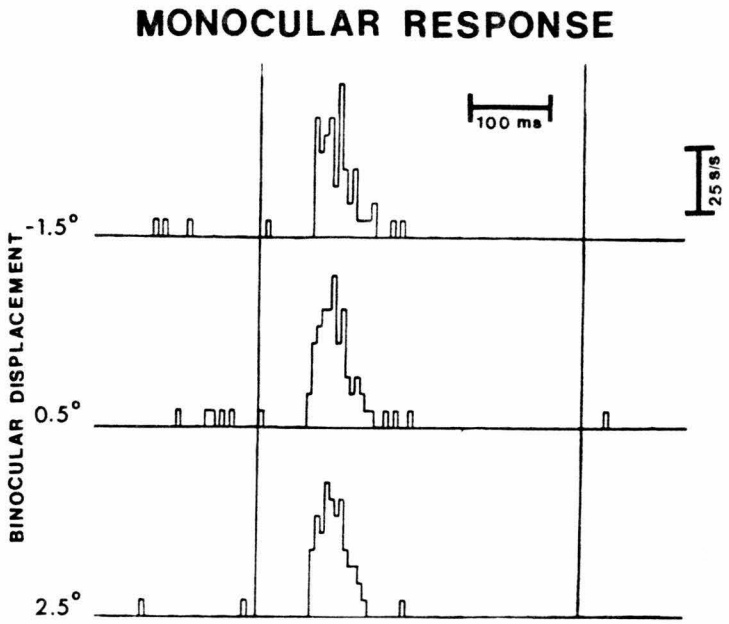

Figure 5

3. RESULTS

3.1 General

Sixty-one LGN cells were plotted from a series of nine adult cats. Twenty-one (34%) were CONTRA-On, twelve (20%) were CONTRA-Off, sixteen (26%) were IPSI-On, nine (15%) were IPSI-Off, two (3%) were CONTRA-Unclassified, and one (2%) was IPSI-Unclassified. Usable Binocular Difference Histograms (BDHs) were obtained from forty-four of these units. Binocular Feedback (BF)[1] was found in the majority of LGN cells.

Each unit was tested for BF varying as many different parameters of the visual stimuli as were possible until its spike was lost. A BDH was computed for each parameter, filtered to $p < 0.005$, and a firing frequency for each interval of inhibition and facilitation was calculated as described in METHODS. Thirty-seven (84%) cells showed significant binocular facilitation and forty-three (98%) had significant binocular inhibition for some visual stimuli. The number of stimulus parameters (velocity, direction, etc.) that could be tested varied from cell to cell and one might expect that the probability of finding BF would be less for cells given fewer tests. When cells tested for less than three computer runs are excluded, a larger percentage show clear BF, with twenty-six (93% of 28) showing facilitation and twenty-eight (100% of 28) showing inhibition.

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1. LGN cells receive only monocular retinal input, and so all binocular interactions are referred to as "feedback" without necessarily presuming the source (e.g., interlaminar, cortico-geniculate, etc).

Maximum facilitation and inhibition can be compared to a typical[2] monocular response firing frequency for each cell (Figure 6). The typical firing frequency for all cells ranged from 40 spikes/sec (s/s) to 247 s/s, with an average at 119 s/s. The mean maximum binocular facilitation was 52 s/s (0 to 156 s/s) and the mean maximum binocular inhibition was 71 s/s (0 to 147 s/s). These values are most likely an underestimate of the actual values. Removing the cells tested for less than three runs increases the facilitation mean to 62 s/s and the inhibition mean to 81 s/s. No significant correlation between monocular response amplitudes and BF amplitudes was seen. Twenty-one (48% of 44) cells showed facilitation exceeding 50% of their typical firing frequencies and six (14%) exceeded 85% of the typical monocular response. Similarly, twenty-seven (61%) had binocular inhibition to a level 50% below the typical monocular level and eleven (25%) below the 85% level. Clearly, the majority of the LGN cells tested showed clear and strong binocular facilitation and inhibition with appropriate visual stimuli.

The occurrence and magnitude of BF was not significantly different for CONTRA versus IPSI cells or for On versus Off cells (Figure 6). Cells with more than three computer runs and with receptive fields estimated to be within five degrees of the Area Centralis (AC) averaged 43 s/s for maximum binocular facilitation while similarly run cells with fields more than five degrees away averaged 80 s/s for facilitation. No difference was found between these groups for binocular inhibition. BF was therefore plotted against estimated RF

2. "Typical" is defined as the median of the peak monocular firing frequencies measured in all tests.

Figure 6

Maximum significant binocular facilitation and inhibition is plotted for each cell against its typical monocular firing frequency. "Typical" is defined as the median of the peak responses found in all runs for that cell. No significant difference in the distribution of Binocular Feedback (BF) is found between CONTRA and IPSI or between On and Off cells. No clear correlation is seen between typical firing frequency and BF amplitude.

Figure 7

Maximum significant binocular facilitation and inhibition for each cell is plotted against the estimated distance of its monocular receptive field (RF) to the Area Centralis (AC). Only cells for which three or more computer runs were taken are included. No significant correlation is seen. The triangle plot-points are facilitation and the circles are inhibition.

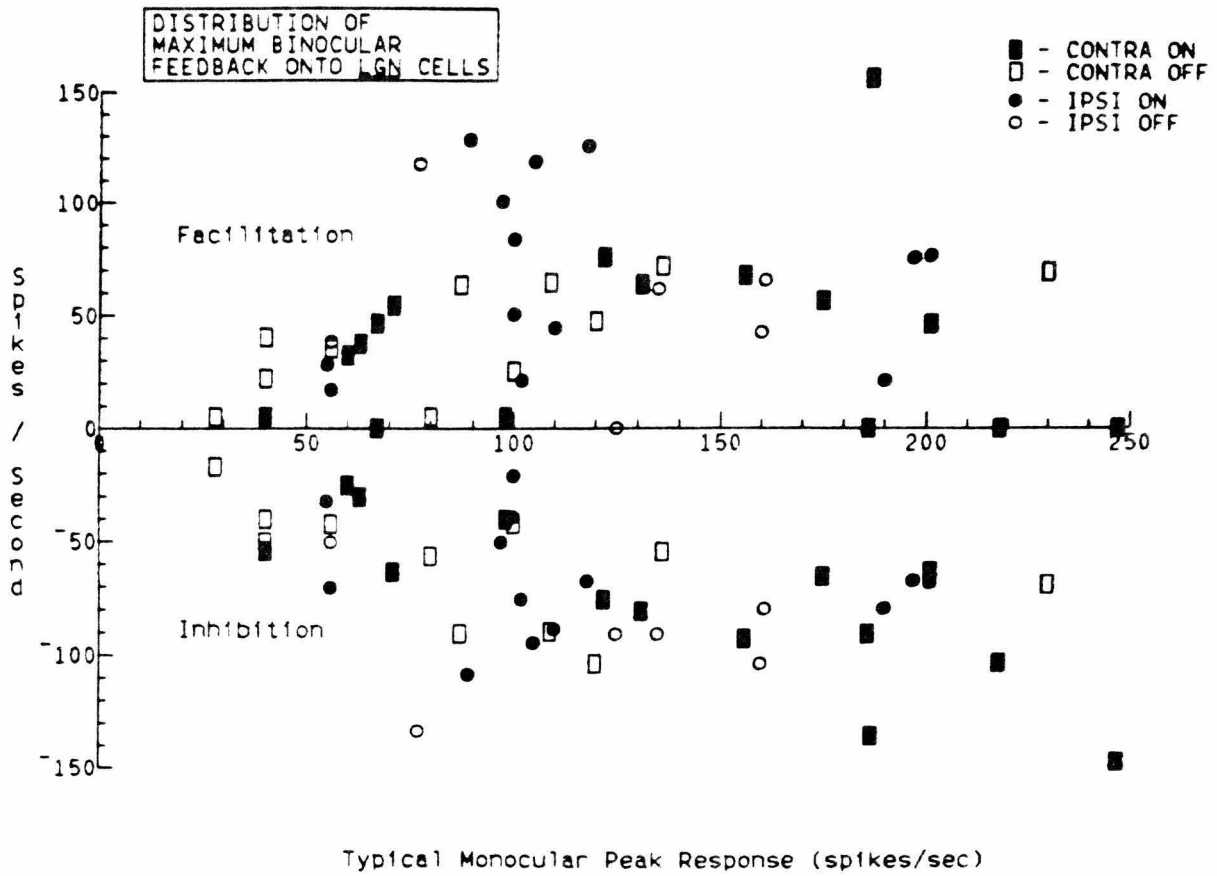

DISTRIBUTION OF
MAXIMUM BINOCULAR
FEEDBACK ONTO LGN CELLS
■ - CONTRA ON
□ - CONTRA OFF
● - IPSI ON
○ - IPSI OFF
Facilitation
Inhibition
Spikes / Second
150
100
50
0
-50
-100
-150
50
100
150
200
250
Typical Monocular Peak Response (spikes/sec)

Figure 6

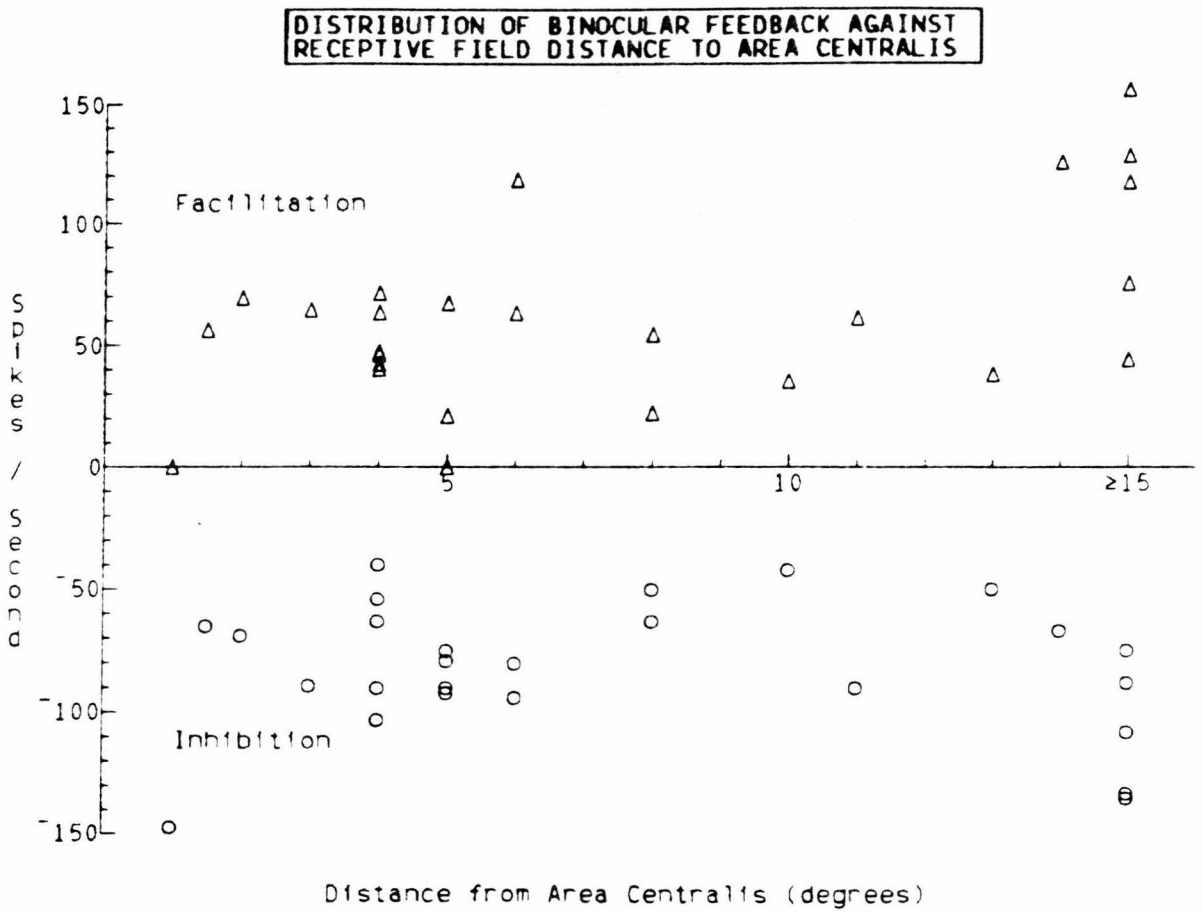

DISTRIBUTION OF BINOCULAR FEEDBACK AGAINST
RECEPTIVE FIELD DISTANCE TO AREA CENTRALIS
150
100
50
0
-50
-100
-150
Facilitation
Inhibition
Spikes / Second
5
10
≥15
Distance from Area Centralis (degrees)

Figure 7

distance from the Area Centralis (Figure 7). However, no clear or statistically significant correlation is found across these measures and no difference in facilitation between central and peripheral cells is reliably demonstrated.

It is most likely that these measures of the occurrence and maximum amplitude of BF in LGN cells are in general less than the actual values. Differences between binocular and monocular responses were not taken as BF unless significance exceeded 99.5% on the more demanding double-sided paired t test. Further, as will be described in later sections, BF is often well tuned to variations in parameters of visual stimuli. Reliably measured maximum BF must always be equal to or less than the maximum obtainable BF with totally ideal stimuli. Given the limited time available in testing for BF, the idea that the above measures are underestimates is supported.

The large majority of LGN cells tested show strong and significant BF under at least some conditions of visual stimulation. The amplitude of the maximum BF to be found for each cell under optimal conditions is largely independent of the size of its monocular responses, and for half or more of the cells exceeds a typical monocular response by at least 50%. Binocular facilitation occurred only slightly less often than inhibition, and the average amplitude of facilitation was just slightly less than that of inhibition. The frequency of occurrence and the amplitudes of maximum BF were not found to be related to IPSI versus CONTRA or On versus Off categorization. Cells further from the AC showed an apparent increase in facilitation

amplitude, but this was not statistically significant.

3.2 Location of Binocular Feedback in Visual Space

Typically a unit was studied with a long vertical slit moving horizontally across its RF. A computer driven variable prism was placed in front of one of the two eyes to test BF at different relative binocular displacements (see METHODS). Most often, BDHs were generated in one run for a range from four degrees converged to four degrees diverged, sampled at one degree intervals. Further runs were often done to expand the range or to focus in on a particular range with finer test intervals. Other parameters of the visual stimuli were chosen either on the basis of other earlier tunes, if any, of BF for that cell (e.g., using the velocity that yielded the greatest BF) or on the basis of producing a clear and strong monocular response. This technique revealed many regions of BF that are well tuned for relative retinal disparity.

A composite map of the locations of BF in visual space was produced for each cell tested (Figure 8). The meaning of BF location maps can be made clearer by considering how the ocular location of a region of BF would reflect on this type of map (Figure 9). A region of BF with a specific location only on the dominant retina shows as a horizontal band if the variable prism is placed over the non-dominant eye and as a diagonal band when the prism is over the dominant eye. Similarly, BF localized only on the non-dominant retina shows as a diagonal band in the former case and horizontal in the latter case. If the BF is found only over a limited range of binocular displacements, suggesting a requirement for the binocular retinal disparity

Figure 8

Maps of binocular feedback are created in a series of stages. Cell LA3-8A (CONTRA-On, RF 4^{o} from AC) was tested with a vertical slit moving horizontally at 8^{o}/sec towards the AC. The variable prism was placed over the non-dominant (IPSI) eye and 9 different vergences were tested. The monocular responses at each setting are similar. The BDHs show a clear region of binocular inhibition that is approximately 2^{o} wide (horizontally) on the retina but that can be elicited only in a sub-range of binocular displacements; from -1^{o} to 3^{o}, clearly peaking at 1^{o}. The BDHs are filtered to $p < 0.005$ to identify regions of BF, and the regions are mapped graphically to demonstrate their location in visual space. The abscissa ("Relative Retinal Position") refers only to the dominant eye, as the position on the non-dominant eye shifts by 1^{o} for each 1^{o} of displacement. The dotted line represents the relative location of the unit's monocular receptive field. The amplitudes of responses seen in BDHs will in general be less than in the maps because BDHs are constructed with large boxcars (see METHODS). In this paper, negative displacements are convergent for CONTRA cells and divergent for IPSI cells. In this and all figures, "s/s" is an abbreviation for "spikes per second".

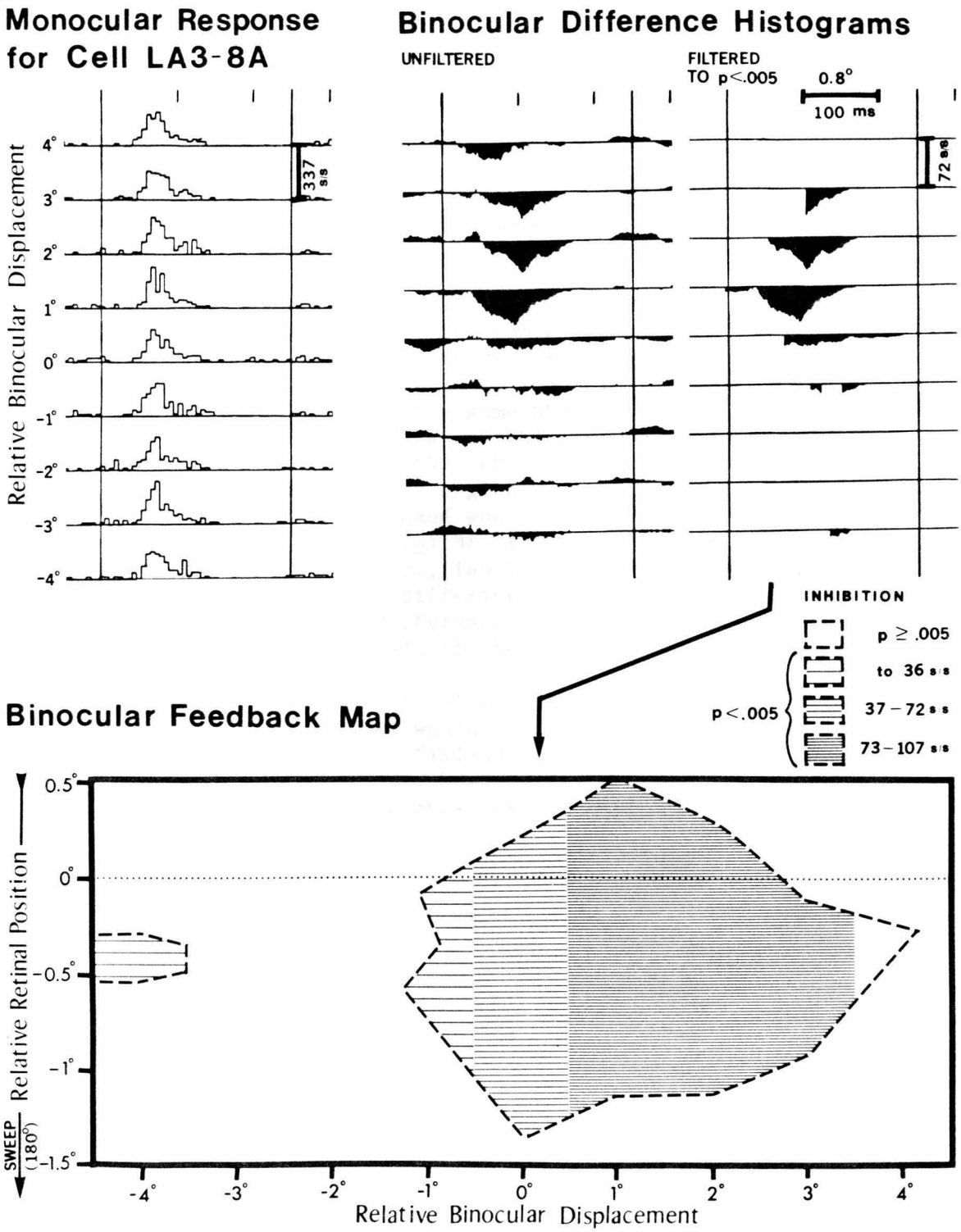

Monocular Response for Cell LA3-8A
Relative Binocular Displacement
4°
3°
2°
1°
0°
-1°
-2°
-3°
-4°
337 s/s
Binocular Difference Histograms
UNFILTERED
FILTERED TO p<.005
0.8°
100 ms
72 s/s
INHIBITION
p ≥ .005
to 36 s/s
p<.005
37 – 72 s/s
73 – 107 s/s
Binocular Feedback Map
Relative Retinal Position
0.5°
0°
-0.5°
-1°
-1.5°
SWEEP (180°)
-4°
-3°
-2°
-1°
0°
1°
2°
3°
4°
Relative Binocular Displacement

Figure 8

Figure 9

BF location maps are more clearly understood in terms of ocular location. The left-most column represents the position of idealized regions on the dominant and non-dominant retinas in relation to a slit sweep at various binocular displacements. The center column represents idealized BDHs for three arrangements of BF and the third column represents the resulting BF location maps. This figure assumes the variable prism is placed over the non-dominant eye.

Region on Dominant Retina: BF driven from a specific region on the dominant retina (and with no specific location on the other retina) would produce the same BDH no matter what the binocular displacement. Maps of this type of region would contain a horizontal band, the thickness of which would represent the width of the region. If the prism is placed over the dominant eye, the band would be diagonal.

Region on Non-Dominant Retina: BF driven from a region on the non-dominant retina (e.g., inhibition from the other LGN lamina) would produce BDHs differing only in the time of occurrence of the peak difference. The map would contain a diagonal band (or horizontal, if the prism is over the dominant eye).

Disparity Tuned Region: BF requiring specific binocular displacements (or disparities) would produce peaks on only some BDHs. The map would contain "islands" representing the BF: its location on the retina shown by its abscissa value and its location in depth-space shown by its ordinate value.

MAPPING AS A FUNCTION OF OCULAR LOCATION

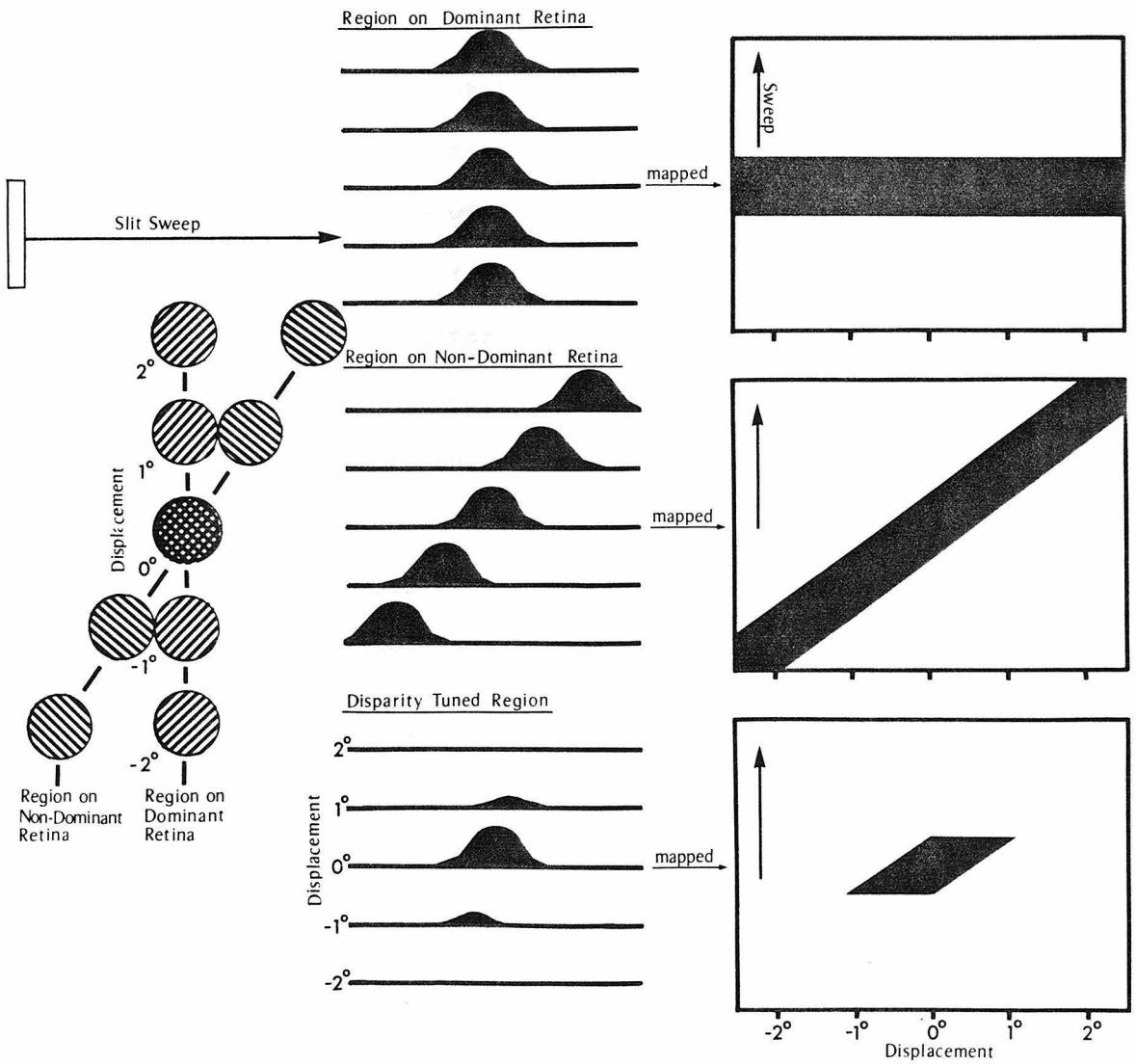


Figure 9

of the stimulus, an "island" would show on the map. Figure 8 contains a clear example of such an island. Further, in all cases, the width of the region on the retina can be determined from the width of the band or island along the abscissa of the map.

Complete BF location maps were made for twenty-five cells using vertical slits or edges moving horizontally across the retina. In many cases, maps were made at different velocities, sweep directions, etc., and maps from the same cell under differing stimuli parameters were often quite different. A total of thirty-nine maps were made. Every cell and every map showed considerable BF. Further, the majority had multiple regions of BF with both facilitation and inhibition occurring at different locations. Figure 10 shows histograms made from a unit with a clear facilitory island next to an inhibitory island. This cell also shows another feature commonly found: the presence of strong BF at the onset and at the offset of the slit sweep, even though the slit comes on and goes off at up to 8^{o} away from the monocular receptive field. This onset and offset phenomenon will be described more fully later.

Of the twenty-five cells, only one had a map of pure inhibition (Figure 8) and only one had a map of pure facilitation (containing two distinct islands). A more common arrangement consisted of an island of BF surrounded on the location map by BF of the opposite polarity (Figure 11). A similar mapping seen consisted of a large region of BF with a smaller region of BF of the opposite polarity, where the smaller region (a "peninsula") is not contained by the

Figure 10

This figure shows one of the computer runs used in making the BF location maps for LGN Cell LA9-10 (IPSI-Off, RF 11° from AC). The computer driven variable prism was placed over the dominant eye in this case and as a result the monocular response shifts by 1° for each degree of binocular displacement. The dotted line on the BDHs represents the position of the RF as determined by the monocular response peaks. Clear neighboring islands of inhibition (peaking at -2° to -3° displacement) and facilitation (peaking at +3° displacement) are seen, each located differently on the retina and in relative depth space. Also clear is the presence of sweep onset and offset binocular inhibition. (A complete map of BF from this cell is shown in Figure 32).

Binocular Feedback Mapping: Cell LA9-10

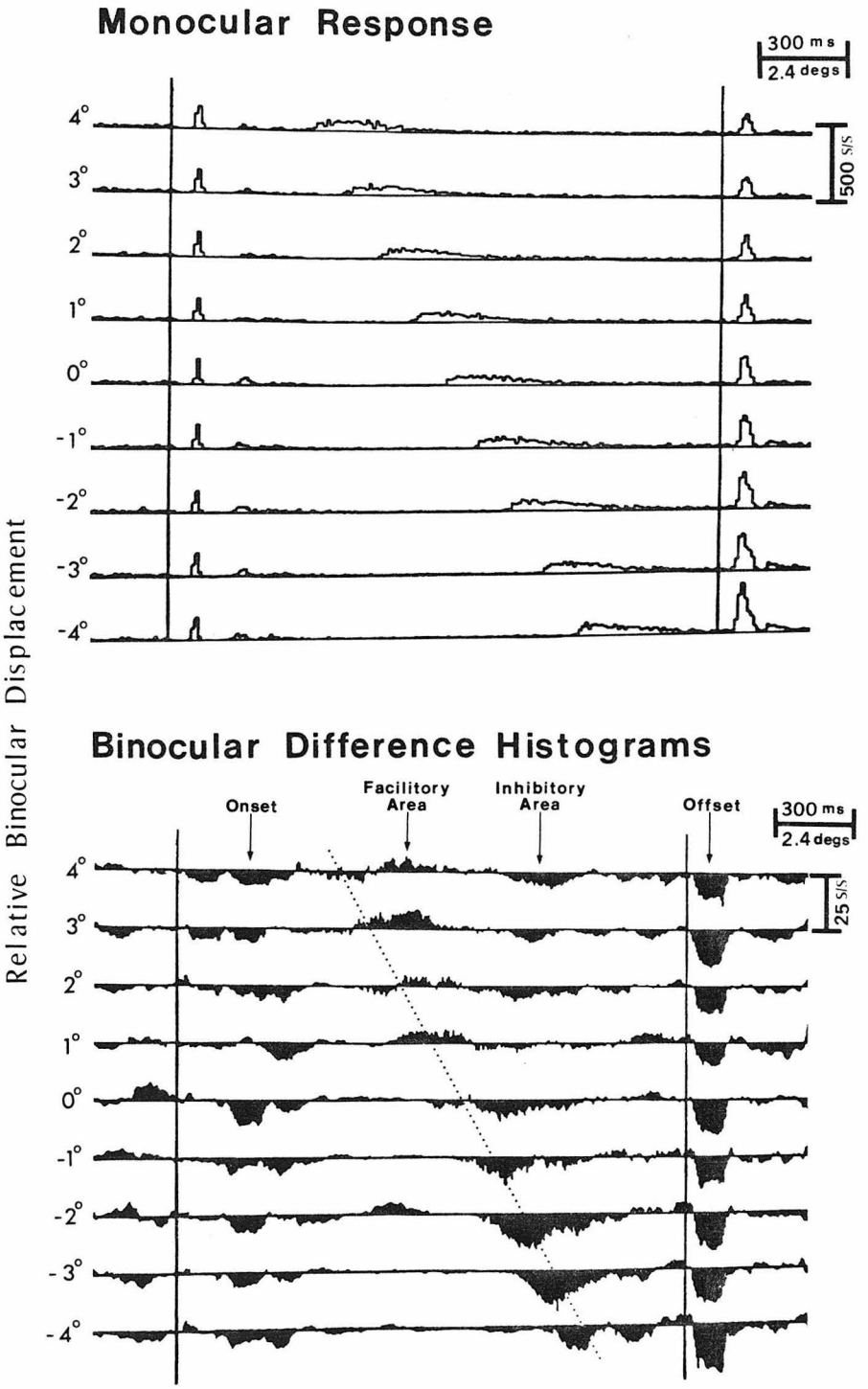


Figure 10

Figure 11

This figure shows the binocular feedback map for LGN cell LA5-6 (IPSI-Off, RF 4° from AC) taken with a vertical slit moving horizontally towards the AC at 12°/sec. A clear island of binocular facilitation is seen to be imbedded in a larger region containing binocular inhibition. The requirement for both binocular displacement and retinal position is sharper in this cell for facilitation than inhibition. The dotted line represents the position of the monocular RF of the cell. The variable prism was placed in front of the non-dominant eye for this test. The BF seen at sweep onset and offset is also depicted.

Figure 12

This figure shows the binocular feedback map for cell LA9-7 (CONTRA-On, RF 14° from AC) taken with a vertical slit moving horizontally away from the AC at 8°/sec. A large region of binocular facilitation is seen next to a smaller region of inhibition. Tests were not done at displacements more than 4° divergent for this cell and it is only clear that inhibition at least requires displacements greater than or equal to 3° divergent. The dotted line represents the position of the monocular RF of the cell. The variable prism was placed over the dominant eye for this test. No BF was found at sweep onset. The offset BF consisted of facilitation followed by inhibition, as indicated by the triangular splitting on the map.

MAP OF BINOCULAR FEEDBACK FOR CELL LA5-6

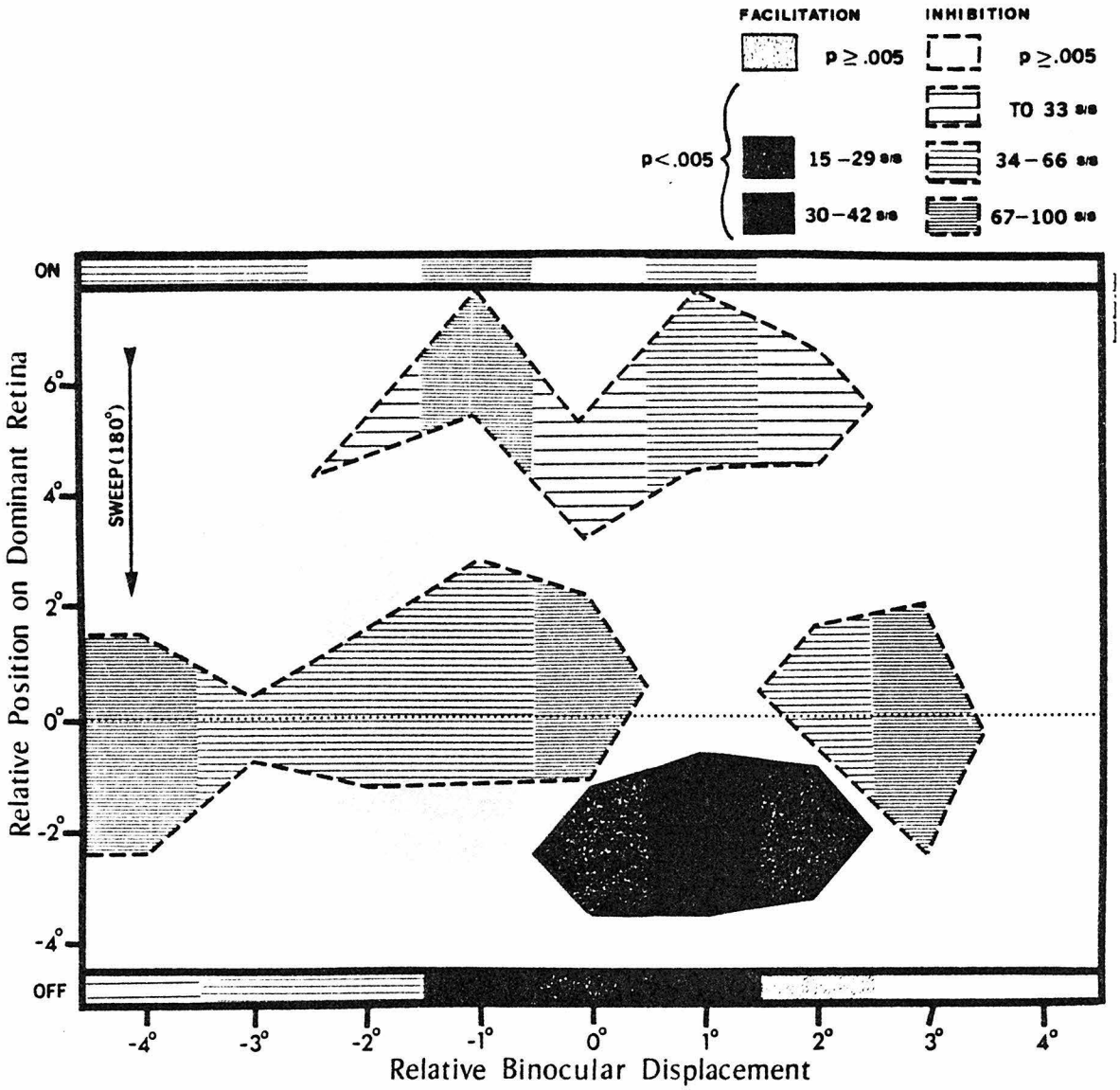


Figure 11

MAP OF BINOCULAR FEEDBACK FOR CELL LA9-7

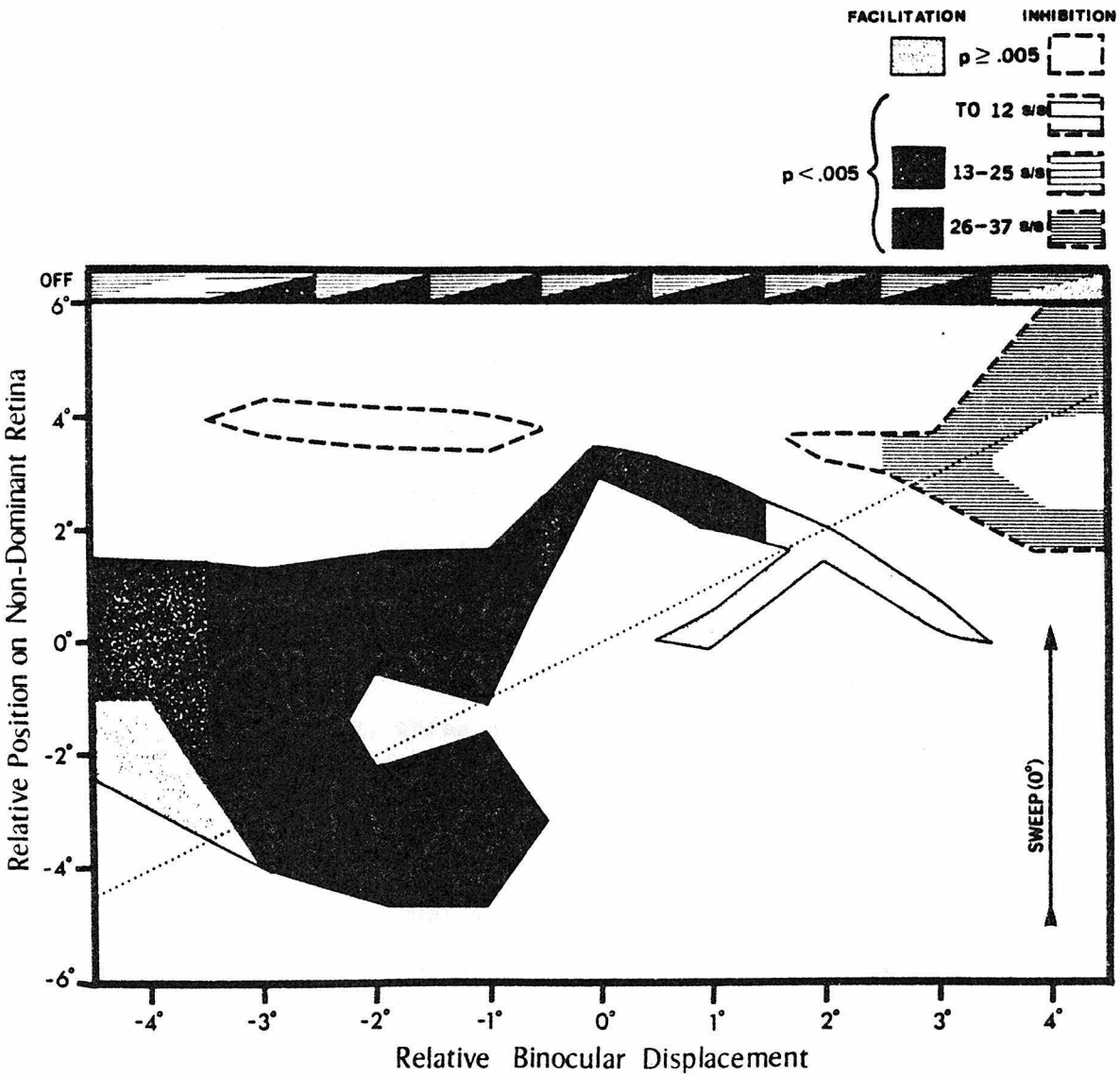


Figure 12

larger region and the smaller region occurs on one of the extreme displacements tested (Figure 12). Five cells showed a single island of facilitation surrounded by inhibition. An additional two cells showed a single facilitation peninsula and larger regions of inhibition. A single inhibition island surrounded by facilitation was seen in three cells and two cells showed inhibitory peninsulas next to extensive facilitation. Two cells showed a single island of facilitation paired with a single island of inhibition. The most common arrangement, however, consisted of two or more regions of facilitation and two or more regions of inhibition. This was seen in seventeen maps taken from twelve cells. BF clearly can be found, it is seen, in a number of different arrangements.

Every map from every cell contained at least one island - a region at a specific retinal location and at a range of specific binocular displacements. Nine cells also showed bands of BF as described above, demonstrating the existence of BF regions which have a specific location on the retina but which lack a strong requirement for binocular displacement (Figure 13). Four of the cells had a single band of facilitation, three had a single band of inhibition, and two had one of each. As described above, the orientation of the band (horizontal versus diagonal) can be used to indicate whether the region has a well defined location on the dominant or non-dominant retina. Four of the cells had a band indicating the dominant retina, four indicating the non-dominant, and one had a band for each (see Figure 32). It should be noted that even within bands, increases in BF amplitude are often seen at particular displacements, which

Figure 13

This figure shows a binocular feedback map for LGN cell LA2-3 (CONTRA-On, RF 12° from AC) taken with a vertical slit moving horizontally away from the AC at 12°/sec. Three strong regions of BF are indicated, two facilitory and one inhibitory. The central inhibitory region spans all displacements tested and forms a band parallel to the monocular RF (dotted line), thus indicating a weaker requirement for binocular displacement than the cells depicted in the two previous figures. The tests were run with the variable prism over the non-dominant eye.

MAP OF BINOCULAR FEEDBACK FOR CELL LA2-3

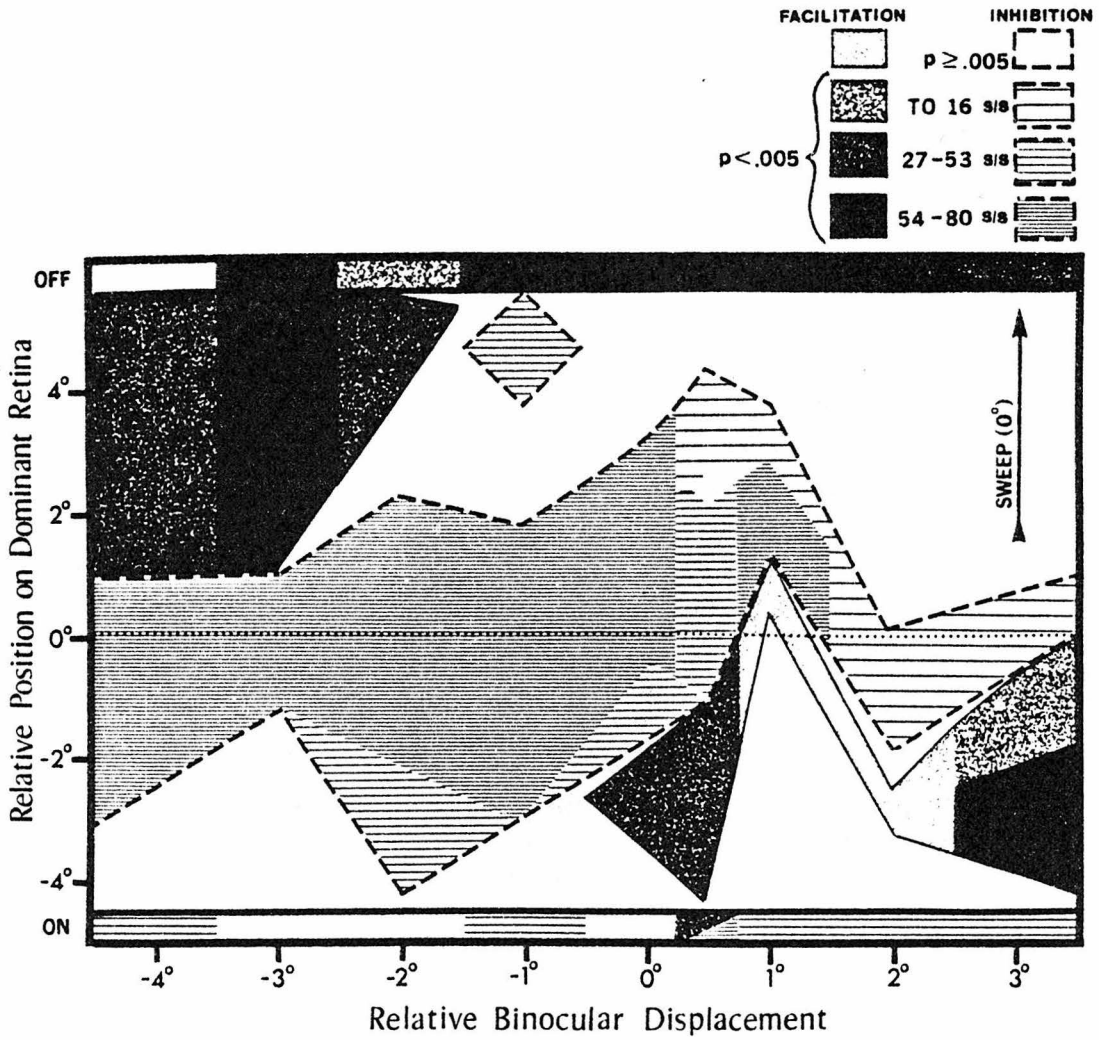


Figure 13

indicates some preference for a particular retinal disparity.

Inhibition and facilitation were fairly evenly distributed among the population of cells tested. Twelve maps from ten cells could be classified as predominantly containing inhibition, fifteen maps from twelve cells containing mostly facilitation, and the remaining twelve maps from eleven cells had roughly equal amounts of facilitation and inhibition. The relative predominance of one polarity of BF could in fact switch in the same cell depending upon the visual stimulus presented (see Figure 32).

All of the maps were checked to see if any particular arrangement of BF could be correlated with other factors. No significant difference was found in BF arrangement, predominance of inhibition or facilitation, or the occurrence of banding for IPSI versus CONTRA, On versus Off, or central versus peripheral cells.

Although most regions of binocular inhibition and facilitation are similar in that they both have specific requirements for binocular displacement, they are quite different in their distribution in vergence space (Figure 14). The number of islands of facilitation (15 of 51; 29%) found at an estimated zero degrees displacement almost doubled the number of inhibitory islands found there (8 of 54; 15%). Special precautions were taken to get an accurate measure of the vergence of the eyes, often including the use of reference cortical units (METHODS). Although the relative vergence of the retinas of a paralyzed cat can be hard to measure, and is believed to have a slow drift of less than one degree in an experiment, the tendency of

Figure 14

51 islands of facilitation and 54 islands of inhibition from 39 maps from 25 cells were plotted in the bin representing each one's optimal binocular displacement. In this figure, negative displacements are convergent. Although errors in measuring actual retinal displacements would tend to cause a "spreading out" of both histograms, the increased tendency of facilitory islands to lie at zero degrees displacement is clear. There is a also a tendency for islands of both facilitation and inhibition to require convergent displacements (see Text). So-called "peninsulas" have been excluded from this figure, due to the uncertainty of their actual preferred displacements.

Binocular Feedback Locations: Optimal Binocular Displacements

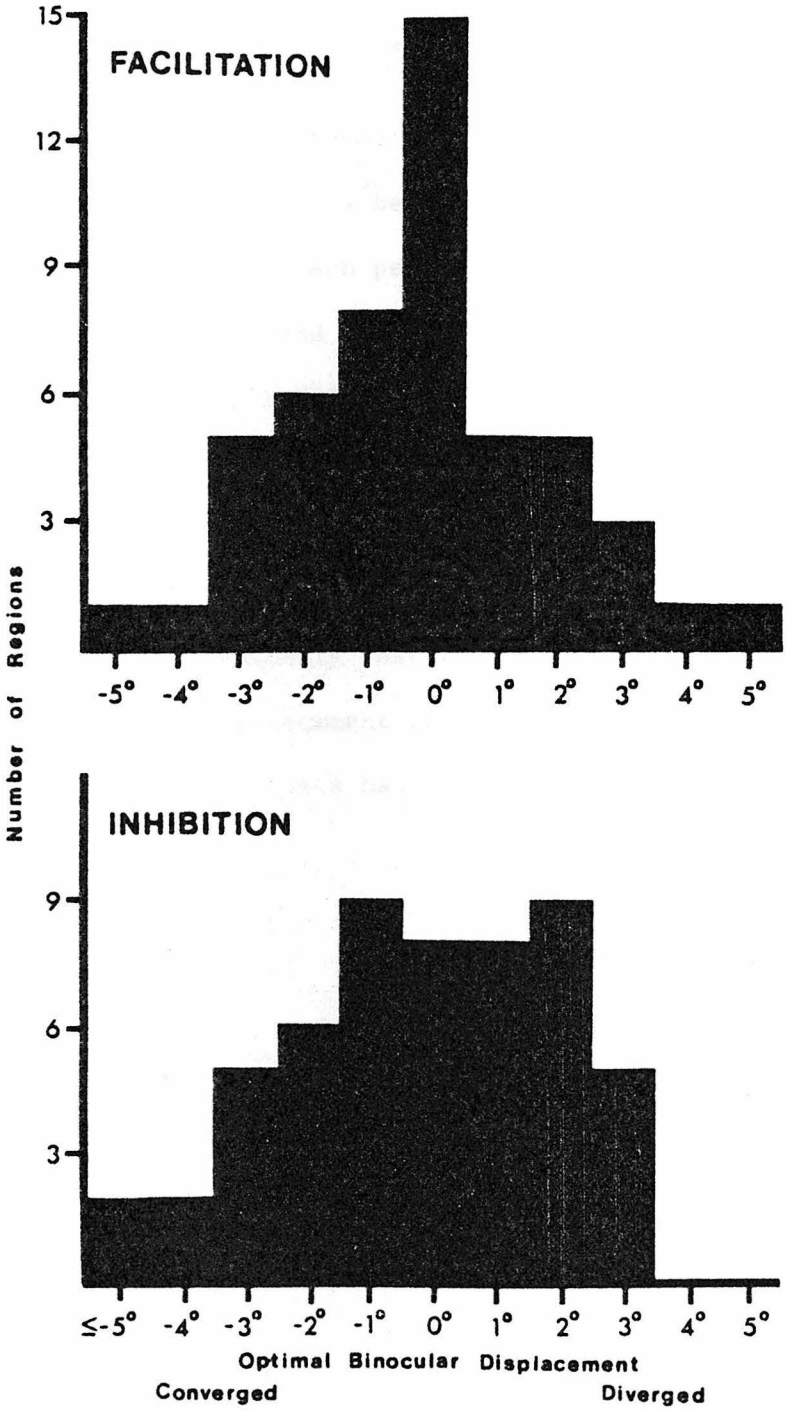


Figure 14

such errors would be to flatten out the histograms in Figure 14 and to do so equally to facilitory and inhibitory regions. The difference between facilitation and inhibition is even more striking in light of this and it is likely that the data represent an underestimate of the number of regions that actually lie at zero degrees displacement.

BF also showed a tendency to be convergent. Although "peninsulas" are not included in Figure 14 because their optimal displacement is not clear, the vergence of each peninsula is clear. Including them gives 65 convergent regions and 56 divergent regions. Inhibition and facilitation are not strongly different in this tendency. It should also be noted that the 40 peninsula regions not included in Figure 14 all exist at the more extreme displacements, as described above, and BF was found even as extreme as six degrees diverged and eleven degrees converged. It is unlikely that this is totally due to error in measuring retinal displacement as in three cats four successive cells on the same electrode track had BF located over large ranges of displacements (Table 1).

Cat	Layers Crossed	RF Distance to AC (degs)	Range of Displacements Found: Facilitation (degs, C=converged, D=diverged)	Inhibition
LA1	A1	15	5C to ≥6D	≥4C to 2.5D
LA2	A to A1	16 to 6	4C to 4D	11C to 4D
LA7	A to A1	4	7C to 4.5D	5C to 6D

Ranges of Optimal Binocular Displacements
in Single Tracks of Four Units Each

Table 1

Comparisons of optimal vergence were made between different cell categories. No significant differences were found between IPSI and CONTRA, On and Off, or peripheral and central.

Regions of BF can also be described in terms of their retinal location relative to the location of their monocular RF on the dominant eye. The relationship is depicted in Figure 15. The majority of regions lies in the same place as the monocular RF, although a number do not. The mean distance for all regions is 0.2^{o} with a standard deviation of 2.4^{o} indicating fair scatter. These measures are considered as very accurate because the position of a region of BF and the monocular RF are determined simultaneously from the same sweeps of the visual stimulus. No difference is found between inhibitory or facilitory BF.

Figure 16 shows the size distibution of regions of BF. Horizontal width ranged from under 0.1^{o} to as large 5.8^{o}. Facilitation averages 1.4^{o} and inhibition averages 2.0^{o}. These measures are most

Figure 15

This figure shows the distribution of the distances of the center of a region of BF on the dominant retina from the center of its unit's monocular RF. All regions of BF that could be located on the dominant retina from their BF maps are included in this histogram. Because all maps were made with vertical slits moving horizontally, the distances depicted are horizontal. Negative distances are on the AC side of the monocular RF. The mean distance for all regions is 0.2^{o} with a standard deviation of 2.4^{o}. There is no difference between facilitation and inhibition.

Figure 16

This figure shows the distribution of sizes of regions of BF on the retina. Size is calculated as the region over which the binocular difference is reliable beyond the 99.5% cutoff and is thus probably an underestimate. As depicted, the average region of facilitation is smaller than the average region of inhibition.

Regions of Binocular Feedback: Positions Relative to Monocular RF

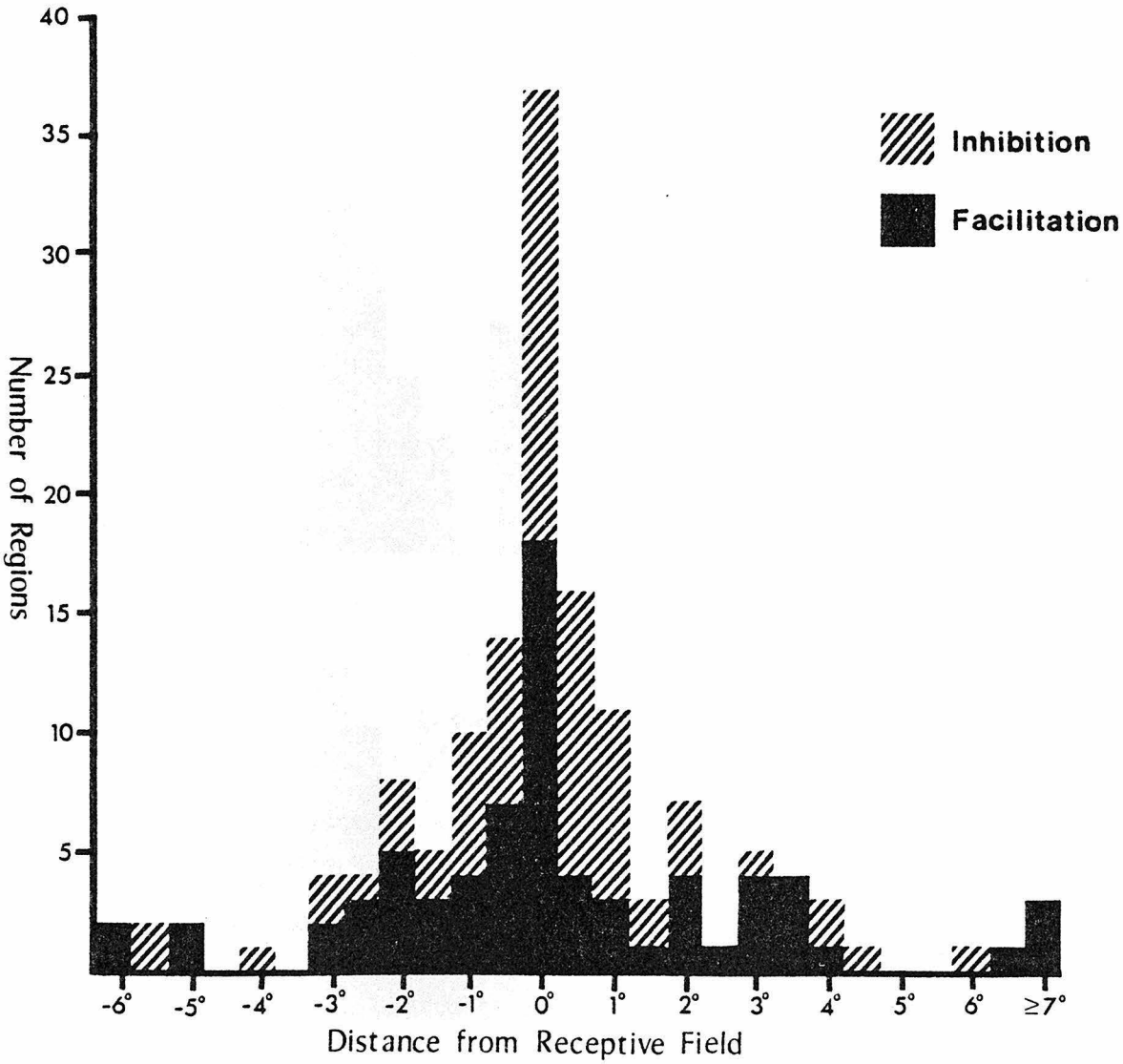


Figure 15

Regions of Binocular Feedback: Size Distribution

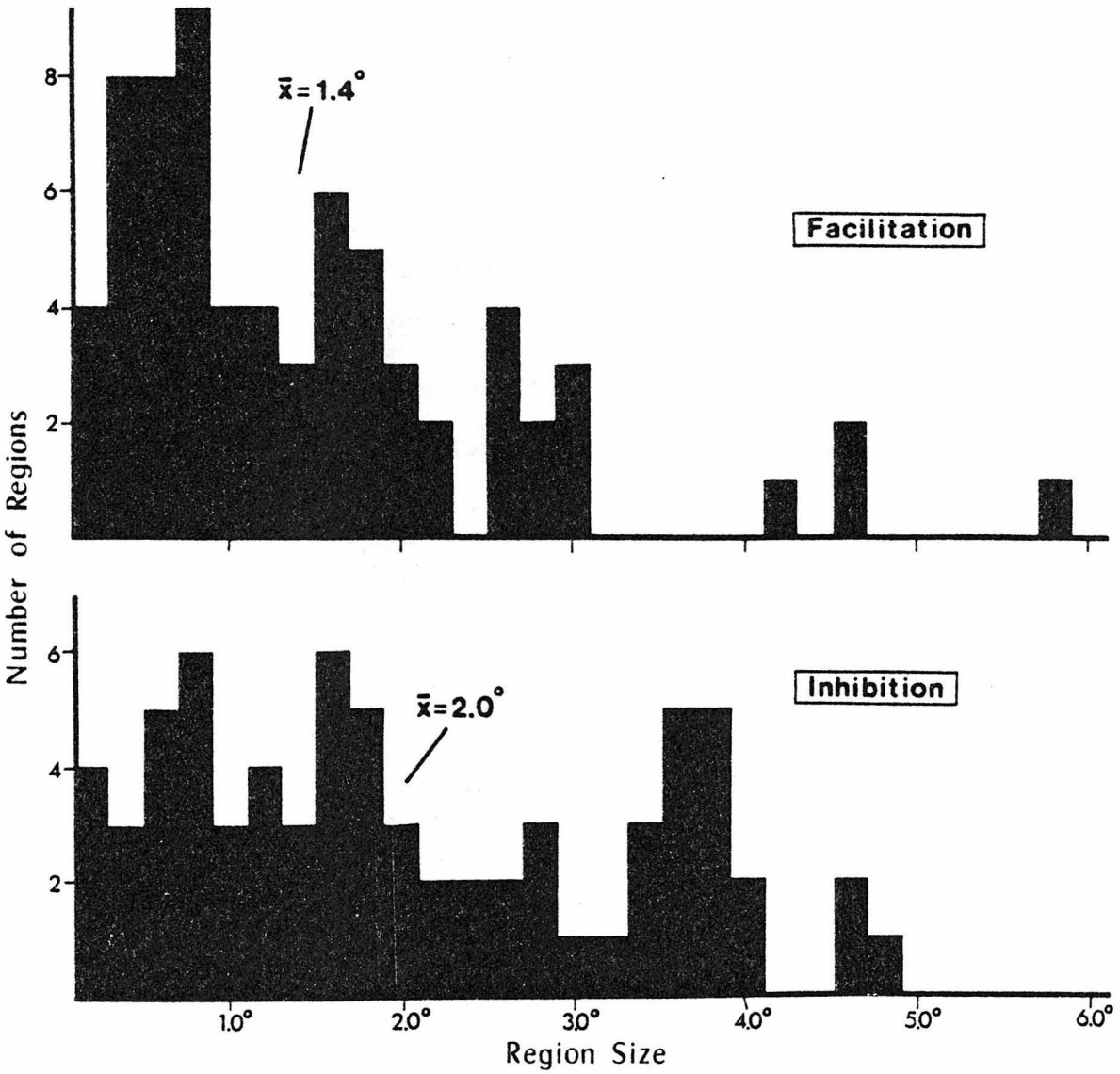


Figure 16

likely underestimates because they represent only the area over which the binocular difference measured exceeds 99.5% reliability. No difference is found for size distribution or distance to monocular RF for IPSI versus CONTRA, On versus Off, or central versus peripheral.

Binocular feedback, it is shown, occurs most often as areas with specific retinal locations and specific requirements for binocular displacement. The majority of cells have multiple regions of facilitation and inhibition, each with their own location in retinal and depth space. Facilitation tends to occur more often at zero binocular displacement than inhibition. Neither inhibition nor facilitation predominate under the conditions tested. Most regions of BF lie on or near the monocular RF, although a significant number can be more than a few degrees away. Regions of BF can vary considerably in size, possibly from as small as less than 0.1^{o} to larger than 5.8^{o}. On the average, inhibitory regions are larger than facilitory.

2.3 Velocity Tuning

Thirty-four cells were tested to see if BF varies with the velocity of visual stimuli sweeping over the region around the monocular RF. In general, vertical gratings, slits, or edges were used. Other parameters of the visual stimuli (e.g., direction of sweep, relative binocular displacement) were sometimes chosen on the basis of other tests on the cell, but more often these tests could not be analyzed soon enough, so partly arbitrary values were used. Despite the difficulty in optimizing the visual stimuli for BF, sharp velocity tuning was found to be far more common for BF than for the monocular response of each cell.

As with displacement tuning, BDHs were constructed and amplitudes extracted from regions of significant BF, in this case at each velocity tested (Figures 17 and 18)[1]. Forty-six complete and usable tunes were generated from thirty-two cells. A number of cells were given more than one velocity tune with alterations made in various other parameters of the visual stimuli. All BF velocity tunes could be identified as belonging to one of the following five categories: 1) tuned and containing a sharp peak (Figures 20, 21, and 27), 2) tuned and containing a steep trough (Figure 19), 3) untuned and generally upward-going (from strong inhibition to weak, or from weak facilitation to strong - Figure 22), 4) untuned and generally downward-going (Figure 24), or 5) untuned and basically flat (Figure

1. When more than one region of BF was found on a BDH, the maximum amplitude from all regions of one type was used in the velocity tune. When regions of both inhibition and facilitation were found, a "split" tune was made (as in Figures 24 and 27).

23)[2]. The tuning of the monocular responses could be similarly classified, except that no monocular tunes were found that contained troughs.

Quantitative criteria were set for establishing the existence of peaks, troughs, upward-only, downward-only, and flat tunes. Visual inspection of a tune was considered inadequate because the appearance of possible peaks and troughs could be exaggerated or diminished by variations in a graph's scale. A peak should have both a maximum increase on the lower velocity side and a maximum decrease on the higher side that exceeds a certain slope. A slope equal to 7% of the peak BF per one degree/second was chosen because tunes with multiple small upward and downward fluctuations (as in Figure 23) never had any of their apparent peaks or troughs meeting this requirement. As an example, a cell with 100 s/s facilitation at 16°/sec would have to show a facilitation drop-off to less than 44 s/s at 8°/sec (or above) and at 24°/sec (or below) to qualify as having a real peak at 16°/sec. The criteria for a trough is the same, but inverted in direction. If a tune had no real peaks or troughs it was classified as upward or downward if the average slope of the tune exceeded 1.25% of the peak BF per deg/sec (such as dropping from 75 s/s inhibition at 4°/sec to at least 100 s/s at 24°/sec). If it did not meet these requirements, it was then classified as flat.

Of the forty-six BF velocity tunes, only five (11%) were downward-going, five (11%) were upward-going, and two (4%) were flat.

2. In all figures showing velocity tunes, inhibition is depicted below the X-axis as negative spikes/second and not as a downward slope or curve.

Figure 17

This figure shows the monocular histograms and BDHs of LGN cell LA5-8 (IPSI-On, RF 5° from AC) as tested by a 1.7° grating moving at velocities ranging from 2°/sec to 14°/sec away from the AC. The filtered BDH is not shown. At 2°/sec, inhibition is very weak, and there is even a small amount of facilitation (slight but in this case significant). Binocular inhibition increases until 12°/sec where it peaks. The tuning is relatively weak in this cell, and it was chosen for depiction because it contains the greatest number of velocities simultaneously tested for any unit. Most often, three to four velocities would be tested at once. An entire tune could consist of from one to four tests of separate sets of velocities. This tune also demonstrates that onset inhibition can occur with gratings and that for this cell the onset BF is not as tuned to velocity as is the response during the sweep.

Figure 18

This figure shows the monocular histograms and filtered and unfiltered BDHs for unit LA7-3 (CONTRA-On, RF 5° from AC) as tested by a leading edge moving at velocities 4°/sec to 16°/sec towards the AC. Other velocities were tested and the entire tune can be seen in Figure 20. The "ragged" BDHs are clearer after statistical filtration and the transition from inhibition at 4°/sec to facilitation at 8°/sec back to inhibition at 16°/sec during the sweep becomes clear. Also shown is a strong onset binocular inhibition with some offset inhibition at 4°/sec and possibly some offset facilitation at 16°/sec. Notice that the cell also has a monocular onset and offset response.

Partial Velocity Tune for Cell LA5-8

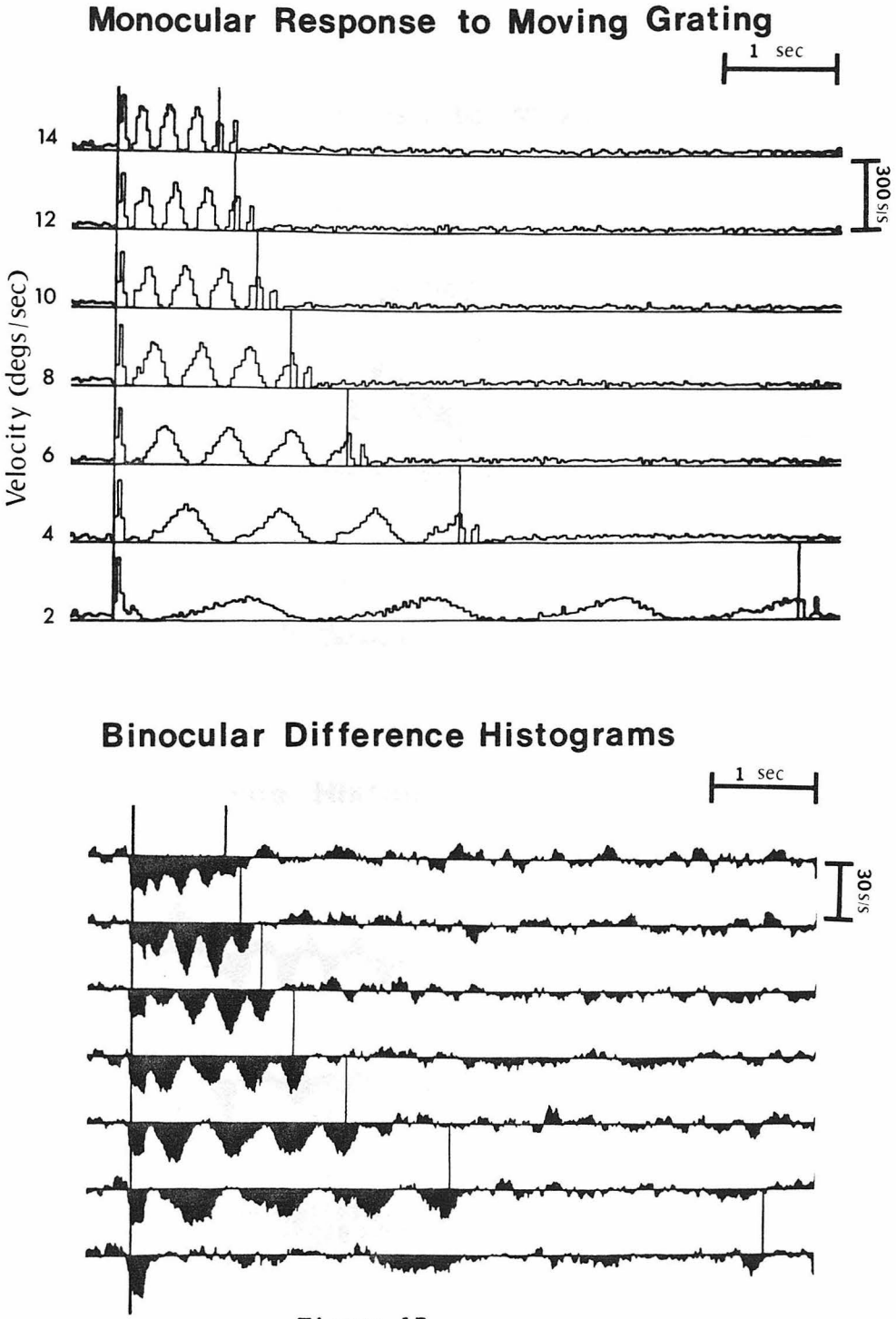
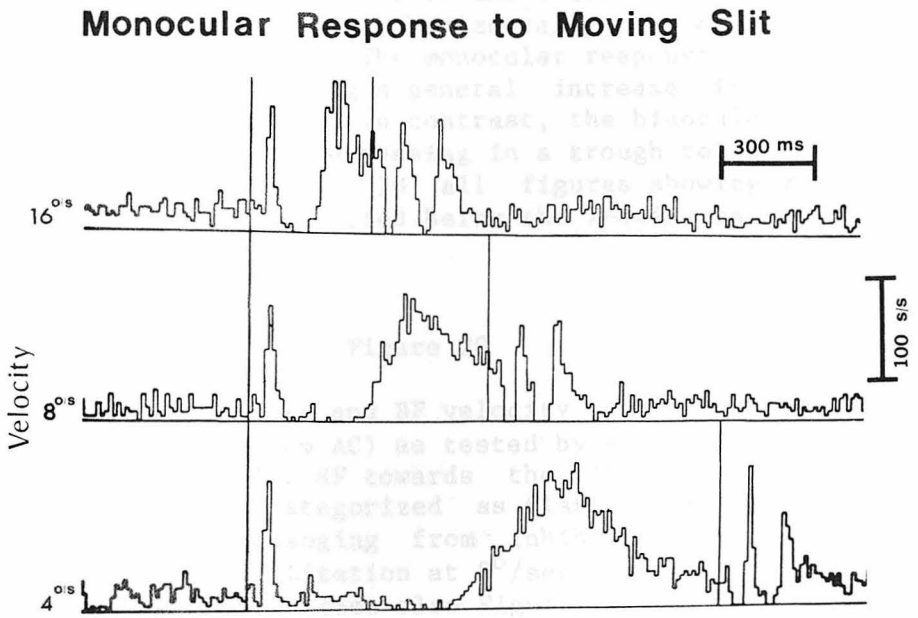


Figure 17

Partial Velocity Tune for Cell LA7-3



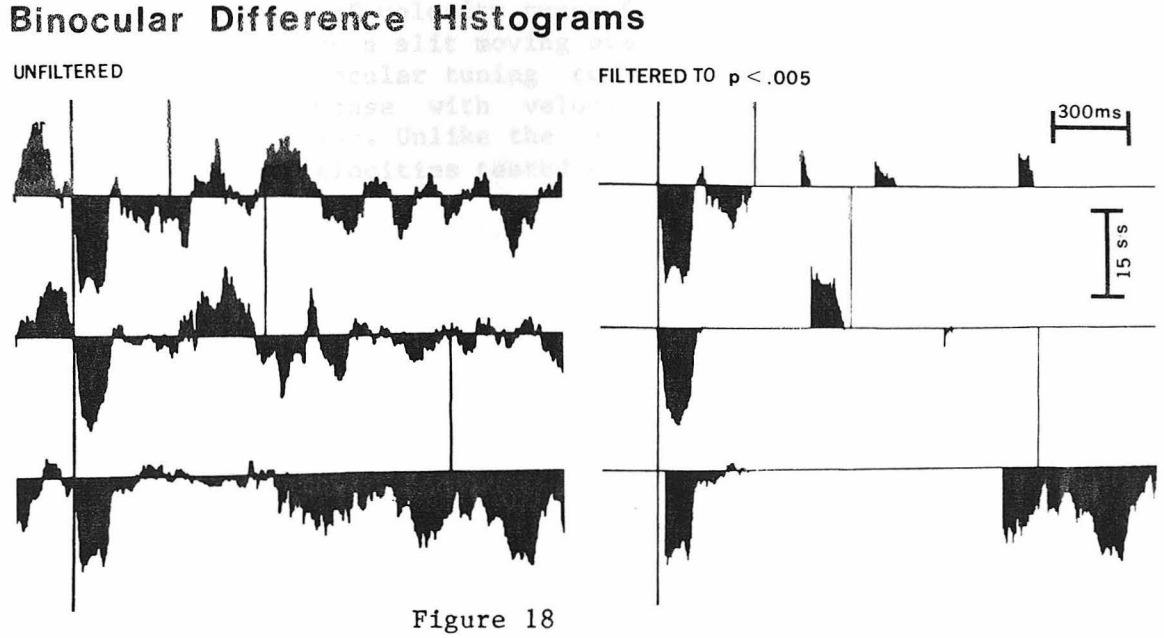


Figure 18

Figure 19

This figure shows the velocity tunes of the monocular response and of the BF of unit LA5-6 (IPSI-Off, RF 4° from AC) to a 1.7° grating moving horizontally over the monocular RF away from the AC. The monocular response is not well tuned to velocity, showing a general increase in response with increased velocity. In contrast, the binocular inhibition is sharply tuned, decreasing in a trough to a maximum inhibition at 12°/sec. In all figures showing velocity tunes, inhibition is depicted below the X-axis as negative spikes/second.

Figure 20

Shown are the monocular and BF velocity tunes for cell LA7-3 (CONTRA-On, RF 5° from AC) as tested by a leading edge moving over the monocular RF towards the AC. This monocular velocity tune is categorized as flat. The BF is strongly tuned to velocity, changing from inhibition at low edge speeds to a peak facilitation at 8°/sec back to inhibitition at a higher velocity. (See also Figure 18.)

Figure 21

The monocular and BF velocity tunes for cell LA2-5 (IPSI-On, RF 5° from AC) to a slit moving over the RF towards the AC are shown. The monocular tuning consists only of a slow decrease in response with velocity, whereas the BF has a clear peak at 5°/sec. Unlike the unit in Figure 20, the entire range of velocities tested produced binocular facilitation.

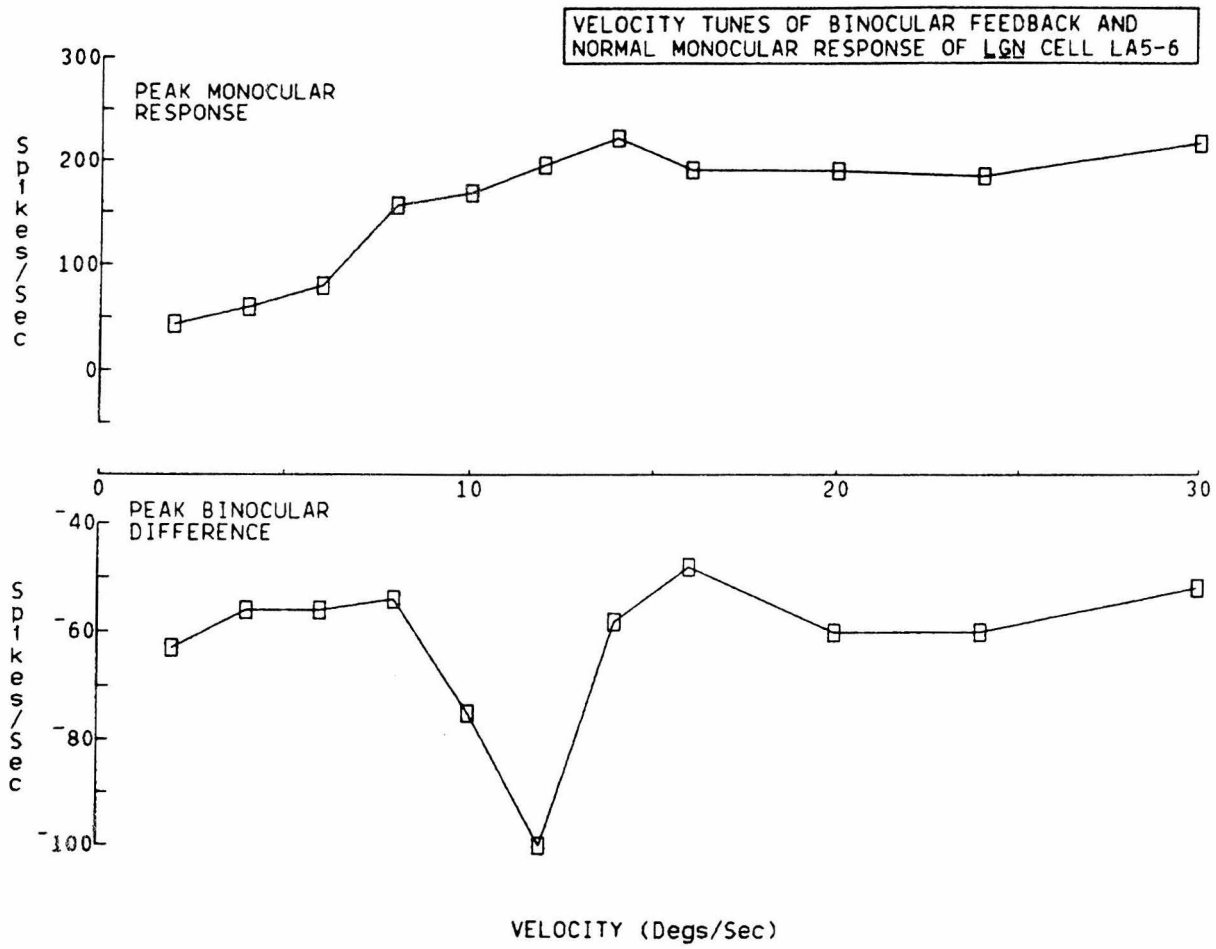

VELOCITY TUNES OF BINOCULAR FEEDBACK AND NORMAL MONOCULAR RESPONSE OF LGN CELL LA5-6
PEAK MONOCULAR RESPONSE
Spikes/Sec
300
200
100
0
0
10
20
30
PEAK BINOCULAR DIFFERENCE
Spikes/Sec
-40
-60
-80
-100
VELOCITY (Degs/Sec)

Figure 19

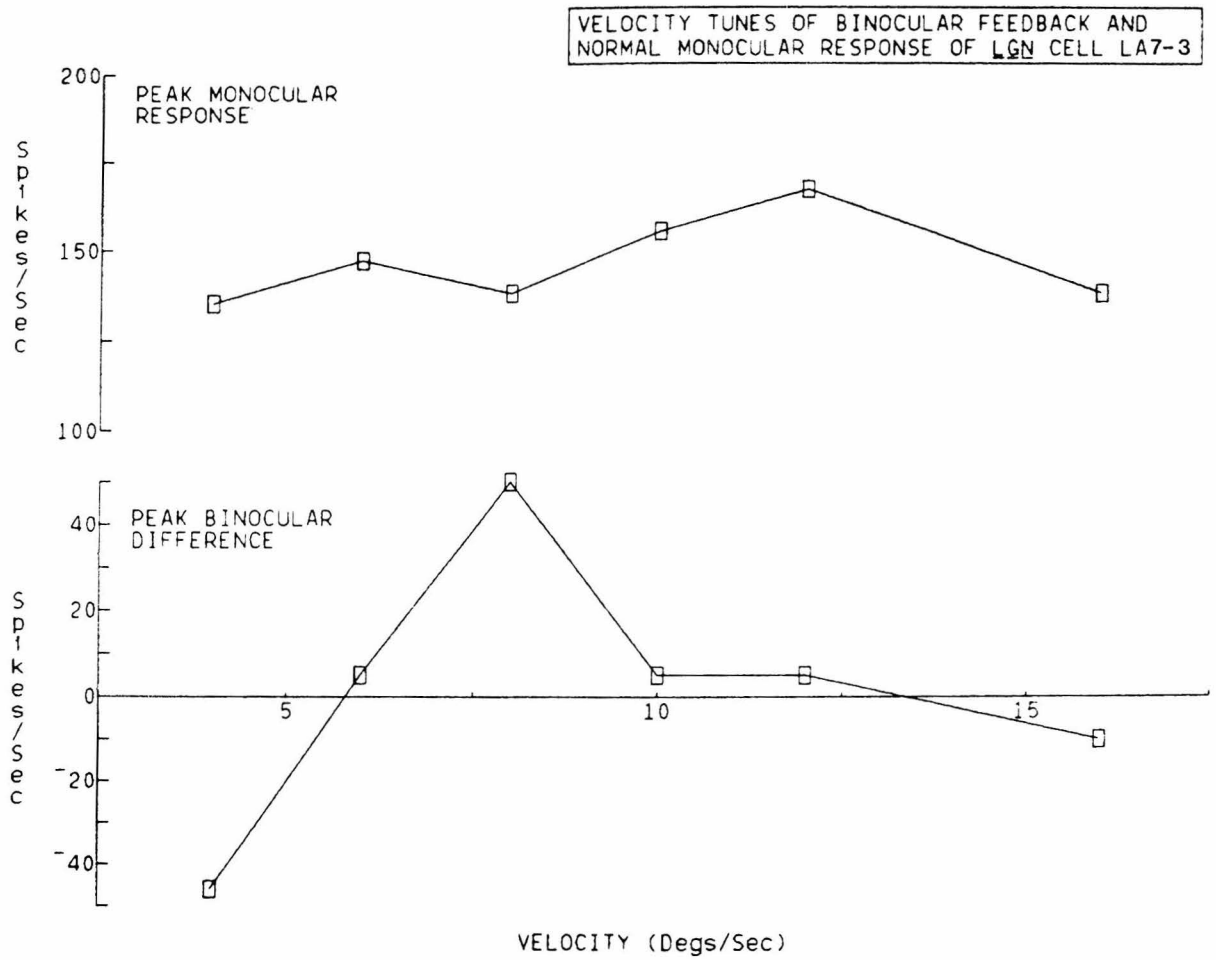

VELOCITY TUNES OF BINOCULAR FEEDBACK AND NORMAL MONOCULAR RESPONSE OF LGN CELL LA7-3
PEAK MONOCULAR RESPONSE
Spikes/Sec
200
150
100
PEAK BINOCULAR DIFFERENCE
Spikes/Sec
40
20
0
-20
-40
5
10
15
VELOCITY (Degs/Sec)

Figure 20

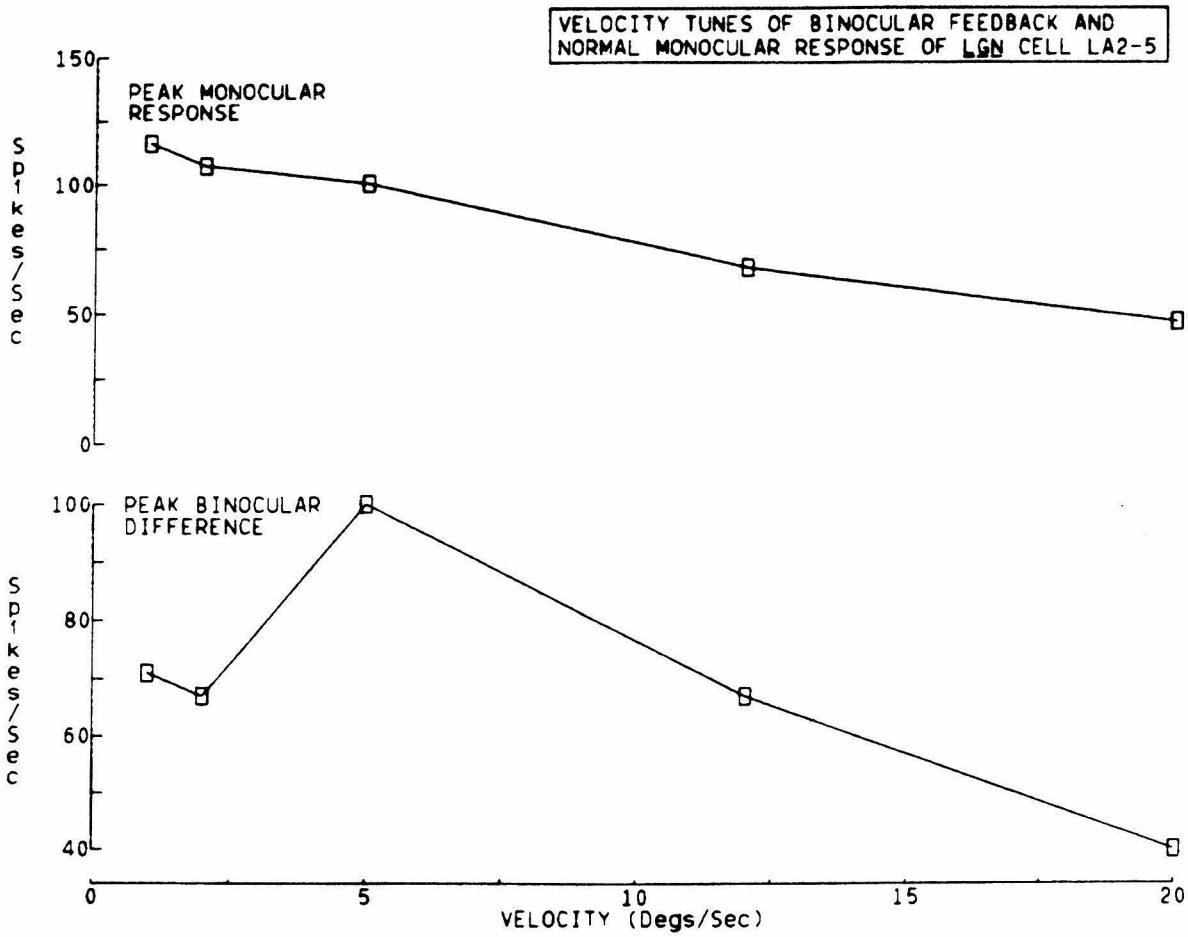

VELOCITY TUNES OF BINOCULAR FEEDBACK AND NORMAL MONOCULAR RESPONSE OF LGN CELL LA2-5
PEAK MONOCULAR RESPONSE
Spikes/Sec
150
100
50
0
PEAK BINOCULAR DIFFERENCE
Spikes/Sec
100
80
60
40
0
5
10
15
20
VELOCITY (Degs/Sec)

Figure 21

Figure 22

This figure shows monocular and BF velocity tunes for LGN cell LA6-4 (CONTRA-On, RF more than 15^{o} from AC) to a 1.7^{o} grating moving over the RF away from the AC. This cell is an example of those with BF that show only a slow upward trend as velocity increases. The same trend is seen with the monocular response.

Figure 23

Unit LA5-5 (CONTRA-Off, 4^{o} from AC) shows BF that is relatively invariant with velocity and a monocular response that slowly increases with higher sweep speeds. These tunes were done with a 1.7^{o} grating moving over the RF away from the AC.

Figure 24

Cell LA2-3 (CONTRA-On, RF 6^{o} from AC) shows BF that shows a slow downward trend with increased velocities and a monocular response with an opposite upward trend. The tests were done with a slit moving over the RF away from the AC. The BF measure is split at 2^{o}/sec because in that sweep, regions of both facilitation and inhibition were found. The values plotted represent the maximum of each seen in the sweep. This "splitting" was not uncommon.

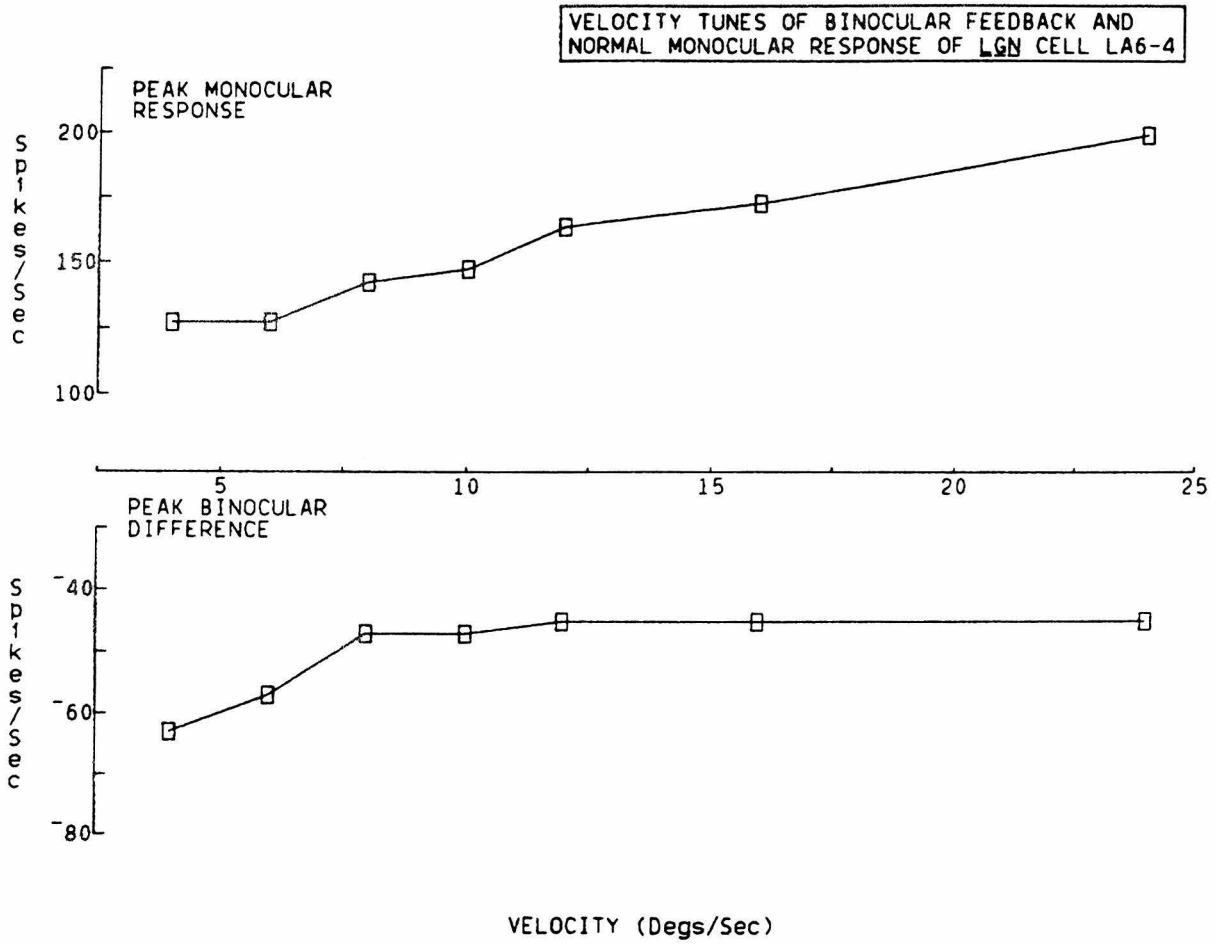

VELOCITY TUNES OF BINOCULAR FEEDBACK AND NORMAL MONOCULAR RESPONSE OF LGN CELL LA6-4
PEAK MONOCULAR RESPONSE
Spikes/Sec
200
150
100
5
10
15
20
25
PEAK BINOCULAR DIFFERENCE
Spikes/Sec
-40
-60
-80
VELOCITY (Degs/Sec)

Figure 22

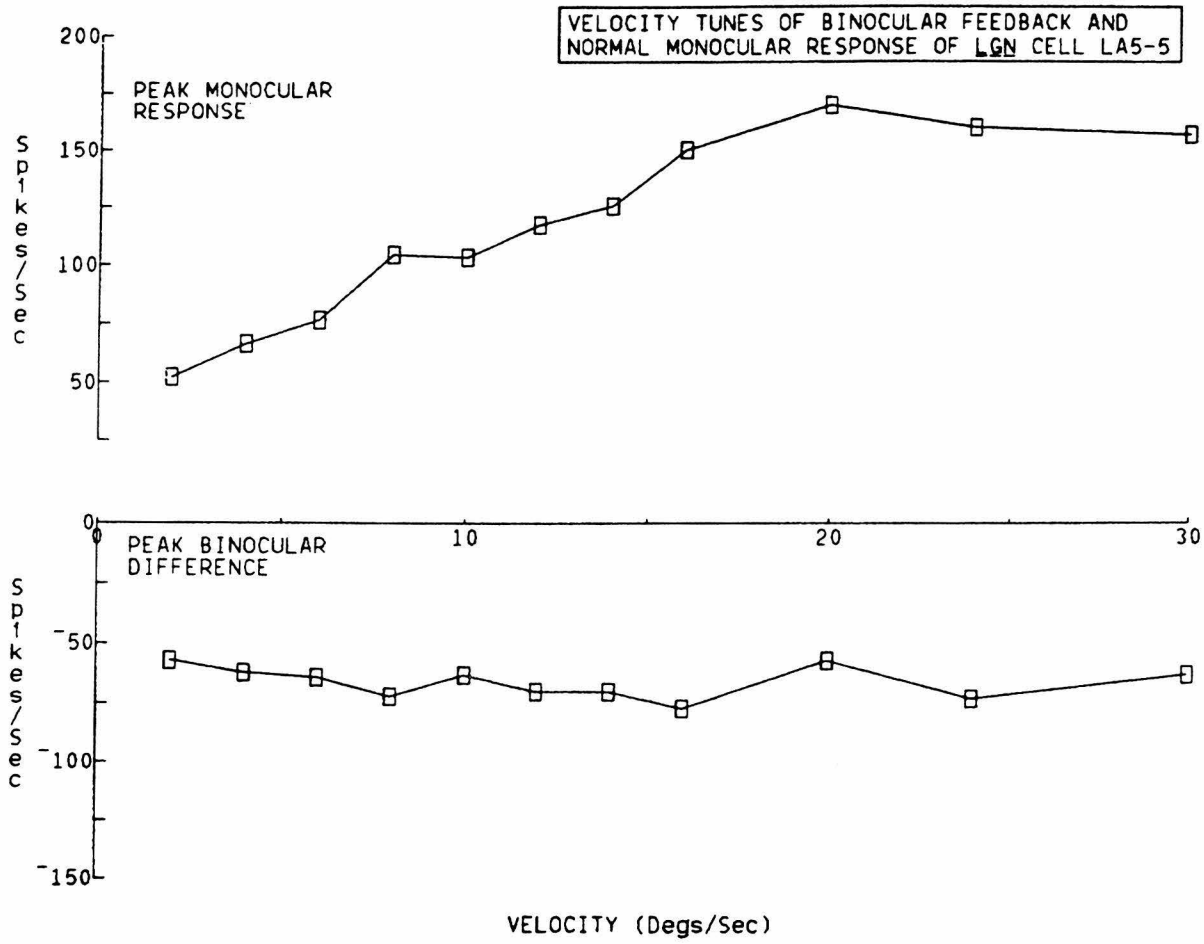

VELOCITY TUNES OF BINOCULAR FEEDBACK AND NORMAL MONOCULAR RESPONSE OF LGN CELL LA5-5
PEAK MONOCULAR RESPONSE
Spikes/Sec
200
150
100
50
0
10
20
30
PEAK BINOCULAR DIFFERENCE
Spikes/Sec
-50
-100
-150
VELOCITY (Degs/Sec)

Figure 23

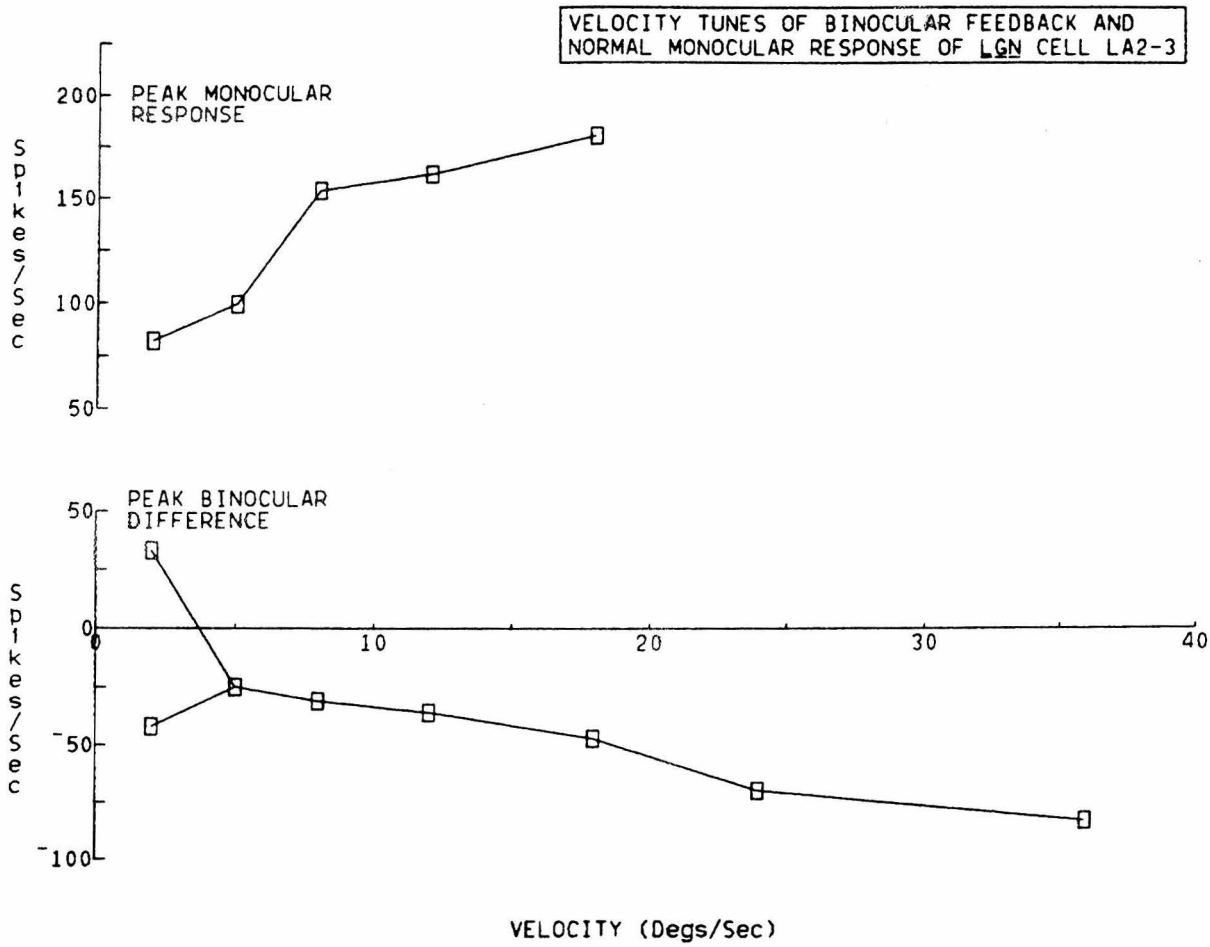

VELOCITY TUNES OF BINOCULAR FEEDBACK AND NORMAL MONOCULAR RESPONSE OF LGN CELL LA2-3
PEAK MONOCULAR RESPONSE
Spikes/Sec
200
150
100
50
PEAK BINOCULAR DIFFERENCE
Spikes/Sec
50
0
-50
-100
0
10
20
30
40
VELOCITY (Degs/Sec)

Figure 24

The majority, 33 (72%), had real peaks and/or troughs. Of these, thirteen (40%) had a single peak, fourteen (42%) had a single trough, five (15%) had both a peak and a trough (as in Figure 25), and one (3%) had a trough, a peak, and then a trough (Figure 26). Of the twenty-one trough minima identified, nineteen were inhibitory and two were at zero (and thus were troughs in a range of facilitation). Seventeen of the nineteen peak maxima were facilitory and two were inhibitory. It should be noted that in many cases the velocity tune for a cell spanned both facilitation and inhibition (as in Figures 20, 24, 25, 26 and 27). In almost every case, the BF for each individual cell was strikingly more precisely tuned for velocity than its monocular response to the same stimuli (as in Figures 19, 20, 21, 25, 26 and 27).

BF tends to be best tuned at a particular range of velocities (Figure 28). Peaks and troughs occur far more often between 6 and 12°/sec than any other interval, with 19 (48% of 40) falling at 8°/sec. No difference in distribution is seen between peaks and troughs.

An average BF amplitude was calculated for each of the thirteen BF tunes containing no peaks or troughs (and thus considered untuned). Twelve (92%) of these were inhibitory (as in Figures 22, 23, and 24). All of the BF tunes that were upward-going or downward-going, forms most often seen in monocular responses, were primarily inhibitory, with the averages for each tune ranging from 7 to 71 s/s.

Figure 25

The monocular and BF velocity tunes for LGN cell LA6-3 (CONTRA-On, RF more than 15° from AC) taken with a 1.7° grating moving across the RF away from the AC. The monocular tune is upward-going whereas the BF tune has both a peak (at 14°/sec) and a trough (at 24°/sec). The point at 14°/sec is just at threshold (see Text) for classification as a real peak.

Figure 26

This figure shows the monocular and BF velocity tunes for unit LA5-7 (CONTRA-Off, RF 8° from AC) for a 1.7° grating moving over the RF away from the AC. This cell was unique in that it shows a trough, a peak, and then a trough. Notice also that the tune includes both facilitation and inhibition. The monocular tune is of the typical upward-going type.

Figure 27

Shown here are the BF and monocular velocity tunes for cell LA7-1A (CONTRA-Off, RF 4° from AC) for a 1.7° grating moving across the RF away from the AC. The BF is split at 6°/sec because both facilitation and inhibition were found at that velocity. The monocular tune is one of three that has a real peak, which is nevertheless fairly weak.

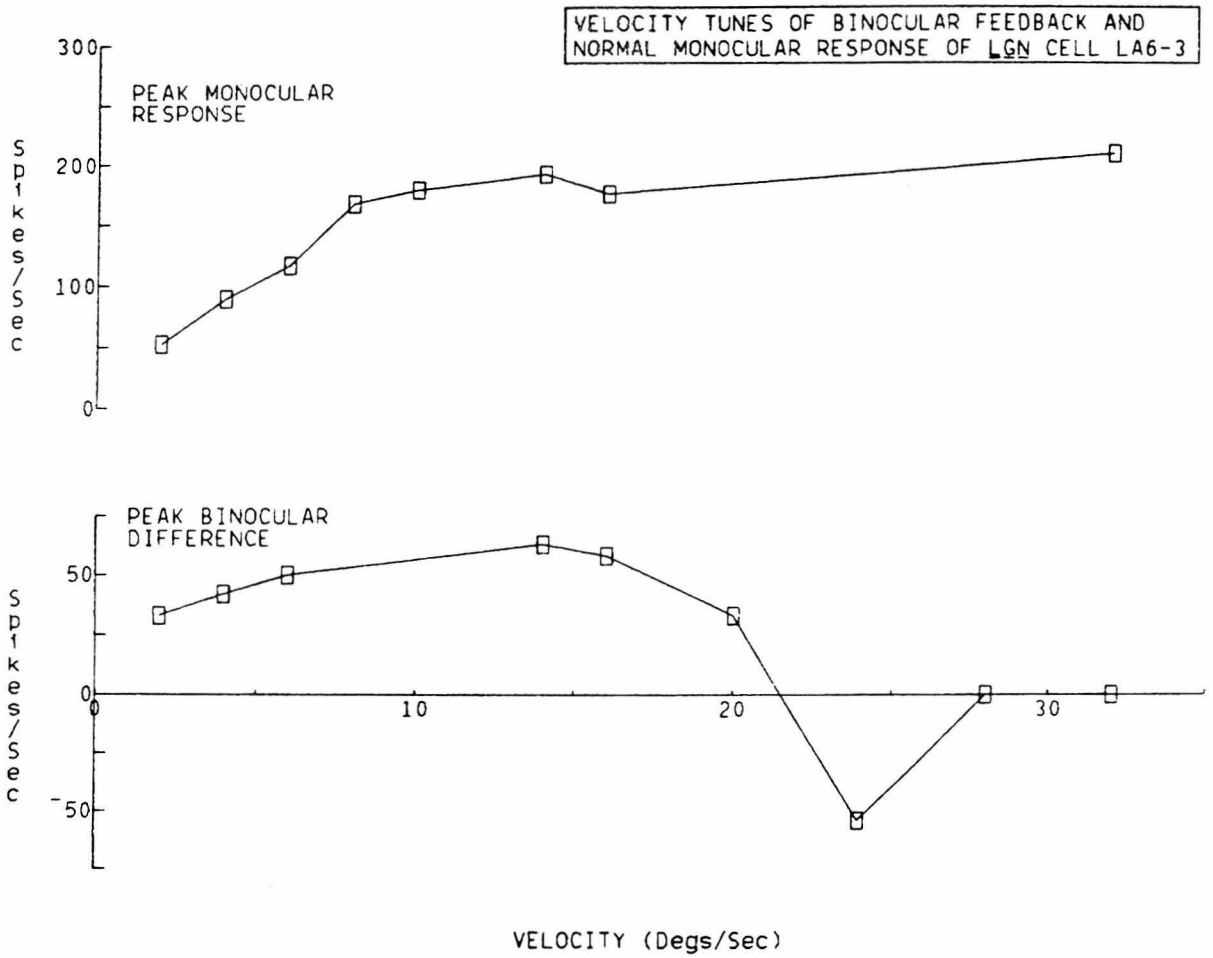

VELOCITY TUNES OF BINOCULAR FEEDBACK AND NORMAL MONOCULAR RESPONSE OF LGN CELL LA6-3
PEAK MONOCULAR RESPONSE
Spikes/Sec
300
200
100
0
PEAK BINOCULAR DIFFERENCE
Spikes/Sec
50
0
-50
0
10
20
30
VELOCITY (Degs/Sec)

Figure 25

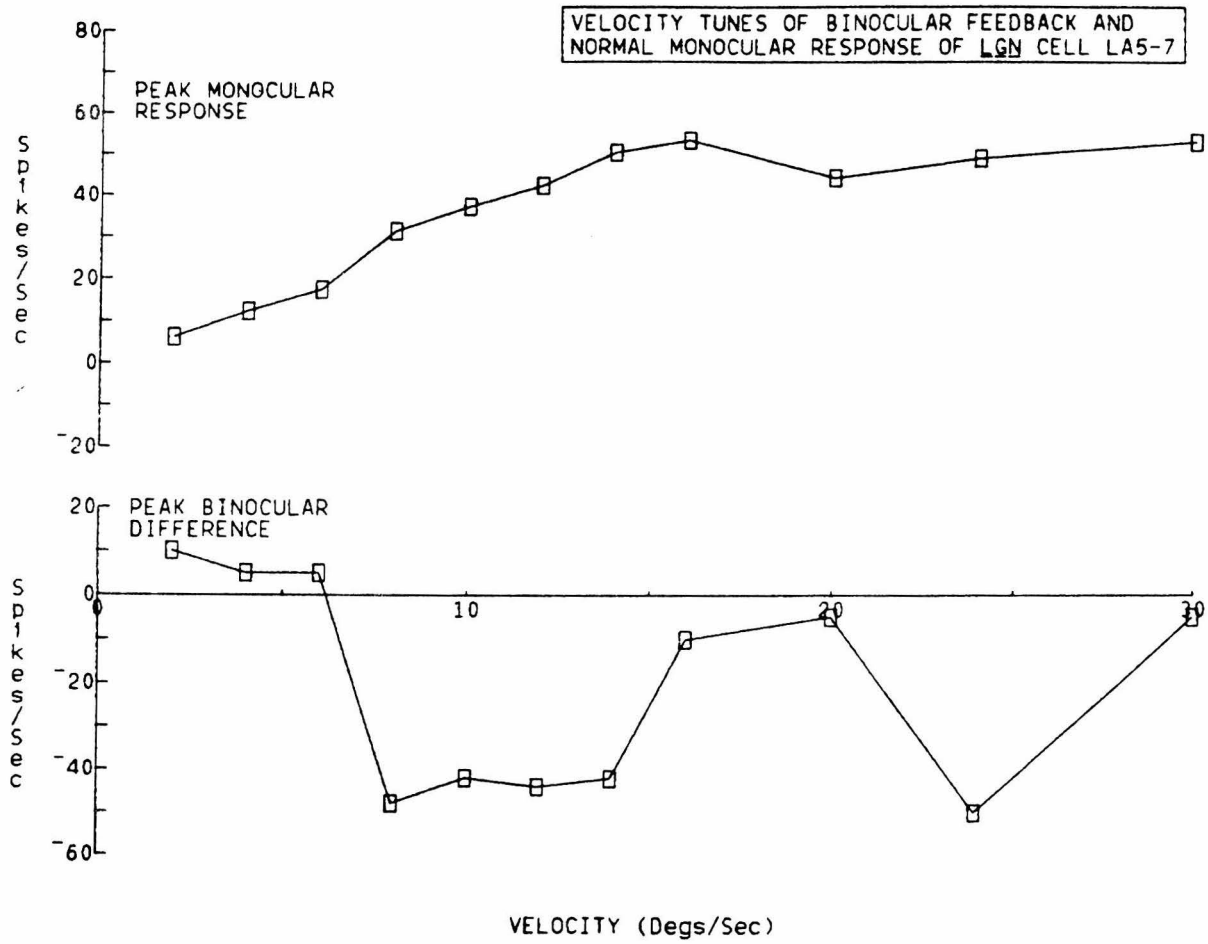

VELOCITY TUNES OF BINOCULAR FEEDBACK AND
NORMAL MONOCULAR RESPONSE OF LGN CELL LA5-7
PEAK MONOCULAR
RESPONSE
Spikes/Sec
80
60
40
20
0
-20
PEAK BINOCULAR
DIFFERENCE
Spikes/Sec
20
0
-20
-40
-60
10
20
30
VELOCITY (Degs/Sec)

Figure 26

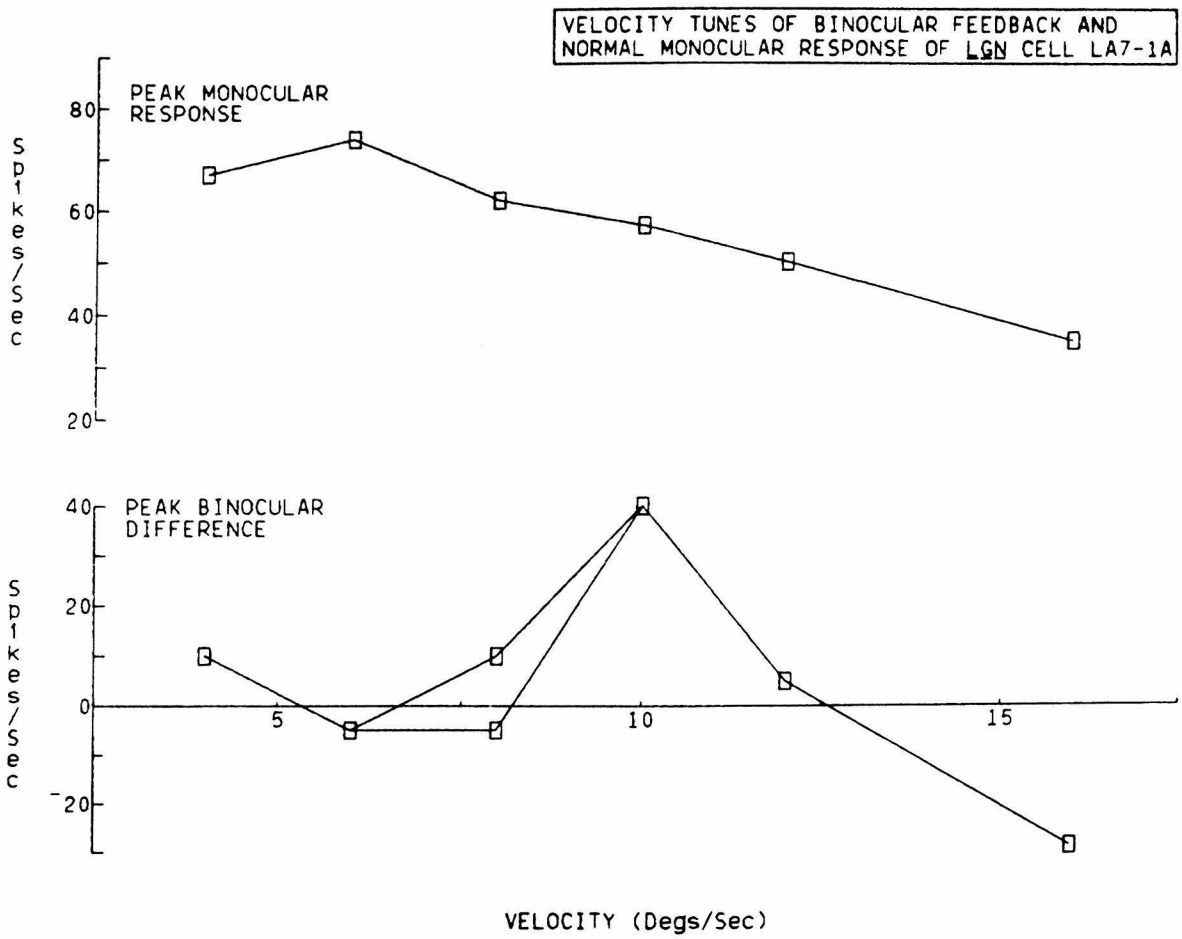

VELOCITY TUNES OF BINOCULAR FEEDBACK AND
NORMAL MONOCULAR RESPONSE OF LGN CELL LA7-1A
PEAK MONOCULAR
RESPONSE
Spikes/Sec
80
60
40
20
PEAK BINOCULAR
DIFFERENCE
Spikes/Sec
40
20
0
-20
5
10
15
VELOCITY (Degs/Sec)

Figure 27

Figure 28

This figure shows two ways of representing the velocities at which peaks and troughs were found (called here "critical" velocities). In both cases, a clear concentration of critical velocities is within the 6°/sec to 12°/sec range with a smaller secondary grouping around 24°/sec. Also, in both cases no significant difference is seen between peaks and troughs.

Figure 28-A: Simple histogram showing the number of peaks and troughs that were found for each velocity bin (which are 2°/sec wide).

Figure 28-B: Velocity tunes were done at often differing test points. A peak at 8°/sec might be isolated between points as close as 7 and 10°/sec or as far apart as 4°/sec and 16°/sec. Each peak and trough could be better identified by a confidence interval of velocities over which it falls (such as 7.5°/sec to 9°/sec versus 6°/sec to 12°/sec). This histogram shows the number of peak and trough confidence intervals that contain each velocity. The broadening of this histogram over the one above results from including the range of uncertainty for each point. Even with this correction, the concentration of critical velocities is clear.

VELOCITY TUNING OF BINOCULAR FEEDBACK: Distribution of "Critical" Velocities

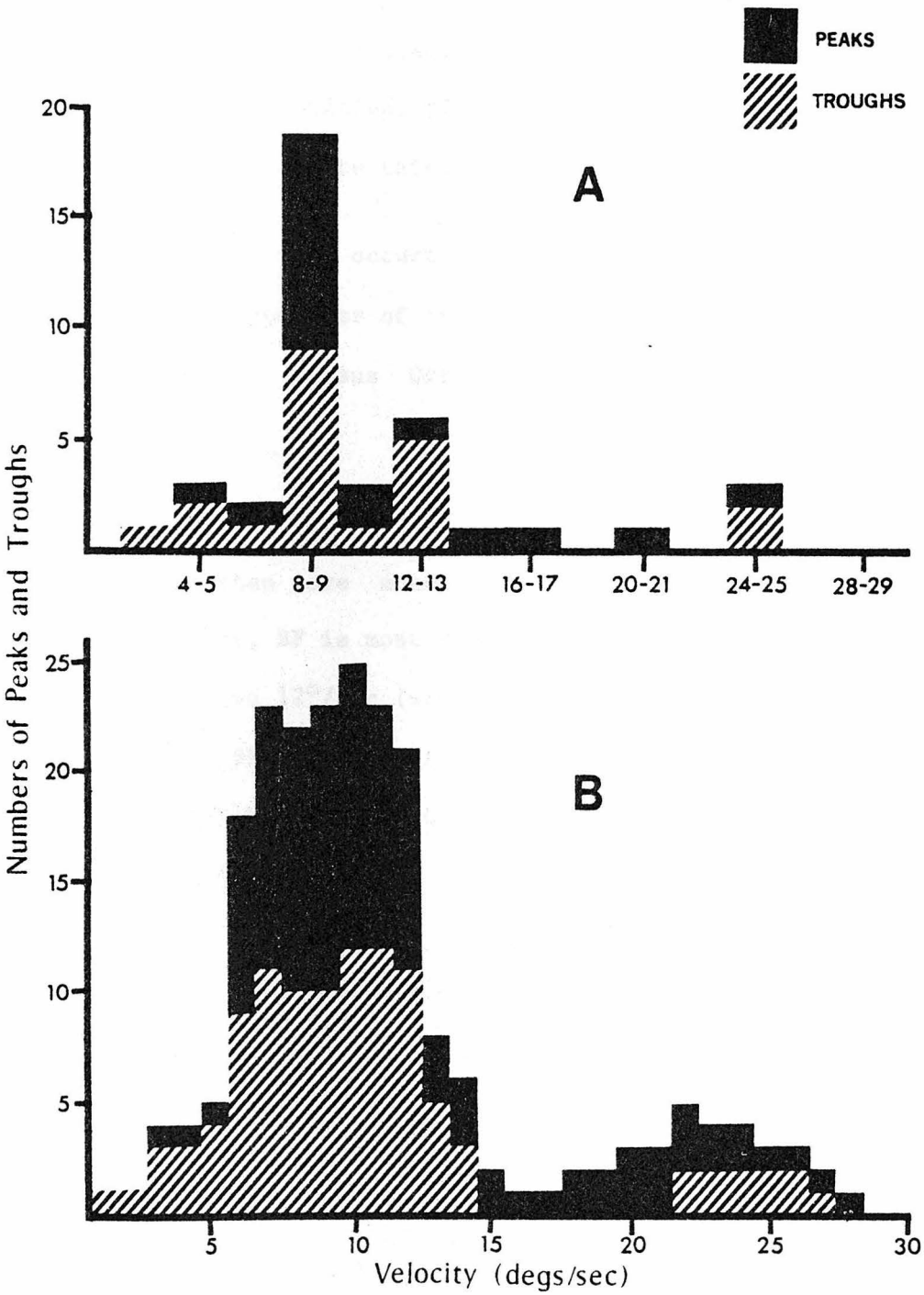


Figure 28

It was possible in one case to do a BF location map at three different velocities (Figure 30). In general, the overall organization of the map was similar at different velocities, but the intensity of the various regions of BF changed considerably. It also appears that the preferred displacement for a region of BF could be shifted at different velocities, although many more examples would be needed to clearly demonstrate this.

No correlation of the occurrence or amplitude of peaks and troughs, of tune type, or of tuning steepness could be found with IPSI versus CONTRA, On versus Off, or central versus peripheral cells.

In summary, BF was found to be considerably more sensitive to velocity changes than are monocular responses to the same stimuli (Figure 29). Further, BF is most sensitive to changes occurring in the range of 6^{o}/sec to 12^{o}/sec (with possibly a secondary grouping at 24^{o}/sec). Cases of BF that are similar to the common monocular profile of being poorly tuned to velocity are shown in general to consist mostly of inhibition.

Figure 29

This figure shows all of the velocity tunes taken. The upper figure contains all of the monocular tunes and the lower shows all of the BF tunes. The scaling is the same for both. A strong difference can be seen in that the monocular tunes are for the most part linear, giving a fairly smooth and even appearance. The lower figure consists of many tunes with slopes that change rapidly with velocity, particularly around the 6 to 12°/sec range, thus giving a more ragged appearance. A comparison of the two yields a striking demonstration suggesting a difference in the processing of velocity information between a monocularly stimulated LGN and a binocularly stimulated LGN.

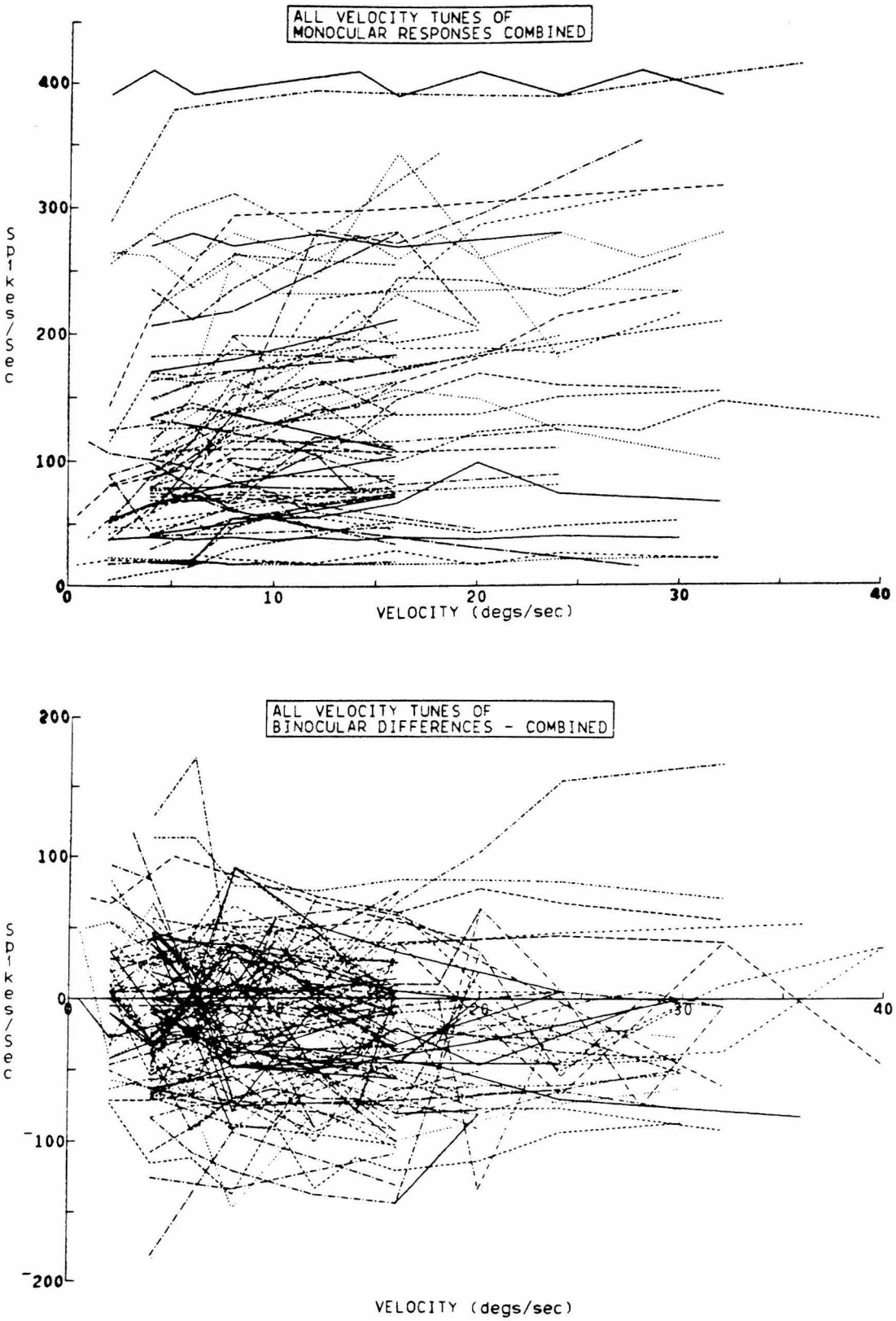

ALL VELOCITY TUNES OF
MONOCULAR RESPONSES COMBINED
Spikes/Sec
400
300
200
100
0
0
10
20
30
40
VELOCITY (degs/sec)
ALL VELOCITY TUNES OF
BINOCULAR DIFFERENCES - COMBINED
Spikes/Sec
200
100
0
-100
-200
0
10
20
30
40
VELOCITY (degs/sec)

Figure 29

Figure 30

This figure shows three BF location maps taken at different velocities for LGN cell LA9-3 (IPSI-Off, RF 13° from AC) taken with a slit moving across the RF towards the AC. At least two islands of facilitation are seen in each map, with both showing slight shifts in optimal position in visual space. The amplitudes of these shifts are not large and are possibly due to eye movements or other measurement errors. The shift in amplitude of the right island of facilitation to a maximum at 8°/sec cannot be accounted for by such errors. The inhibitory regions also show similar changes with velocity, with a maximal area of distribution at 4°/sec. The onset and offset BF are included and also change considerably with velocity. The depiction of onset and offset BF is as described in Figure 12.

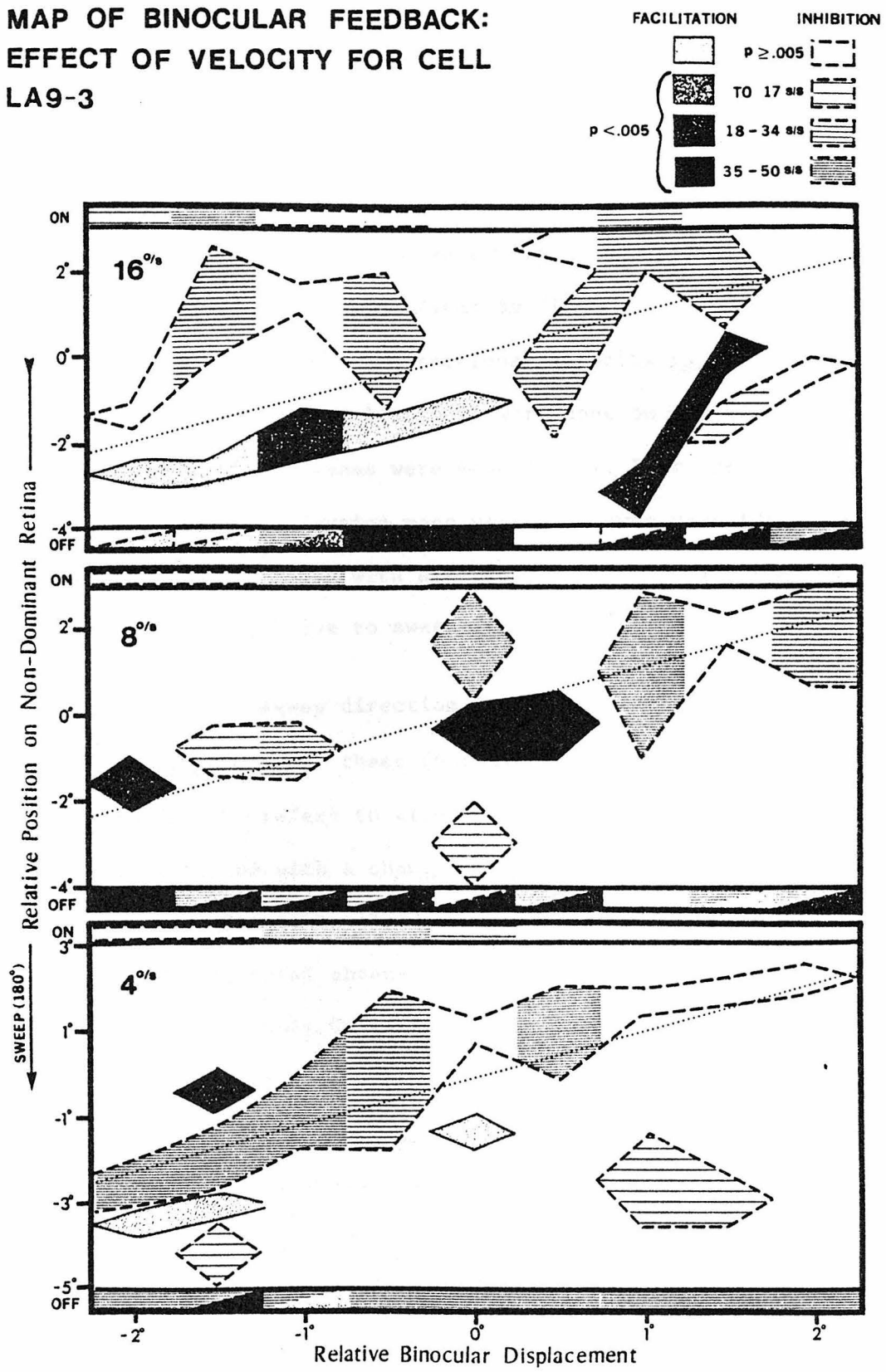

MAP OF BINOCULAR FEEDBACK:
EFFECT OF VELOCITY FOR CELL
LA9-3
FACILITATION
INHIBITION
p ≥.005
p <.005
TO 17 s/s
18 - 34 s/s
35 - 50 s/s
16°/s
8°/s
4°/s
ON
OFF
2°
0°
-2°
-4°
3°
1°
-1°
-3°
-5°
Relative Position on Non-Dominant Retina
SWEEP (180°)
-2°
-1°
0°
1°
2°
Relative Binocular Displacement

Figure 30

3.4 Directional Selectivity

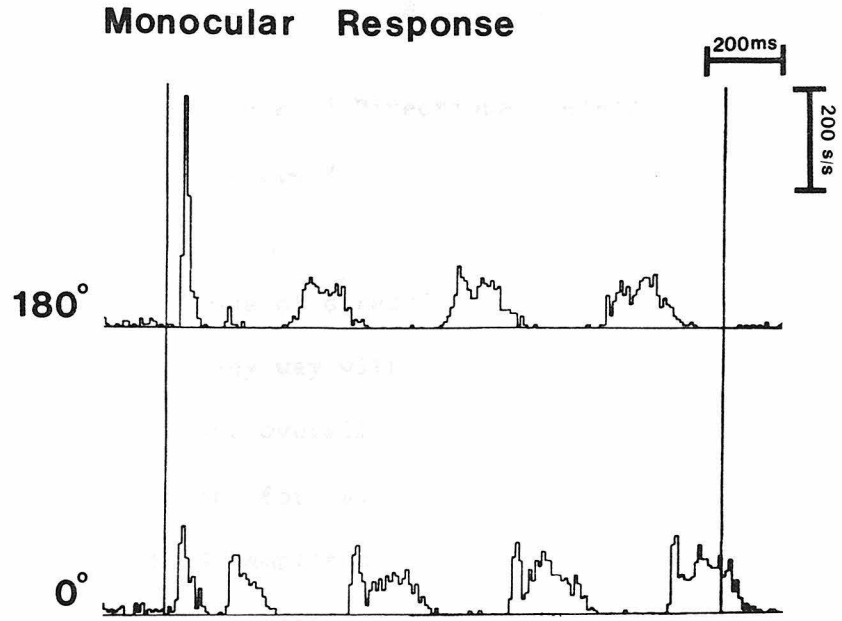
Nineteen cells were tested to see if BF varies with the direction of visual stimuli sweeping over the monocular RF. Vertical gratings, slits, and edges moving horizontally were used to compare BF found for sweeps moving toward the AC (notated as "180°") with sweeps moving away from the AC (0°). Often directional selectivity tests with varied parameters of the visual stimuli were done on the same cell. Twenty-seven such direction tunes were made in all. Four cells were studied to see how the BF location maps vary and seven were tested to see how velocity tuning varies with sweep direction. BF in the LGN was found to be very sensitive to sweep direction.

BF could vary with sweep direction in one of four ways. Table 2 shows the distribution of these four types. The most common type ("Change in Amplitude") refers to either an increase or decrease in the magnitude of the BF with a change in sweep direction, as seen in eight cells (42% of 19) and in eleven tunes (41% of 27). The second most common showed the total absence of BF at one direction and clear BF for the other ("BF - Only One Dir"). This was found in five cells (26% of 19) and in eight tunes (30% of 27). The third involved cells that had multiple regions of BF with at least one region present for one direction and not for the other ("Extra Region"). Three cells (16% of 19) and five tunes (19% of 27) showed this pattern. The fourth and most striking kind of directional selectivity was the reversal of the polarity of BF, such as from inhibition to facilitation (Figure 31). Three cells (16% of 19) and three tunes (11% of 27)

Figure 31

This figure shows the effect of sweep direction on the BF of LGN cell LA4-3 (CONTRA-On, RF 1.5° from AC). A 1.7° grating was swept at 8°/sec over the RF toward the AC (180°) and away from the AC (0°). The BDHs show binocular inhibition during the sweep for 180° switching to facilitation at 0°. The monocular sweep response does not change significantly with direction. Also note the presence of a strong monocular and BF onset. The onset is mostly inhibition, and does not switch polarity.

Binocular Feedback as a Function of Sweep Direction for Cell LA4-3



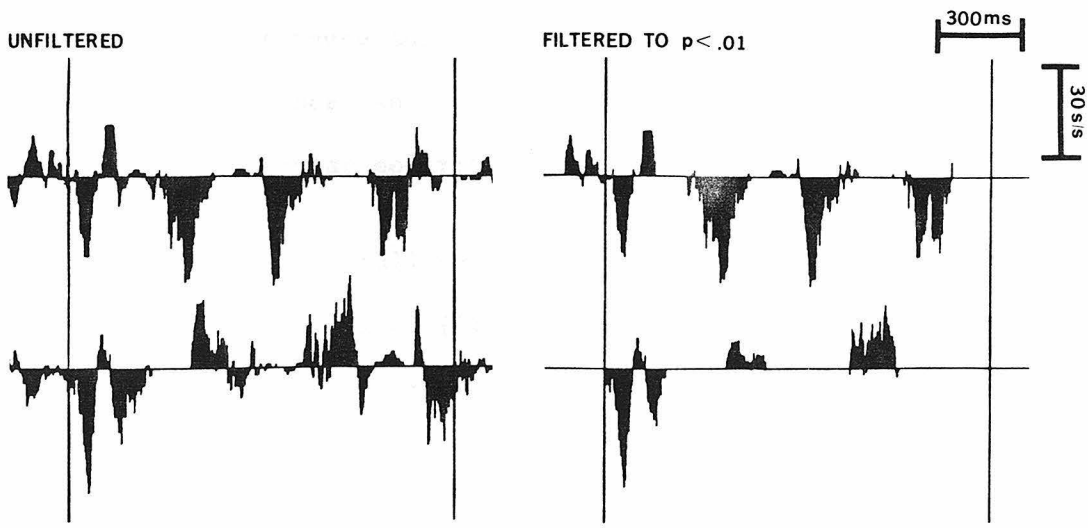


Figure 31

showed this type ("Polarity Reversal").

Change in Amplitude:					BF - Only	Extra	Polarity	
0-20%	21-40%	41-60%	61-80%	>80%	One Dir	Region	Reversal	
0	2	2	3	1	5	3	3	= 19 cells
1	4	2	3	1	8	5	3	= 27 tunes

Occurrence and Magnitude of Directional Selectivity

Table 2

The occurrence and magnitude of directional selectivity of BF could not be correlated in any way with IPSI versus CONTRA or On versus Off. It was also found that overall, neither inhibition nor facilitation was more prevalent for sweeps toward or away from the AC. Further, an increase in BF amplitude was not seen to be more common for a reversal in either direction.

For four cells, full BF location maps were made for both 0^{o} and 180^{o} sweeps (Figure 32). All four cells showed significant shifting in the organization of these maps. In general, when sweep direction was changed the occurrence and magnitude of regions and/or the predominance of a particular polarity of BF would also change.

Seven cells were given full velocity tunes for both directions and six showed clear differences (Figure 33). In each of these six cases, reversal of direction resulted in shifts of the types listed in Table 2, but not uniformly at all velocities. For two cells, another BF region appeared, but only at some velocities. Three cells showed large increases in BF amplitude at some velocities with

Figure 32

This figure shows complete BF location maps taken at two different sweep directions for LGN cell LA9-10 (IPSI-Off, RF 11° from AC) using a slit travelling over the RF at 8°/sec. The entire arrangement of BF is shifted by changing sweep direction. The most striking changes are the increased prevalence of facilitation and the loss of a region of inhibition with the shift from 180° to 0°. This type of selectivity is referred to as "Extra Region" in Table 2. The binocular displacement was controlled by a variable prism placed over the dominant eye. The dotted line shows the position of the peak monocular response (and thus the RF).

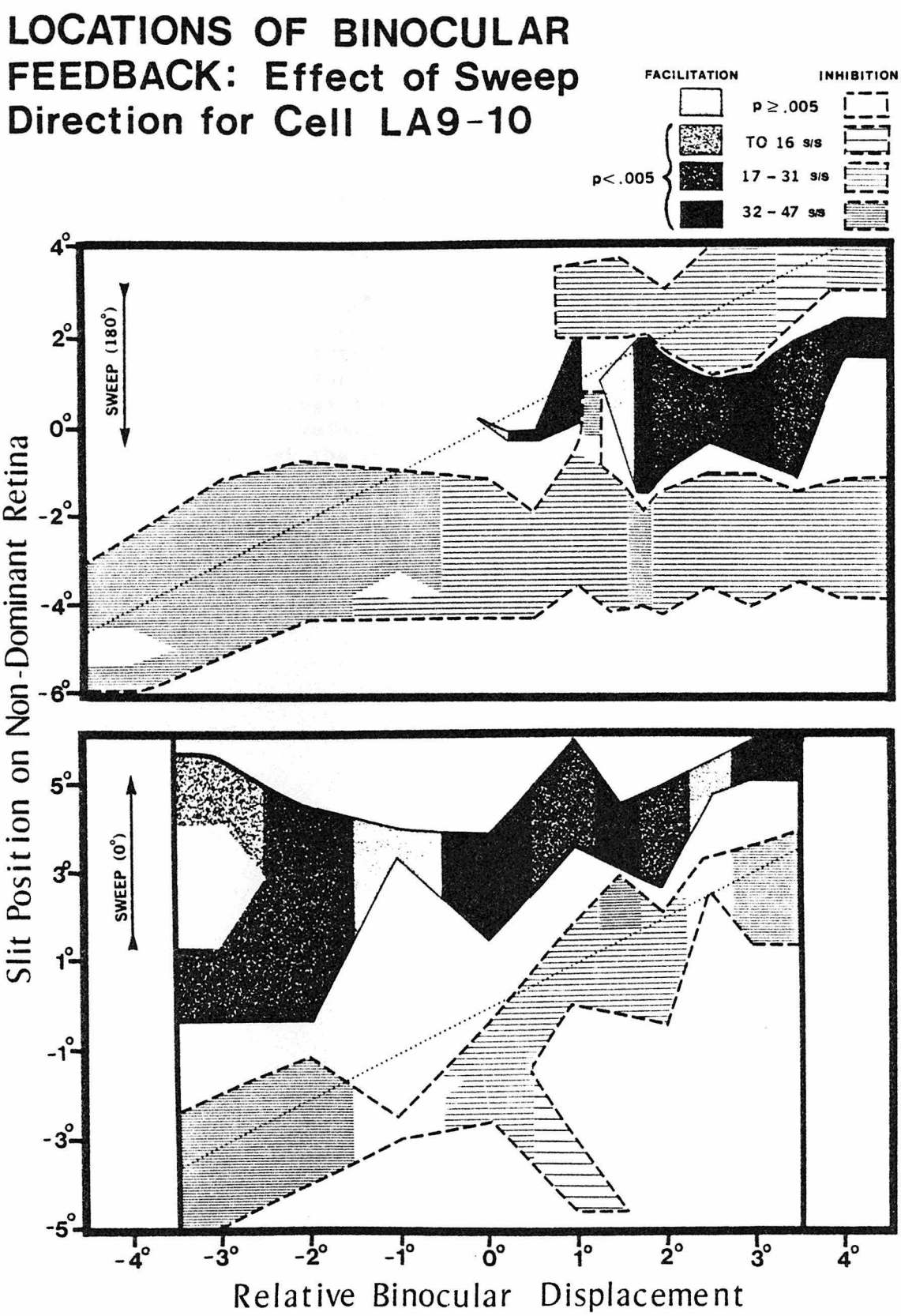

LOCATIONS OF BINOCULAR FEEDBACK: Effect of Sweep Direction for Cell LA9-10
FACILITATION
INHIBITION
p ≥ .005
p<.005
TO 16 s/s
17 - 31 s/s
32 - 47 s/s
SWEEP (180°)
SWEEP (0°)
Slit Position on Non-Dominant Retina
Relative Binocular Displacement
4°
2°
0°
-2°
-4°
-6°
5°
3°
1°
-1°
-3°
-5°
-4°
-3°
-2°
-1°
0°
1°
2°
3°
4°

Figure 32

Figure 33

This figure shows the monocular and BF velocity tunes for cell LA2-5 (IPSI-On, RF 5° from AC) to a slit moving over the RF for sweeps toward (180°) and away from (0°) the AC. The monocular tuning consists only of a slow decrease in response with velocity for both directions. The BF has a clear peak at 5°/sec for 180° and a clear trough at 5°/sec for 0° (as well as a region of low facilitation). In this case, the critical velocity was the same for both sweep directions even though the polarity and amplitude of the BF varied.

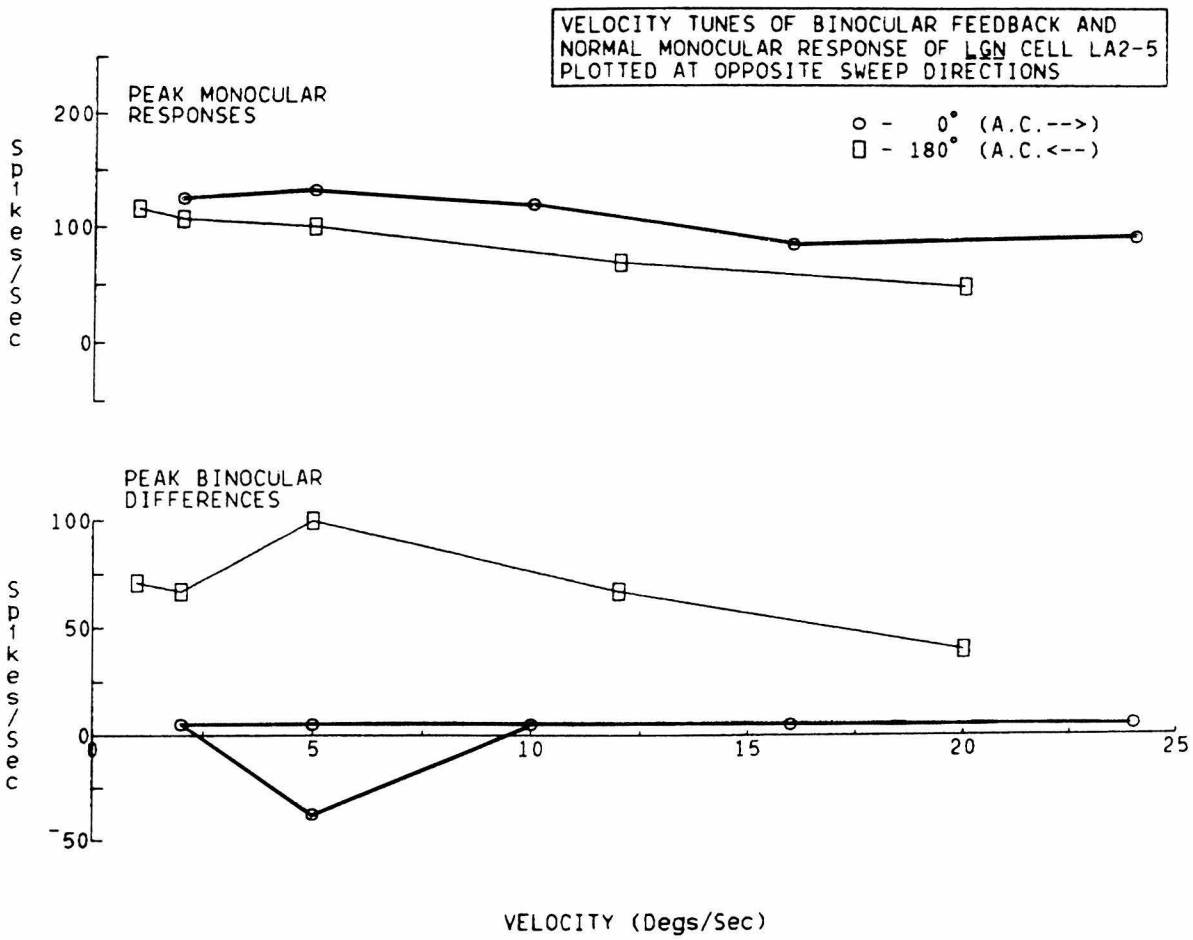

VELOCITY TUNES OF BINOCULAR FEEDBACK AND
NORMAL MONOCULAR RESPONSE OF LGN CELL LA2-5
PLOTTED AT OPPOSITE SWEEP DIRECTIONS
PEAK MONOCULAR
RESPONSES
o - 0° (A.C.-->)
□ - 180° (A.C.<--)
Spikes/Sec
200
100
0
PEAK BINOCULAR
DIFFERENCES
100
50
0
-50
0
5
10
15
20
25
VELOCITY (Degs/Sec)

Figure 33

direction change and one cell showed a switch in polarity only at one velocity (Figure 33).

Orientation tunes were attempted for eight cells. However, as described in Section 3.2, BF often occurs in multiple regions distributed over the retina around the area of the monocular RF. Oriented stimuli swept so as to totally cover the monocular RF at all sweep angles do not necessarily cover all regions of BF for that cell. Although the bi-directional sweeps described above stimulate exactly the same region of the retinas with a stimulus of the same angle (but a different polarity of direction), this is not true for an orientation tune. It would be possible to mask off all visual space except for a particular region of BF and then to do a complete orientation tune over that region. However, the computation and analysis required to discover from experimental runs the size and location of each region was impractical in the time a cell was normally held. One would expect simple orientation tunes without such corrections to produce multi-modal results with amplitudes and even existences of BF regions that vary non-uniformly with angle of sweep. This is what was found for these cells, and orientation tunes were abandoned for this study. However, BF did vary in every case with orientation, if non-uniformly. Figure 4 shows the BF of one cell at four different orientations.

In summary, all cells tested showed a degree of directional selectivity for BF, ranging from changes in amplitude to shifts in the polarity of the BF. Further, directional selectivity varied at

different velocities and at different locations on the retina and in binocular displacement space.

3.5 Other Observations Concerning Binocular Feedback

One striking feature of many BDHs was the existence of strong and significant BF at the onset and/or the offset of the sweep of the visual stimuli, as mentioned above. From forty-two cells, forty-one showed onset and/or offset BF under some conditions (for example, see BDHs in Figures 10, 17, 18, and 31). The source of these phenomena is unclear and for gratings could simply result from the flashing on of the stimuli over regions of BF. However, in the twenty-seven cells tested with slits, whose sweeps start and stop up to 8^{o} away from the RF, eighteen (67%) cells showed onset BF, twenty-two (81%) showed offset BF, and fifteen (56%) showed both. Many cells also showed a monocular onset and/or offset response (also in Figures 10, 17, 18, and 31). It was found possible for either to occur with or without the other. Four (15% of 27) showed onset BF with no onset monocular firing, and six (22%) showed offset BF with no similar monocular response. Four cells (15%) showed monocular onset with no BF, and two (7%) showed monocular offset with no BF. Fourteen (52%) had both onset responses and sixteen (59%) had both offset responses.

It is likely that these responses do not result only from scattered light. Often the onset and/or offset BF would occur only at particular binocular displacements (Figures 11, 12, 13, and 30) and at particular velocities. In some cases, they would have a velocity tuning different from each other and from that of the BF occurring during the sweep (Figure 30). As with RF located responses, the onset/offset monocular responses tended not to be well tuned to velo-

city. This type of BF is similar in amplitude to the above described sweep BF, with the average maximum (for each cell) onset facilitation at 66 s/s, onset inhibition at 63 s/s, offset facilitation at 57 s/s, and offset inhibition at 66 s/s (compare to Figure 6).

Unlike sweep BF, which shows approximately equal occurrence of inhibition and facilitation, onset binocular inhibition occurs in almost twice as many cells as onset facilitation (15 of 27 = 57% versus 9 of 27 = 33%). More than three times as many cells show predominantly onset inhibition than show predominantly onset facilitation (10 of 27 = 37% versus 3 of 27 = 11%). No such asymmetry was found for offset BF. Differences between IPSI and CONTRA or On and Off for this type of BF could not be substantiated.

Another type of observation about BF should be mentioned. With the set-up used, a crude, wide bin histogram showing monocular and binocular responses in tandem was produced in real time during an experiment. It was often the author's impression that initially strong differences between the monocular and binocular histograms would diminish as more trials were run. The possibility that BF fatigues was looked at more closely for two cells. A velocity tune was run for unit LA4-4 for 28 minutes, and the BDHs were compared for the first and last 14 minutes. This unit showed a region of facilitation at 4, 8, and 16°/sec and a region of inhibition at 4 and 8°/sec during the first 14 minute run. The second 14 minute run showed only the inhibitory region, and only at 4°/sec. A similar test was done on unit LA6-4, with a direction tune run continuously for almost a

half-hour. Initially, two regions of facilitation and one of inhibition was seen. By 11.3 minutes, the regions of facilitation had disappeared. The tune was continued and the facilitation did not reappear within the remaining 13 minutes. Further, the initial amplitude of inhibition seen was reduced on an average of 23% to the final values seen in the last 13 minutes. This is suggestive that BF can fatigue, that inhibition may be more resistant to fatigue, and that long runs testing for BF and averaging over the whole run may produce underestimates of its magnitude.

It should be noted that in about one half of the cells looked at, the response of the non-dominant eye alone to the visual stimuli was also taken together with the dominant and binocular responses. In general, the amplitude of modulation of spontaneous activity by stimulation of the non-dominant eye alone was from 0 s/s to 8 s/s and could not account for the BF found.

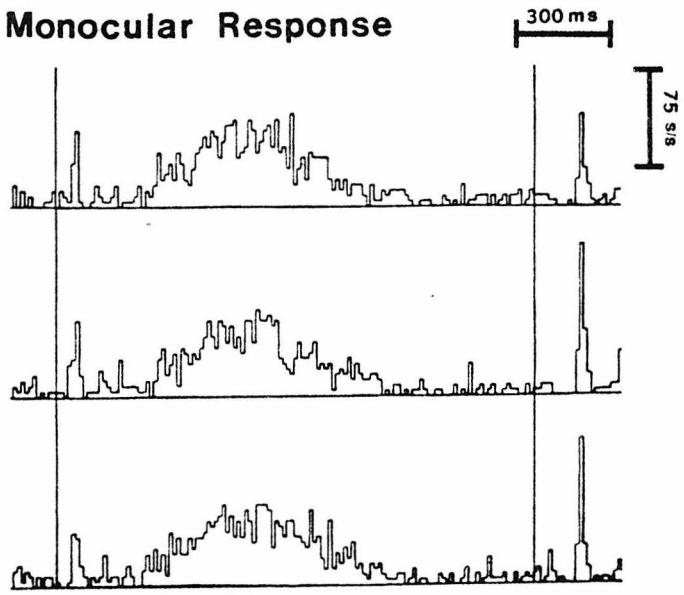
Finally, one cell produced a BDH with a very unusual pattern (Figure 34). Unfortunately, the data about the cell and the run were scrambled by the computer and lost. Further, the unusual effect was not statistically significant. It is included only for completeness.

In summary, BF occurring at the onset and offset of a slit sweep was common and similar in amplitude to sweep BF. Monocular onset/offset responses were also commonly seen, and either monocular or binocular responses could occur alone or in combination with the other. These effects could also be located in binocular displacement space and have particular velocity requirements. Some evidence exists

Figure 34

This figure shows the monocular responses and BDHs for a cell that was probably an On unit, tested with a slit. The cell and run data were scrambled by the computer and lost. The unusual effect seen in the unfiltered BDH was not statistically significant. The figure is included only for completeness.

Binocular Feedback Pattern for Cell LA6-?



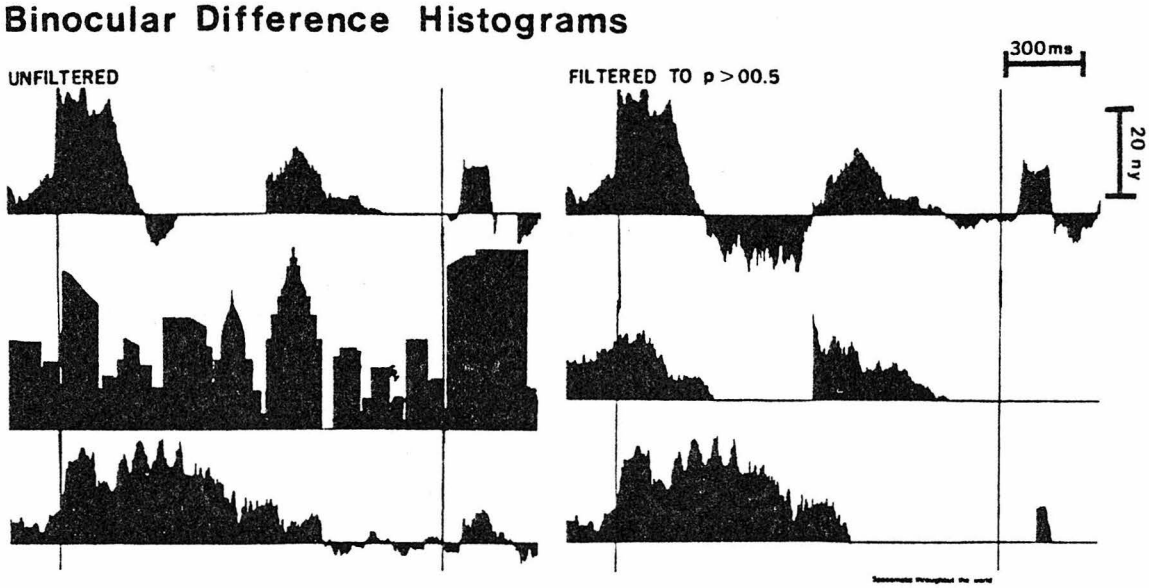


Figure 34

that for onsets, inhibition is more prevalent than facilitation. Further, some evidence was generated that suggests that BF can fatigue over the order of minutes, and that facilitation may be more sensitive than inhibition. Lastly, pure non-dominant visual stimulation was excluded as a significant source of the effects seen in BDHs.

5. DISCUSSION

The vast majority of LGN relay cells showed both binocular facilitation and inhibition when tested with oriented stimuli that were systematically altered along parameters that profoundly affect cortical unit firing. The amplitudes of these interactions were strong; in as many as half of the cells studied they exceeded 50% of the cell's normal firing rates. The typical LGN cell had multiple regions of binocular feedback (BF) with facilitation only slightly less strong and prevalent than inhibition. Regions tended to be very close to the cell's monocular RF on the retina, with a maximum distance of 6^{o} away. Regions ranged in size from 0.1^{o} to 6.0^{o}, with facilitation averaging 1.4^{o} and inhibition 2.0^{o}.

The BF found in this way was highly tuned to a number of parameters of visual stimuli. The majority of regions had specific requirements for retinal disparity. Facilitation was optimal at zero disparity twice as often as was inhibition, and both had more regions requiring convergent disparities than divergent. In most cases, the BF was well tuned to velocity, with peaks and troughs seen in equal numbers. Most peaks and troughs occurred in the interval between 6^{o}/sec and 12^{o}/sec. Monocular responses were not well tuned to velocity. Further, most BF was directionally selective. Changes in amplitude, disappearance of regions of BF, and even polarity reversals were seen with a 180^{o} change in sweep direction. BF varied with stimulus orientation, but in a non-uniform fashion. Technical considerations made conclusions about orientation tuning difficult (see

RESULTS).

Although BF was found to be sensitive to many variables of visual stimuli, no significant differences were seen in any way between CONTRA and IPSI cells and between On and Off cells. Some indication was found that facilitation is stronger in the retinal periphery than in the center. Evidence was presented that suggests that some of the BF can fatigue in the order of minutes. The phenomenon of sweep onset and offset BF was found and described.

5.1 Relationship to Previous Work

Various new techniques were used in this study. LGN binocular responses were taken in tandem with monocular responses to eliminate errors due to variability in neuron responsivity. Earlier studies relied primarily on a sequence of a monocular run, then binocular, then monocular, and so on to find BF, or simply on the response of the non-dominant eye alone (Singer, 1970; Sanderson et al., 1971; Fukuda and Stone, 1976; Rodieck and Dreher, 1979). Here, histograms were constructed of the full sweep of the difference between a binocular and monocular response of a cell, thus showing BF which doesn't necessarily fall during the peak firing of the cell. Statistical filtering was used to identify intervals of significant BF. Finally, studies were conducted with oriented stimuli controlled for parameters that influence cortical activity.

In general, the present study found BF more often (particularly facilitation) and at higher amplitudes. Sanderson et al. (1971) for example, shows inhibition from the non-dominant eye on the order of 5 s/s to 10 s/s, whereas this study found average inhibition and facilitation amplitudes of 50 s/s to 70 s/s. In light of the finding that BF is very tuned to various aspects of a visual stimulus and that this study involved systematic searches through these aspects, it is not suprising that more BF and larger amplitudes were found. Other problems could have prevented earlier workers from seeing as much BF as is present. Typically, in past studies the maximum firing rate of the binocular response was compared to that of the monocular response

so differences that did not fall at the time of peak firing could have been missed. In addition, evidence was presented here that some BF fatigues. Most of our runs were done with just enough trials to get good statistics. This may not have been true in the earlier works, and fatigue could have diluted measured amplitudes. Thus, there are several reasons why earlier studies did not see as much BF as is reported here.

Suzuki and Kato (1966) and Suzuki and Takahashi (1970) reported binocular inhibition occurring for IPSI cells three to four times as often as for CONTRA whereas the present work found no distinction between IPSI or CONTRA in any way related to BF. They used electric shocks to optic nerves to test for binocular interactions. Other workers found a much smaller asymmetry, if any, using visual stimuli (Sanderson et al., 1971; Singer, 1970; and Rodieck and Dreher, 1979) and, as stated above, earlier reported BF was of low amplitude. The current work used exclusively visual stimuli and found high amplitude BF. It is easily conceivable that optimal visual triggering of BF shows no asymmetries while suboptimal triggering or non-visual stimuli could emphasize a small IPSI over CONTRA bias.

The description of arrangements of fields of BF extends earlier works. Sanderson's inhibition fell primarily on the same retinal position as the monocular RF; it is shown here that this is also true for facilitation, and that both types of BF occasionally lie as far as 6^{o} away from the RF. Because both positions are simultaneously recorded in this study, it is difficult to ascribe this result to

errors in measuring eye position. Sanderson et al. found fields from 1.5° to 6° wide and Schmielau & Singer (1977) found facilitory regions 0.5° to 2° wide. The current report is similar. However, the size of inhibitory regions reported by Schmielau and Singer was 5° to 10°. Inhibitory regions found here with oriented stimuli averaged 2° wide and never exceeded 6° and multiple regions for each cell were commonly found. Their study was done with flashed spots. It is surprising that they were able to find cortico-geniculate feedback using stimuli that typically do not drive cortical cells. The current results were obtained with stimuli optimized for cortical neurons and it is not unlikely that they would reveal a different arrangement of BF. It is conceivable that their technique grouped multiple regions into one.

The present study, in general, extends the concept of BF to include multiple regions that are well tuned to visual parameters not usually thought to be important in the LGN.

5.2 Source of Binocular Feedback

The earlier study of Schmielau and Singer (1977) demonstrated that most of the binocular facilitation and some of the inhibition found in the LGN under their test conditions disappeared when the visual cortices were cooled. This work also suggests that BF is cortical in origin.

Tight tuning of cortical units to relative retinal disparity has been demonstrated in the cat (Barlow et al., 1967; Pettigrew et al., 1968b; Bishop et al., 1971), in the monkey (Hubel and Wiesel, 1970) and in sheep (Ramachandran et al., 1977). This work shows that the majority of BF regions also have tight tuning to retinal disparity, which suggests input from the visual cortex.

Neurons of the visual cortex have been shown to be tuned to the velocity of visual stimuli (Pettigrew, 1968a). Recent studies generally agree that simple cells are tuned to lower velocities, with reports of 2^{o}/sec to 4^{o}/sec as the average optimal, and that complex cells are tuned to higher velocities, 16^{o}/sec to 18^{o}/sec as the average optimal velocity (Movshon, 1975; Gilbert, 1977; Goodwin and Henry, 1978; Hess, 1979). The greatest number of cortical cells of both categories combined were tuned to velocities from 5^{o}/sec to 10^{o}/sec, which is very close to the range found here for BF, 6^{o}/sec to 12^{o}/sec. Studies of cortical layer VI cells indicate that the cortico-geniculate system includes both simple and complex units. (Gilbert, 1977; Harvey, 1978). It is likely that BF that comes from the cortico-geniculate system would reflect the tuning properties of

layer VI cells, which have been specifically confirmed to be well tuned to velocity (Leventhal and Hirsch, 1978). Both the present study and earlier studies confirm that for the most part LGN cells show poor or no velocity tuning when tested monocularly and it is thus unlikely that interlaminar input is responsible for the BF found (Dreher and Sanderson, 1973; Hess and Wolters, 1979; and in the monkey, Lee et al., 1979). The comparison of untuned monocular responses with well tuned BF (see RESULTS) is striking. Further, the report by Daniels et al. (1977) that small orientation biases in LGN cell response disappear at stimuli velocities above 20^{o}/sec is consistent with this interpretation.

Many cortical cells have also been shown to be very directionally selective (Pettigrew et al., 1968a) and Gilbert (1977) reports that layer VI cells are the most consistently directionally selective cells in area 17. The current finding that BF is also directionally selective lends further support for the notion that it is cortical in origin. The evidence that BF can fatigue is also consistent with cortically mediated multi-synaptic feedback. Finally, the maximum amplitudes of the BF found with cortical trigger features with the current techniques far exceed the amplitudes of interlaminar inhibition found earlier (that survives cortical cooling - Singer, 1970; Sanderson, et al., 1971). The simplest explanation currently available to account for the data is that the BF found originates in the visual cortex.

It is of course posssible that this BF doesn't originate in the cortex, but instead in some other area. The cortico-geniculate input is an anatomically dominating feature of LGN structure (see below) and it is the most plausible source. Future studies would best demonstrate that cortical cooling eliminates the kinds of BF described.

It should be noted that some BF was found that was most likely interlaminar in origin and not cortical. A small number of cells showed BF that was not tuned to velocity and in twelve out of thirteen cases it was inhibitory (see Figures 22, 23 and 24). Interlaminar inhibition is well substantiated and one would expect it not to be more velocity tuned than LGN monocular responses. Binocular displacement tunes also revealed a few cases of BF that could easily be interlaminar. As described in RESULTS, regions of inhibition or facilitation falling solely on the non-dominant retina would show up as a band on the BF location maps. Five such bands were seen and four of them were inhibitory. That the current techniques suggest interlaminar inhibition makes it unlikely that some kind of technical or systematic error is responsible for data suggesting a cortical origin for the other BF.

The data suggest a few ideas about the organization of feedback from the visual cortex to the LGN. First, it is possible that multiple cortical units functionally converge on each LGN cell. Most LGN units showed multiple regions of BF, each with different polarities and retinal disparity requirements. To date, no one has reported cortical cells that are tightly tuned to more than one disparity.

Also, some cells showed BF that changes polarity with a change in sweep direction. It seems less likely that one cortical unit could be both facilitory and inhibitory than that more than one unit could converge on each LGN cell. Second, there is no evidence that the BF found is related to the CONTRA-IPSI or On-Off classification, as if the incoming cortical fibers make no distinction between these types. From both of these ideas, an image emerges of cortical fibers converging on LGN cells with little specificity, other than topographic.

5.3 Functional Significance

The cortico-geniculate feedback system is very large, with more than half the cells in layer VI of area 17 projecting to the LGN and about half of the synapses in the LGN of the type that degenerate when the cortex is removed (Jones and Powell, 1969; Guillery, 1971; Gilbert and Kelly, 1975). Only 30% of LGN synapses are retinal in origin. It is likely this system plays a very important role in visual information processing; however, this role is still unclear. Schmielau and Singer (1977) have suggested that the system may be used to highlight a distinction between foreground and background. This idea is supported by the current evidence that facilitation is found much more often than inhibition at zero retinal disparity. This would have the effect of increasing the LGN's response to features on the plane of fixation while inhibiting responses to features not on that plane. Even though such corrections could be done in a higher center where individual neurons are more directly responsive to both eyes, there could be an advantage to feeding back binocularly derived information to a relay center that has not yet fully mixed the two retinal images. The idea that the LGN acts as a general preprocessing area upon which modifying feedback arrives from many higher centers has already been reviewed by Singer in 1977 and by Burke and Cole in 1978.

The finding that BF shows increased facilitation and increased inhibition at velocities 6^{o}/sec to 12^{o}/sec might be explained in the following way. Visual features moving at these velocities in partic-

ular would be more strongly facilitated when on the plane of fixation and more strongly inhibited when off of that plane than features moving at other velocities. Pritchard and Heron (1960) reported that a cat's eyes show "flicks" averaging 13^{o}/sec, and Ditchburn et al. (1959) showed that stabilized images on human retinas preventing similar flicks (4^{o}/sec to 8^{o}/sec) destroy image integrity. Although in the Pritchard and Heron preparation these flicks were rare, freely moving cats might show more frequent flicks. The BF mechanism could be designed to maximize highlighting of the plane of fixation during these eye movements.

In general, the eyes are constantly moving and the brain must deal with creating a single stable world image from two rapidly changing images. The BF mechanism is clearly concerned with feature velocity and direction and could be involved in other ways in this processing. It could be directly interested in the velocities of objects in addition to or instead of eye movements. It might be part of the difficult task of stimulus matching that is necessary for the cortex to measure the depth of a feature (Pettigrew, et al., 1968a). Finally, the velocity and direction specificity of BF might be unimportant to the functioning of the cortico-geniculate system and be simply an artifact of the specificity of the cortical units involved.

It is felt that the function of the cortico-geniculate system is still unclear. It is possible that the description of characteristics of the system given here is essentially complete, but it is not clear to the author why such a massive system would evolve for the limited,

though important roles suggested above. Perhaps further elucidation of the nature and functioning of the areas that receive input from the LGN will illuminate the importance of the mechanisms detailed here.

References

Barlow, H.B., Blakemore, C. & Pettigrew, J.D. (1967). The neural mechanism of binocular depth discrimination. J. Physiol. 193: 327-342.

Bishop, P.O. & Davis, P. (1953). Bilateral interaction in the lateral geniculate body. Science. 118: 241-243.

Bishop, P.O., Kozak, W., Levick, W.R. & Vankur, G.J. (1962). The determination of the projection of the visual field onto the lateral geniculate nucleus in the cat. J. Physiol. 163: 503-539.

Bishop, P.O., Henry, G.H. & Smith, C.J. (1971). Binocular interaction fields of single units in the cat striate cortex. J. Physiol. 216: 39-68.

Burke, W. & Cole, A.M. (1978). Extraretinal influences on the lateral geniculate nucleus. Rev. Phys. Bioch. Pharm. 80: 105-166.

Cleland, B.G., Dubin, M.W. & Levick, W.R. (1971). Simultaneous recording on input and output of lateral geniculate neurons. Nature 231: 191-192.

Coenen, A.L. & Vendrik, A.H. (1972). Determination of the transfer ratio of cat's geniculate neurons through quasi-intracellular recordings and the relation with level of alertness. Exp. Br. Res. 14: 227-242.

Daniels, J.D., Norman, J.L. & Pettigrew, J.D. (1977). Biases for oriented moving bars in lateral geniculate nucleus neurons of normal and stripe-reared cats. Exp. Br. Res. 29: 155-172.

Ditchburn, R.W., Fender, D.H. & Mayne, S. (1959). Vision with controlled movements of the retinal image. J. Physiol. 145: 98-107.

Dreher, B. & Sanderson, K.J. (1973). Receptive field analysis: rsponses to moving visual contours by single lateral geniculate neurons in the cat. J. Physiol. 234: 95-118.

Dubin, M.W. & Cleland, B.G. (1977). Organization of visual inputs to interneurons of lateral geniculate nucleus of the cat. J. Neurophys. 40: 410-427.

Duckworth, W.E. (1968). Statistical Techniques in Technological Research, pp. 39-43. London: Methuen & Co.

Fukuda, Y. & Stone, J. (1976). Evidence of differential inhibitory influences on X- and Y- type relay cells in the cat's lateral geniculate nucleus. Br. Res. 113: 188-196.

Gilbert, C.D. (1977). Laminar differences in receptive field properties of cells in cat primary visual cortex. J. Physiol. 268: 391-421.

Gilbert, C.D. & Kelly, J.P. (1975). The projections of cells in different layers of the cat's visual cortex. J. Comp. Neurol. 163: 81-106.

Goodwin, A.W. & Henry, G.H. (1978). The influence of stimulus velocity on the responses of single neurones in the striate cortex. J. Physiol. 277: 467-482.

Guillery, R.W. (1967). Pattern of fiber degeneration in dorsal lateral geniculate nucleus of the cat following lesions in the visual cortex. J. Comp. Neurol. 130: 197-222.

Guillery, R.W. (1971). Patterns of synaptic interconnections in the dorsal lateral geniculate nucleus of cat and monkey: a brief review. Vis. Res. Sup. 3: 211-227.

Harvey, A. R. (1978). Characteristics of corticothalamic neurons in area 17 of the cat. Neurosci. L. 7: 177-181.

Hendrickson, A.E., Wilson, J.R. & Ogren, M.P. (1978). The neuroanatomical organization of pathways between the dorsal lateral geniculate nucleus and the visual cortex of old world and new world primates. J. Comp. Neurol. 182: 123-136.

Hess, R. & Wolters, W. (1979). Responses of single cells in cat's lateral geniculate nucleus and area 17 to the velocity of moving visual stimuli. Exp. Br. Res. 34: 273-286.

Hollander, H. (1972). Autoradiographic evidence for a projection from the striate cortex to the dorsal part of the lateral geniculate nucleus in the cat. Br. Res. 41: 464-466.

Hubel, D.H. & Wiesel, T.N. (1961). Integrative action in the cat's lateral geniculate body. J. Physiol. 155: 385-398.

Hubel, D.H. & Wiesel, T.N. (1962). Receptive fields, binocular interaction, and functional architecture in the cat's visual cortex. J. Physiol. 160: 106-154.

Hubel, D.H. & Wiesel, T.N. (1970). Stereoscopic vision in Macaque monkey. Nature 225: 41-44.

Hull, T.F. (1968). Corticofugal influence in the macaque lateral geniculate nucleus. Vis. Res. 8: 1285-1298.

Jones, E.G. & Powell, T.S. (1969). An electron microscope study of the mode of termination of cortico-thalamic fibers within the sensory relay nuclei of the thalamus. Proc. Roy. Soc. B 172: 173-185.

Kaas, J.H., Guillery, R.W. & Allman, J.M. (1972). Some principles of organization in the dorsal LGN. Br., Behav., Evol. 6: 253-299.

Kalil, R.E. & Chase, R. (1970). Cortico-fugal influence on activity of lateral geniculate neurons in the cat. J. Neurophys. 33: 459-474.

Kawamura, S., Sprague, J.M. & Niimi, K. (1974). Corticofugal projections from the visual cortices to the thalamus, pretectum, and superior colliculus in the cat. J. Comp. Neurol. 158: 339-362.

Lee, B.B., Creutzfeldt, O.D. & Elephant, A. (1979). The reponses of magno- and parvo- cellular cells of the monkey's lateral geniculate body to moving stimuli. Exp. Br. Res. 35: 547-557.

Leventhal, A.G. & Hirsch, H.B. (1978). Receptive field properties of neurons in different lamina of visual cortex of the cat. J. Neurophys. 41: 948-962.

Levick, W.R. (1972). Another tungsten microelectrode. Med. biol. Engng. 10: 510-515.

Lund, J.S., Lund., R.D., Hendrickson, A.E., Bunt, A.H. & Fuchs, A.F. (1975). The origin of efferent pathways from the primary visual cortex, area 17, of the macaque monkey as shown by retrograde transport of horseradish peroxidase. J. Comp. Neurol. 164: 287-304.

Malcolm, L.J., Bruce, I.C. & Burke, W. (1970). Excitability of the lateral geniculate nucleus in the alert, non-alert and sleeping cat. Exp. Br. Res. 10: 283-297.

Movshon, J.A. (1975). The velocity tuning of single units in the cat striate cortex. J. Physiol. 249: 445-468.

Nikara, T., Bishop, P.O. & Pettigrew, J.D. (1968). Analysis of retinal correspondence by studying receptive fields of binocular single units in cat striate cortex. Exp. Br. Res. 6: 353-372.

Noda, H., Tamaki, Y. & Iwama, K. (1972). Binocular units in the lateral geniculate nucleus of chronic cats. Br. Res. 41: 81-99.

Pettigrew, J.D., Cooper, M.L. & Blasdel, G.G. (1979). Improved use of tapetal reflection for eye-position monitoring. Inv. Opthal. & Vis. Sci. 18: 490-495.

Pettigrew, J.D., Nikara, T. & Bishop, P.O. (1968a). Responses to moving slits by single units in cat striate cortex. Exp. Br. Res. 6: 373-390.

Pettigrew, J.D., Nikara, T. & Bishop, P.O. (1968b). Binocular interaction on single units in cat striate cortex: simultaneous stimulation by single moving slit with receptive fields in correspondence. Exp. Br. Res. 6: 391-410.

Pritchard, R.M. & Heron, W. (1960). Small eye movements of the cat. Canad. J. Psych. 14: 131-137.

Ramachandran, V.S., Clarke, P.H. & Whitteridge, D. (1977). Cells selective to binocular disparity in the cortex of newborn lambs. Nature 268: 333-335.

Rodieck, R.W., Pettigrew, J.D., Bishop, P.O. & Nikara, T. (1967). Residual eye movements in receptive field studies of paralysed cats. Vis. Res. 7: 107-110.

Rodieck, R.W. (1973). Inhibition in cat lateral geniculate nucleus: role of Y system. Proc. Aust. Phys. Pharm. Soc. 4: 167.

Rodieck, R.W. & Dreher, B. (1979). Visual suppression from non-dominant eye in the lateral geniculate nucleus: a comparison of cat and monkey. Exp. Br. Res. 35: 465-477.

Sanderson, K.J., Bishop, P.O. & Darian-Smith, I. (1971). The properties of the binocular receptive fields of lateral geniculate neurons. Exp. Br. Res. 13: 178-207.

Schmielau, F. & Singer, W. (1977). The role of the visual cortex for binocular interactions in the cat lateral geniculate nucleus. Br. Res. 120: 354-361.

Singer, W. (1970). Inhibitory binocular interaction in the lateral geniculate body of the cat. Br. Res. 18: 165-170.

Singer, W. & Bedworth, N. (1973). Inhibitory interaction between X and Y units in the cat lateral geniculate nucleus. Br. Res. 49: 291-307.

Singer, W., Tretter, F. & Cynader, M. (1975). Organization of receptive field properties with afferent and efferent connections. J. Neurophys. 38: 1080-1098.

Singer, W. (1977). Control of thalamic transmission by corticofugal and ascending reticular pathways in the visual system. Phys. Revs. 57: 386-420.

Stevens, J.K. & Gerstein, G.L. (1976). Interactions between cat lateral geniculate neurons. J. Neurophys. 39: 239-256.

Suzuki, H. & Kato, E. (1966). Binocular interaction at cat's lateral geniculate body. J. Neurophys. 29: 909-920.

Suzuki, H. & Takahashi, M. (1970). Organization of lateral geniculate neurons in binocular inhibition. Br. Res. 23: 261-264.

Tsumoto, T., Creutzfeldt, O.D. & Legendy, C.R. (1978). Functional organization of the corticofugal system from visual cortex to lateral geniculate nucleus in the cat. Exp. Br. Res. 32: 345-364.

Updyke, B.V. (1975). The patterns of projection of cortical areas 17, 18, and 19 onto the laminae of the dorsal lateral geniculate nucleus in the cat. J. Comp. Neurol. 163: 377-396.

Widen, L. & Marsan, C.A. (1960). Effects of corticopetal and corticofugal impulses upon single elements of the dorsolateral geniculate nucleus. Exp. Neurol. 2: 468-502.