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ABSTRACT

It is widely accepted that the neural mechanism for stereoscopic depth perception can be found in the disparity-sensitive response of single visual neurons. The present study was undertaken to characterize the disparity-sensitive neuron, to elucidate its mechanisms and to investigate the transfer of depth-specific visual information between the two sides of the brain. Binocular visual interactions were examined in single units from the 17/18 border of normal cats and compared to responses from the 17/18 border of cats with large unilateral lesions of the opposite visual cortex. Units were activated with stimuli of varying disparity, moved in the same (sideways motion) and in opposite directions (motion in depth) on the two retinae. In normal cats, neurons showing substantial binocular interactions could be distinguished from disparity-insensitive units by cell type, ocular dominance, directional properties and cortical location. These data indicated clear dimensions in the organization of stereoscopic depth systems in cat visual cortex. Data from both normal and lesioned animals indicated that the critical mechanism of the disparity-sensitive response of single visual cells was binocular inhibition. Unilateral lesions of the visual cortex effected a specific subpopulation of neurons, rendering them unselective for stimulus disparity, and the location of these units, nicely mimicked the known distribution of callosal fibers in cat visual cortex. These data emphasize the role of intrinsic inhibitory circuits in the function of input from the two eyes and suggest that the corpus callosum plays a distinct role in the transmission of stereoscopic depth information between the two sides of the brain.

ABBREVIATIONS

VCL	- Visual cortex lesioned cats
Normal	- Normal cats
BI	- Binocular inhibition
BF	- Binocular facilitation
OD	- Ocular dominance
IN	- In-phase dynamic range
AN	- Antiphase dynamic range
COM	- Combined dynamic range
MIN	- Medial interlaminar nucleus of the thalamus
LGNd	- Dorsal lateral geniculate nucleus of the thalamus
LSVA	- Lateral suprasylvian visual area
AP	- Anterior-posterior
deg/sec	- degrees per second
mm	- millimeter
mg	- milligram
kg	- kilogram
CO_2	- carbon dioxide
O_2	- oxygen

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INTRODUCTION

The horizontal offset of the two eyes in the head provides the geometric basis for binocular disparity and stereopsis. Since each eye views the same visual scene from a slightly differing vantage point, objects separated in depth fall on retinal coordinates which are not in perfect correspondence. This deviation from correspondence, called retinal disparity, was shown by Wheatstone (1838) to be a sufficient cue in the transformation of 2 dimensional retinal input into 3 dimensional visual scenes. Wheatstone's stereoscope, a simple device for producing controlled horizontal retinal disparities, is still in use today, and graphically illustrates the fact that horizontal disparity between the inputs from the two eyes is sufficient <u>in and of itself</u> to produce a vivid sensation of depth.

Presumably, the neural mechanism which appreciates these retinal disparities must be one which involves the convergence and combination of inputs from the two eyes. Since the visual cortex is the first point in the visual pathway where there is significant convergence of input from the two eyes onto single neural elements (Hubel and Wiesel, 1962), it was here that Barlow, Blakemore and Pettigrew (1967) sought the substrate for the neuronal mechanism of stereopsis. Recording from single neurons in cat visual cortex, they found neurons which responded differentially to binocular stimuli as a function of retinal disparity. Cells were encountered which had receptive fields on noncorresponding retinal coordinates, implying that at a fixed point of convergence, different cells would be optimally activated by stimuli of different depths. Other workers (Nikara, Bishop and

Pettigrew, 1968; Joshua and Bishop, 1970; Hubel and Wiesel, 1970; von der Heydt, Adorjani, Hanny and Baumgartner, 1978; Ferester, 1981), while differing with some of the conclusions of Barlow et al., provided confirmation of the essential idea--that visual cortical cells are sensitive to the retinal disparity of binocular stimuli-- a finding which has recently been extended to a variety of frontal-eyed species (Pettigrew and Konishi, 1976; Clark, Donaldson and Whitteridge, 1976; Poggio and Fischer, 1977; Fischer and Kruger, 1979).

The problem of midline stereopsis

Although disparity - sensitive neurons were only quite recently identified, the notion that stereoscopic processing involved the convergence of input from the two eyes onto a particular cortical locus was not a new one. As early as 1900, this idea was expressed by Heine (in Blakemore, 1970) in consideration of what may be called the problem of midline stereopsis. In light of the classic view of a strict nasotemporal division, Heine wondered how input from the two eyes subserving the region of visual space directly around the fixation point could converge onto a single cortical locus. Since it was believed that a partial decussation of fibers at the optic chiasm segregated the output of the nasal and temporal portions of the retina, it seemed that objects lying right in front of, or behind the fixation point, would be imaged respectively on the two temporal or nasal retinae, and that the input from each eye would be transmitted to opposite visual cortices. Thus, there would be no opportunity for information from the two eyes to converge upon a single cortical

locus. This arrangement must have seemed somewhat paradoxical, particularly in light of the knowledge (Helmholtz, 1867) that stereopsis was most acute in regions immediately surrounding the fixation point. Until relatively recently, it was not clear in this situation how or where the neural integration of information from the two eyes occurred.

In the last decade however, anatomical and physiological investigations have identified two independent routes for the transfer of information from the midline of the visual field: (1) retinal fibers from a zone of nasotemporal overlap which project to both optic tracts and (2) the corpus callosum.

The inexactitude of the nastemporal division

One of the first to challenge the widely accepted view of a strict nasotemporal division appears to have been Linksz (1952). He did so in an effort to account for the clinical phenomenon of "macular sparing". Macular or "foveal sparing" refers to a perceptual phenomenon observed in patients who have undergone removal of one occipital lobe. Not surprisingly, the lesion produces a homonymous hemianopsia--a loss of vision in the contralateral half of the visual field. In cases of macular sparing however, the separation between the blind and the normal half of the visual field occurs about 1° from the midline, toward the blind half of the visual field. Since the removal of one visual hemisphere functionally eliminates the callosal pathway, any vision beyond the midline must be attributable to other mechanisms. Linksz thought that the most likely explanation was an inexactitude of the nasotemporal division. He felt that hemidecussation at the optic chiasm was a statistical rather than an

absolute process and suspected that there must be a projection of at least some temporal retinal cells toward the opposite side of the brain. The size of the area of spared macular vision and the phenomenon itself would suggest that these fibers represent at least 1^{o} of binocular overlap and that they alone are sufficient to subserve midline vision.

Linkz's suspicion, that hemidecussation was inexact, has since been born out by a a number of anatomical studies in both cat (Stone, 1966; Stone and Fukuda, 1974; Kirk, Levick, Cleland and Wassle, 1976; Kirk, Levick and Cleland, 1976) and monkey (Stone, Leicester and Sherman, 1973; Bunt, Minckler and Johanson, 1977). In primates a 1^{o} strip of retina has been found which straddles the vertical meridian and projects to both optic tracts. A similar amount of overlap, about 1.2^{o}, has also been seen in the cat retina, among brisk-sustained units (Kirk, Levick, Cleland and Wassle, 1976) and X-cells (Stone and Fukuda, 1974). Larger amounts of overlap have been observed in brisk-transient units (Kirk, Levick, Cleland and Wassle, 1976) Y-cells (Stone and Fukuda, 1974) and in cells with slowly conducting axons (Stone and Fukuda 1974; Kirk, Levick and Cleland; 1976). Fibers from this zone of nasotemporal overlap have been found to project to the medial edge of the cat dorsal lateral geniculate nucleus (LGNd) whence the thalamic fibers project to the border between areas 17 and 18. (Sanderson and Sherman, 1971; Kinston, Vadas and Bishop, 1969). Fibers terminate in all main laminae of both LGN's and in the adjoining region of the medial interlaminar nucleus (MIN). In general, larger amounts of overlap have been found in the thalamus and visual cortex (Hubel and Wiesel, 1967; Nikara, Bishop and Pettigrew,

1968; Blakemore, 1969; Joshua and Bishop, 1970) than in the retina.

An electrophysiological demonstration that the input from these overlapping retinal fibers could influence neuronal responses at the level of the visual cortex was provided by Leicester in 1968. Mapping the location of receptive fields along the cat 17/18 border, he found a centrally located strip of bilaterally represented receptive fields which extended .5 to 1^{o} into the ipsilateral hemifield. Sectioning the corpus callosum had no effect on the amount of overlap which was observed. Since any possible influence from the callosum was eliminated with the lesion, the ipsilateral representation of visual fields was attributed to a retino-thalamo-cortical projection. Recently, neurons in the lateral suprasylvian visual area (LSVA) have also been shown to receive ipsilateral activation via a similar projection. In a study by Marzi, Antonini and Legg, (1980) contralateral eye receptive fields in the LSVA extended up to 10^{o} into the ipsilateral half-field after lesions of the corpus callosum. That a greater degree of spared ipsilateral overlap was seen in the LSVA than in the visual cortex corresponds well with the observation that a larger amount of ipsilateral representation can be found in the MIN, the thalamic nucleus which projects to the LSVA, than in the LGNd, the nucleus projecting to the visual cortex (Kingston, Vadas, Bishop, 1969; Sanderson, 1971; Kratz, Webb and Sherman, 1978).

The contribution of the corpus callosum

In addition to a thalamo-cortical projection, a second route for the transmission of input from the central visual fields is, of course, the corpus callosum. Numerous investigations have demonstrated that this commissural pathway is in fact a viable and functionally

efficacious route for the transfer of visual information between the two cerebral hemispheres. One of the first such demonstrations was a study by Choudhury, Whitteridge and Wilson (1965), who, after establishing that fibers ran from the margin of area 17 to their corresponding points in the opposite cortex, isolated the visual input to a single hemisphere by severing one optic tract. They found that in the deafferented visual cortex, responses could be obtained only from cells which had receptive fields located along the vertical meridian. This study was one of the first to show that the influence of this pathway was restricted to the central visual fields and also, that cortical neurons could be activated by input received exclusively via the corpus callosum. A similar experimental approach, was applied in a study by Berlucchi and Rizzolatti (1968) who, in spliting the optic chiasms of cats, restricted the input to each hemisphere to the ipsilateral retinal projection. Recording from units along the 17/18 border, they found neurons which had clearly-defined visual receptive fields in both eyes. Presumably, responses through the ipsilateral eye were mediated by thalamo-cortical connections while responses through the contralateral eye were due to cortico-cortico, callosal connections. Recently, a study by Cynader et al. (1979) has shown that the corpus callosum not only contributes an excitatory input to cells along the opposite 17/18 border, but also, that it specifically mediates disparity-sensitive responses. In these experiments, binocular interactions were measured in cats which had undergone a surgical section of the optic chiasm, and thus again, the only possible route for convergence of input from the two eyes was via the corpus callosum. Binocular interactions in these animals were

reduced relative to normal cats, but there was clear evidence for extensive binocular convergence and of disparity sensitive interactions.

The possible role of the corpus callosum in the transmission of disparity specific information and the relevance of this pathway to the problem of midline stereopsis was an issue considered by Blakemore (1970) in a study of a human patient who had a saggital section of the optic chiasm. In testing this patient's stereoscopic function, Blakemore predicted that since only the temporal retinal pathways remained intact, the subject should be able to discern the depth of stimuli lying immediately in front of the fixation point (crossed disparities) while at the same time being completely blind to objects immediately beyond the fixation point (uncrossed disparities). When measured with stimulus disparities of $.5^{o}$ to 6^{o}, this prediction was confirmed. The data indicated that the callosal pathway integrated information up to 3^{o} within the temporal retina of each eye. Since there was no evidence of stereopsis for uncrossed disparities, and since there was no sign of macular sparing, Blakemore concluded that it was the corpus callosum exclusively which was mediating this residual stereoscopic function.

In the patient described above, section of the optic chiasm did not disrupt convergent, fusional eye movements to a crossed disparate stimulus, and it thus appeared that the corpus callosum was also involved in the mediation of vergence eye movements. Further support for this association came from Westheimer and Mitchell (1969) and Mitchell and Blakemore (1970) who, when testing a subject who had had a surgical division of the callosum, found both a lack of depth perception and a lack of vergence eye movements to centrally located

targets. The subject's stereopsis and vergence eye movements were normal when tested with a target located 5° into the peripheral visual field, but were absent in midline vision for both convergent and divergent disparities of 2°. These data suggested that the corpus callosum enjoys a dual function, being involved not only in the mediation of midline stereopsis, but also, in the generation of vergence eye movements elicited by binocularly disparate stimuli.

Fine and coarse stereopsis

The studies of Blakemore (1970) and Mitchell and Blakemore (1970) suggested that midline stereopsis was principally mediated by the corpus callosum rather than by retinal fibers of the nasotemporal overlap. This is a conclusion however, which has been vigorously criticized by Bishop and Henry (1971) and Bishop (1981). These authors have pointed to the distinction between what appears to be two different stereoscopic subsystems (Ogle, 1950), one for "fine" and the other for "coarse" stereopsis, and they claim that the above studies tested only for coarse stereopsis . They feel that coarse stereopsis may in fact be mediated by the corpus callosum, but that fine stereopsis relies on the direct retinal projection. Since the disparities used for testing in in the above studies were too large to measure fine stereopsis, their conclusion was that Blakemore's claims were too sweeping and that his results indicated only the preservation of a relatively coarse stereoscopic system.

According to the formulation of Bishop and Henry (1971) and Bishop (1981), stereopsis is a dual system composed of separate mechanisms for fine and coarse stereoacuity and fusion which can operate, at least in part, independently of one another. Fine

st reopsis and single vision operates only within a very narrow range of stimulus disparities--probably less than .5°, provides for high-resolution stereoacuity and is always accompanied by coarse fusion. It requires very close similarity between the visual images in the two eyes or else retinal rivalry and suppression of one monocular input occurs. Coarse stereopsis, on the other hand, can operate when there is considerable difference between the two retinal images in form, luminance and the temporal onset of stimuli in the two eyes, and can tolerate up to 7-10° of retinal image disparity. Coarse single vision requires some degree of similarity between the two retinal images, but again, can operate with retinal image disparities of up to 2° and can occur in the absence of fine fusion. Measured clinically, the sensation of depth elicited with large stimulus disparities, presumably activating only the coarse stereoscopic system, is qualitatively different from that obtained with the measurement of fine stereoacuity and single vision.

Studies of disjunctive eye movements have lent support to the notion of dual stereoscopic subsystems and have suggested that the operation of these two systems is complemented by a dual control system for vergence eye movements-one system which initiates such movements and the other which "carries them through to completion" and underlies fusional control (Westheimer and Mitchell, 1969; Mitchell, 1970). As Westheimer and Mitchell (1969) have demonstrated, stimuli which are presented on non-corresponding retinal coordinates elicit disjunctive eye movements, convergent or divergent, which are always appropriate to the sign of the stimulating disparity. For the initiation of vergence movements, retinal disparities can be very

large, up to 5-10°, and the visual images in the two eyes can be significantly different. They can be remarkedly dissimilar in shape, luminance, contrast or in their temporal onset in the two eyes, and still elicit the appropriate vergence eye movement. Nevertheless, although being sufficient for the initiation of a disjunctive eye movement, stimuli differing greatly in image similarity, do not permit its completion. Dissimilar stimuli, adequate for the initiation of eye movements, permit the subjective localization of objects in depth although they do not allow for the images to be subjectively fused. The mechanisms which underlie the initiation of vergence eye movements evoked with large stimulus disparities thus appear more closely associated with the system for coarse than for fine stereopsis.

Although maintaining the distinction between mechanisms for fine and coarse stereopsis, the data of Richards (1970) and Jones (1977) suggested a further subdivision of the coarse stereoscopic system into mechanisms for "near" and for "far" vision. In a psychophysical study, Richards tested the abilities of individuals to distinguish between targets presented at zero disparity ("the same depth as") and from .5° of crossed ("nearer than") and uncrossed ("further than") disparities. He found that a strikingly large proportion , about 30%, of randomly chosen, and apparently normal human subjects, were deficient in at least one of the 3 tasks. All combinations of stereoanomaly were detected and it was found that a person could, for example, have normal abilities for distinguishing crossed or uncrossed disparities, while at the same time be very poor at detecting opposite disparities. With a similar experimental design, these findings were later replicated by Jones (1977) who concurred with Richards on the frequency of stereoanomaly found in the population. However, in a

significant extension to the previous experiment, Jones additionally measured stereopsis in his subjects for retinal disparities of less than .5°--demonstrating that all of his subjects had normal stereoacuity when tested with standard clinical procedures. These data indicated that the systems for fine and coarse stereopsis were dissociable from one another and suggest that the stereoanomalies first described by Richards affected the coarse stereoscopic system only. Jones also examined the vergence movements of his subjects and found an incidence of oculomotor anomaly (20%) only slightly less frequent than perceptual stereoanomalies. Although the converse was not always true, a perceptual stereoanomaly was always found to be accompanied by a vergence anomaly. Not infrequently, vergence anomalies were present in a single dimension only, so that a subject could have normal divergence and anomalous convergence or vice versa. These data thus suggested that the 2 types of eye movements, divergence and convergence, were guided by independent control systems and that deficits could selectively effect only one of these components.

Disparity-sensitive neurons

In recent years neurophysiological investigations (Poggio and Fischer, 1977; Poggio and Talbot, 1981; Fischer and Kruger, 1979; Ferrester, 1981) have focussed on the identifiction of a neural correlate for the psychophysical effects described above. If indeed these observations can be attributed to the response characteristics of binocular visual neurons then there should be at least 3 distinct classes of disparity selective cells: one each for fine stereopsis,

crossed and uncrossed coarse stereopsis, and their associated vergence eye movements. This notion has been supported by the identification in both cat (Fischer and Kruger, 1978; Ferester, 1981) and primates (Poggio and Fischer, 1978; Poggio and Talbot, 1981) of cells which appear functionally capable of providing the substrate for the mechanisms of fine and coarse stereopsis.

The first to describe such cells were Poggio and Fisher (1977), in an experiment involving the use of awake, behaving monkeys, under conditions of normal binocular vision. The procedures utilized in this study had not only the virtue of approaching a natural visual situation, but also permitted a resolution in measurement which was not only far better than had previously been obtained but, was sufficient to reveal that stereoacuity in the non-human primate closely corresponds with that of its human counterpart. Additionally, this experiment indicated, in contrast to a previous study (Hubel and Wiesel, 1970), that disparity sensitive cells can be found in the primary visual cortex of the rhesus monkey. Recording from single neurons in both the striate and parastriate cortex, Poggio and Fischer found 2 major classes of disparity sensitive units. Cells in one group (tuned excitatory and tuned inhibitory neurons) were selective for very small stimulus disparities, averaging .2^{o} around the fixation point, had symmetrical tuning curves and properties which would make them suitable for a system of fine stereopsis. The other group (near and far cells) responded over a broader range of stimulus disparities, had asymmetric tuning curves and were selective for stimuli either in front of or behind the fixation point. These units, with their less specific stimulus demands could provide for a mechanism of coarse stereopsis.

In a previous study of binocular interactions in the cat 17/18 border (Cynader et al., 1979) we have found that animals which had a section of the optic chiasm and therefore received only ipsilateral input to each hemisphere, had units which showed substantial binocular activation, as well as disparity specific binocular interactions. It was obvious to us that the corpus callosum was an effective route for communication between the two visual hemispheres. However, examining the binocular interactions in split-chiasm cats has at least two serious difficulties. Firstly, since chiasm section alters the nature of binocular input to the lateral geniculate nucleus and the cortex on each side of the brain, the properties of callosal projection neurons are unlikely to be the same in split-chiasm cats as in normal cats. Secondly, studies of this type can only reveal those aspects of visual function for which the callosum is sufficient, rather than those for which it is necessary, and thus it was not clear from these data what the role of this projection would be in a relatively intact cortex. A recent approach to this question was that of Payne et al. (1980) who showed that after section of the corpus callosum, there was a dramatic drop in the number of units which could be driven equally by the two eyes, as well as a striking increase in the number of units (OD 1 and 7) which received excitatory input from exclusively one eye. These data suggested that the role of the corpus callosum for binocular connectivity in the opposite visual hemisphere was both substantial and necessary.

In the study of Payne et al., the responses of visual neurons were examined only under conditions of monocular stimulation. The present study was undertaken to examine the contribution of the

callosal projection to binocular interactions in cells along the vertical midline, and to determine if, in addition to the corpus callosum, there was evidence for other mechanisms of binocular convergence in cells with receptive fields located along the vertical midline. Binocular visual interactions were examined in single units from the border of area 17 and area 18 of cat visual cortex, and compared to responses from the 17/18 border of cats with unilateral lesions of the opposite visual cortex. Responses were examined with stimuli which moved in both the same (in-phase movement) and in opposite (antiphase) directions on the two retinae, movement which simulated motion toward or away from the animal or "motion in depth" (Cynader and Reagan, 1978; Poggio and Talbot, 1981). The results showed that stereoscopic processing depends on binocular inhibition in "monocular" neurons and that the corpus callosum plays an active role.

METHODS

In all experiments, subjects were normally-reared adult cats weighing 3-4 kilograms. For single unit recording, animals were initially anesthetized with intravenous Pentobarbital sodium, an endotracheal tube was inserted and paralysis was induced with intravenous Gallamine triethiodide. The skull was exposed and a small bone flap was removed over that part of the visual cortex representing the border between areas 17 and 18. Pentothal was discontinued at this point, Neosynephrine was applied to retract the nictitating membranes and the pupils were dilated with atropine. Contact lenses were chosen by retinoscopy to focus the eyes on a tangent screen 145 cm distant; the lenses contained 4 mm artificial pupils to decrease scattered light and increase depth of focus. A reversing ophthalmoscope was used to plot the two optic discs and <u>areae centrales</u> on the tangent screen. The vertical meridian for each eye was estimated to run through the center of the visual field perpendicular to the floor (Cooper and Pettigrew, 1980). Animals were initially paralyzed with a high dose (.5 cc/kg) of intravenous Flaxedil (Gallamine triethiodide) and then infused continuously with a mixture of Flaxedil (5 mg/kg/hr), D-tubocurarine hydrochloride (.5/mg/kg/hr) and 5% Dextrose in lactated Ringers (1cc/hr). During single unit recording, a level of light anesthesia was maintained by artificially ventilating the animal with a mixture of N_2O and O_2 (70:30) and intravenous anesthesia was discontinued. The animal's body temperature was held near 38° with a feedback-controlled heating pad, and end-tidal CO_2 was monitored continuously and kept near 4.2% by varying the rate of an artificial respiration pump. The cats were

usually maintained for a three day period. At the end of the experimental session, animals were perfused intracardiacally with saline, followed by a mixture of 10% formalin in a .9% saline solution. Brains were blocked in the electrode plane, removed from the skull and allowed to sink in 30% sucrose formalin. Forty micron sections were cut on a freezing microtome and stained with cresyl violet.

Approxminately one month prior to single unit recording, extensive lesions were made of the visual cortex in 5 animals. For surgery, cats were anesthetized with intravenous Alfathesin, fixed in a stereotaxic frame and a bone flap, 3 cm x 2 cm was cut through the skull. Cortex was removed by subpial aspiration, the bone flap was replaced, animals were administered subcutaneous Chloromycetin and returned to a cage for recovery. The lesions (see figure 9) included all of areas 17, 18 and 19 and extended laterally to include the crown of the suprasylvian gyrus and the Clare Bishop area.

Recording and unit classification

In normal cat experiments, a bone flap of approximately 5 mm^2 was removed with bone cutters under direct visual conrol. In an attempt to minimize the extent of dura left exposed after the craniotomy, a different procedure was used on the later-recorded decorticate cats. In these experiments, a small hole was drilled through the skull with a aid of dissecting microscope and less than 1 mm diameter of dura was exposed. In both cases, platinum iridium electrodes were advanced through the unopened dura with a hydraulic microdrive and responses of single units recorded from the 17/18 border. Action potentials were

amplified by conventional methods, monitored over a loudspeaker and displayed on a Tektronix D13 oscilloscope. Following isolation of a single unit, the receptive field was plotted with a hand projector and the following characteristics were noted; 1) the range of orientations over which the unit would respond 2) preferred orientation 3) direction selectivity 4) velocity preference 5) receptive field size 6) level of spontaneous activity 7) ocular dominance and 8) unit type. Moving and flashed stimuli, which included edges and light or dark bars of varied lengths and widths were used to plot receptive fields including edges and light or dark bars. Qualitative methods were generally employed to assess these response properties and quantitative analysis (see below) was reserved for the measurement of disparity sensitivity.

Simple and complex units were classified on the basis of subfield organization as originally described by Hubel and Wiesel (1962). Units were classed <u>simple cells</u> if their receptive fields could be divided into separate 'on' and 'off' areas and/or if responses to leading and trailing edges of moving light stimuli were evoked at different points in the visual field. Cells were classified as <u>complex</u> if both on and off regions and leading and trailing edge discharge regions were intermingled. Four other unit types were distinguished. A cell was classified as <u>hypercomplex</u> if it was selective for the length of a bar positioned along its preferred axis of orientation (Hubel and Wiesel, 1965). If a unit responded poorly or not at all to monocular stimulation but gave a vigorous response to binocularly presented stimuli it was called <u>binocular only</u>. A population of cells encountered gave only on or off responses throughout their receptive fields and these units were considered as

one type, on/off. Some cells did not fit clearly into any of the above categories, or had receptive fields which were difficult to plot, and such units were termed unclassified.

The ocular dominance (OD) of a unit was determined qualitatively and rated on a scale of one to seven according to the scheme of Hubel and Wiesel (1962). Units in OD group 1 receive excitation exclusively through the eye contralateral to the hemisphere under study, and units in higher OD groups receive successively more excitatory input from the ipsilateral eye. Units in group 4 were driven equally through the two eyes, and units in group 7 were excited exclusively by the ipsilateral eye.

Elongated stimuli of the optimum orientation presented at a velocity which evoked vigorous responses from the unit were employed for the assessment of direction selectivity. A unit was defined as "direction selective" if one direction of stimulus movement produced four times as many action potentials as movement in the opposite direction. If twice as many spikes were elicited by one direction of movement than the other, a unit was considered to have a directional preference. Non-directional cells responded with approximately the same number of spikes to either direction of stimulus movement.

Presentation of stimuli for quantitative analysis

Visual stimuli were projected from two similar but independent folded optical systems, each of which was arranged as follows. A slit of variable length and width was positioned in front of a condenser and illuminated by a 300 W tungsten lamp. A 9 cm achromat lens projected an image of the slit onto the tangent screen in front of the

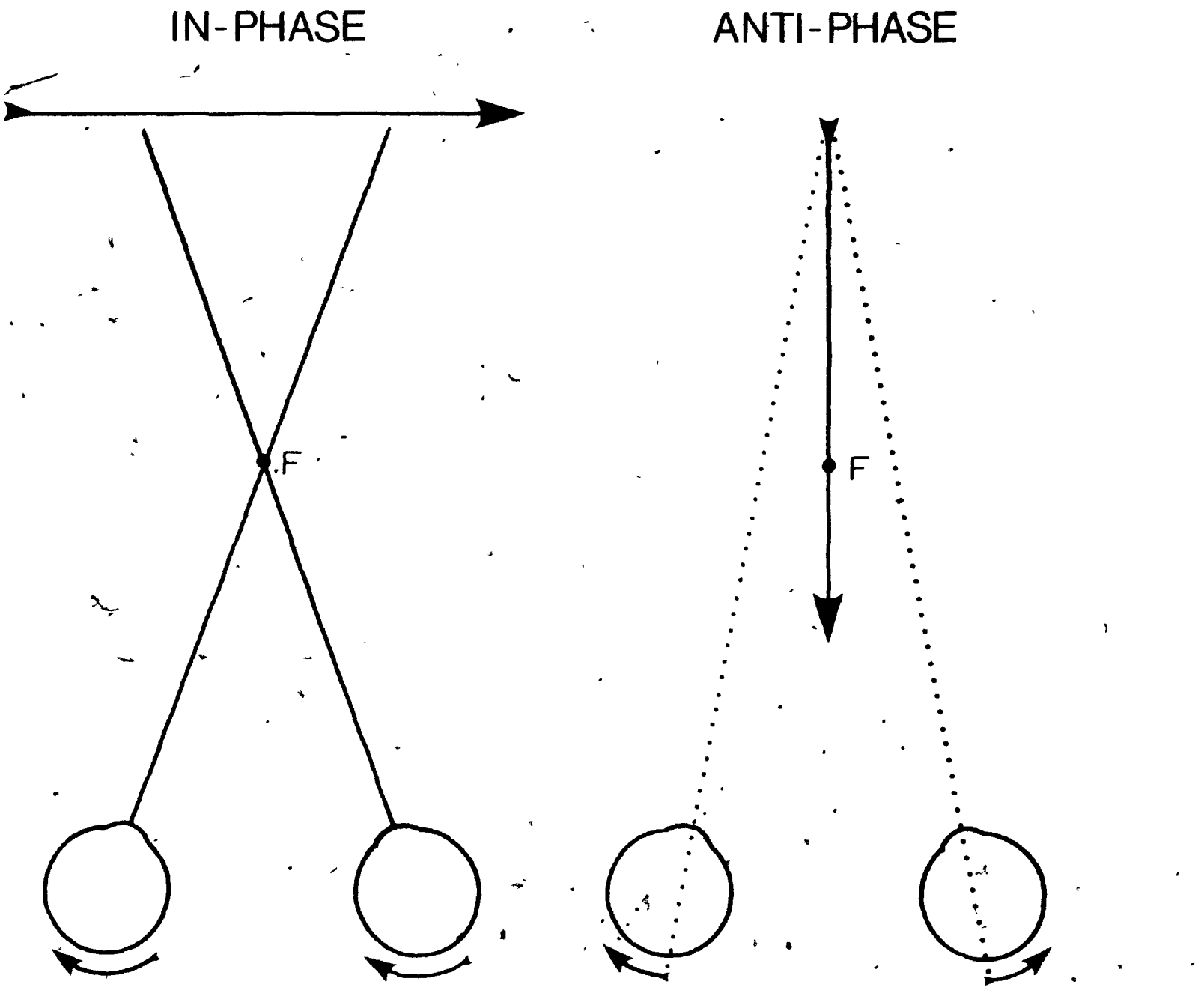
cat's eyes. Before reaching the screen, the beam was first reflected through 90° by a small front-surface plane mirror mounted on a galvanometer motor (General Scanning, type 300 PDT), then passed through a computer-controlled rotator, was again reflected through 90° by a large front-surface plane mirror and finally projected onto the tangent screen. By separating the receptive fields of the two eyes widely with a Risley prism, it was ensured that the receptive field of the left eye could be stimulated by only one of the two projected slits and that of the right eye by the other slit. The luminance of the stimuli was about 2.5 cd/m^2. Stimulus length, width, orientation and velocity were adjusted to match the preferences of the unit under study. The room and projection screen were diffusely illuminated by low-level tungsten light (0.34 cd/m^2). Computer-generated signals fed to the two galvanometer motors oscillated the small mirrors so as to move the bar images from side to side with a ramp wave motion and the positions of the bars were stabilized by positional feedback from the galvanometer. The image rotators were used to vary the orientation of the bars: the direction of movement was always perpendicular to the bars' orientation. The relative speeds and directions of motion could be controlled electrically as could their absolute speeds and repetition frequency.

Computer control of stimulation and recording

Stimulus parameters were set, and stimulus sequences initiated by typing appropriate instructions into a Tektronix model 4010 graphics terminal, which communicted with a PDP 11/34 computer. The terminal provided an on-line display of accumulated spike counts for each

timulus condition. The time of each response after the initiation of stimulus movement was recorded for a fixed interval, the length of which depended stimulus velocity, and the data were recorded on DEC RKO 5 disks for later analysis. In any given experimental run, stimulus velocity was held constant in the dominant eye. The velocity, 5 deg/sec , 10 deg/sec, 20 deg/sec, 40 deg/sec, or 80 deg/sec which gave the best response from that eye was selected. Stimulus excursion was always sufficient to allow the stimuli to start and stop outside the receptive fields. Responses to stimuli moving in the same direction and the same speed in the two eyes (called in-phase motion) were compared with responses to stimuli moving in the opposite directions at the same speeds in the two eyes (called antiphase motion). The direction of stimulus motion was always the preferred direction in the dominant eye and was varied in the nondominant eye. As illustrated in figure 1, in-phase motion on the two retinae simulated sideways movement in the external world and antiphase motion simulated movement toward or away from the animal's nose. This comparison was carried out at seven different disparities separated by 1^{o} or 2^{o} intervals. Responses to 16 or 32 sweeps at each of the seven disparities were summed. Responses through the dominant eye alone were also measured as was the response evoked by stimulation of the nondominant eye alone in both directions of motion. This resulted in a total of 17 stimulus conditions which were individually interleaved. The relative speed with which these data could be collected (5 to 15 min) helped control response variability due to residual eye movement and fluctuations in response rate which occur over time. In the plots presented below, the disparities represented refer to relative disparities between the two receptive fields, and a value of 0

FIGURE ONE In-phase and antiphase stimulus motion. Disparity specific binocular interactions were measured with two types of stimulus motion. Stimuli presented in-phase moved across the two receptive fields in the same direction (figure 1, left), representing sideways motion in the external world. Stimuli presented in antiphase moved across the two receptive fields in opposite directions (figure 1, right), simulating motion toward or away from the animal's nose or motion in depth. Receptive fields were separated with a Risley prism and each eye was stimulated with independently controlled optical systems. In each of the two movement conditions, responses to zero disparity, 3 uncrossed and 3 crossed disparities were measured. Responses were also measured through the dominant eye alone in the preferred direction, and the nondominant eye alone in both directions, resulting in a total of 17 individually interleaved stimulus conditions. In figures 2,3 and 9, crossed disparities are represented with a plus sign, uncrossed disparities with a minus sign.

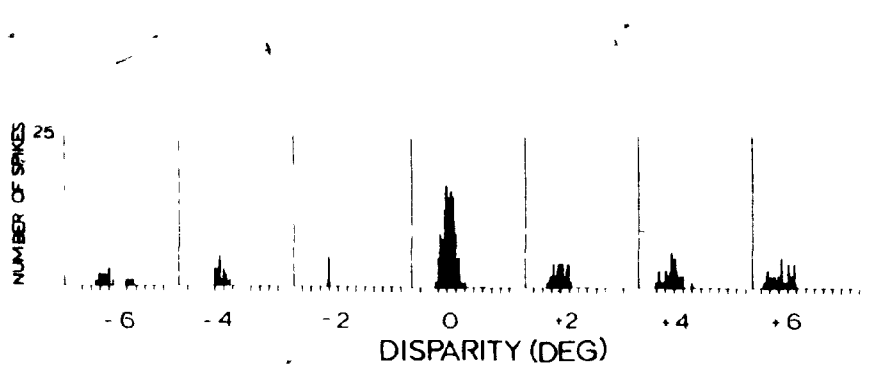

IN-PHASE
ANTI-PHASE
F
F

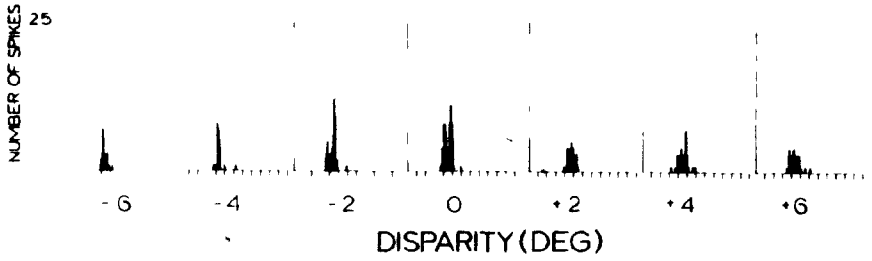
epresents the two centers. Since the use of moving stimuli confounds the variables of space and time (Gardner and Cynader, 1977; Cynader, Gardner and Douglas, 1978; see discussion) no distinction made will be made between "spatial" and "temporal" binocular disparities. The term "binocular interaction" refers to a nonlinear binocular response which is not presumed to be a response to any particular aspect of the binocular stimulus. Likewise, the terms "retinal disparity" and "disparity specific " are general terms which refer to either or both temporal and/or spatial disparities. Moving stimuli were chosen for the present experiment as they are more effective in driving many visual cells than are flashed stimuli, and it was important to sample at regular intervals from an unbiased population. Procedures for data reduction were chosen so that the responses of all units could be quantified and that comparisons could be made across as broad a population as possible. The principles derived from these data are believed to apply to both spatial and temporal mechanisms for stereoscopic depth perception.

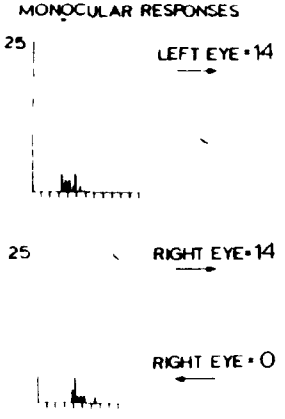
Data analysis

Responses to each of the 17 conditions of visual stimulation were summed and the summed responses and/or individual histograms were displayed on the graphics terminal. Hard copies were made using a Textronix 4610 hard copy unit or 4662 digital plotter. The plots were of the form presented in the top row of histograms in figure 2. In order to compare the degree of binocular interactions in the responses of single units, three indices, binocular inhibition, binocular facilitation and dynamic range, were constructed to indicate the

FIGURE TWO Data reduction. Method of data reduction is shown for a unit which displayed strong disparity specific binocular interactions to in-phase stimulus movement, and was relatively unselective for stimulus disparity with antiphase movement. This unit was recorded within 300 micra of the cortical surface, was direction selective and classified as binocular only. The two rows of post-stimulus time histograms illustrate the responses to 7 different disparities elicited with in-phase (top) and antiphase (bottom) stimulus motion. The number of spikes elicited at each disparity, in each movement condition, is shown in the summary histograms to the right. Responses through the dominant eye alone to the preferred direction and the nondominant eye alone to both directions of motion are also shown. As shown in the insert, the index of binocular facilitation (BF), binocular inhibition (BI) and dynamic range was calculated separately for each of the two movement conditions. There was one index each for combined binocular facilitation, combined binocular inhibition and combined dynamic range and its calculation considered responses across both in-phase and antiphase conditions. Although the procedures employed in quantifying the neuronal responses represent a considerable reduction in raw data, the results of the figures which follow show a high degree of internal consistency, and indicate that the observed effects are robust enough to withstand this degree of data reduction.







		IN-PHASE (IP)	ANTIPHASE (AP)
2-1	BINOCULAR FACILITATION (BF) $\frac{\text{MAXIMUM RESPONSE}}{\text{SUM OF MONOCULAR RESPONSES}}$	$\frac{214}{28}$ 7.6	$\frac{72}{14}$ 5.1
2-2	BINOCULAR INHIBITION (BI) $\frac{\text{MINIMUM RESPONSE}}{\text{SUM OF MONOCULAR RESPONSES}}$	$\frac{6}{28}$ .2	$\frac{24}{14}$ 1.7
2-3	DYNAMIC RANGE $\frac{\text{BINOCULAR FACILITATION}}{\text{BINOCULAR INHIBITION}}$ -10	$\frac{7.6}{2}$ • 38-1 • 37.0	$\frac{5.1}{1.7}$ • 3-1 • 2.0
2-4	COMBINED BINOCULAR FACILITATION MAXIMUM INDEX OF BF, IP OR AP • 7.8		
2-5	COMBINED BINOCULAR INHIBITION MINIMUM INDEX OF BI, IP OR AP • .2		
2-6	COMBINED DYNAMIC RANGE $\frac{\text{COMBINED BF}}{\text{COMBINED BI}}$ -10- $\frac{7.6}{2}$ • 38-1 • 37.0		

degree by which the units' firing departed from that which would be expected on the basis of simple summation of the monocular responses.

The index of binocular inhibition (figure 2-1) for a given unit was derived separately for in-phase and antiphase stimulation by choosing the lowest value in the tuning curve and dividing that value by the sum of the monocular responses. For in-phase stimulation, the denominator of this ratio was the sum of the response evoked by stimulation of the dominant eye in the preferred direction and stimulation of the nondominant eye in the same direction. For antiphase stimulation, the denominator was the sum of the number of spikes evoked by stimulation of the dominant eye in the preferred direction and stimulation of the nondominant eye in the opposite direction. For a cell which shows little or no binocular inhibition this index will show a value of close to 1.0. Increasing degrees of binocular inhibition will result in successively lower values for this index. The index of binocular facilitation (figure 2-2) for a given unit was derived by choosing the maximum value of the disparity tuning curve and dividing it by the sum of the two appropriate monocular responses. This was done separately for in-phase and antiphase responses. Again, a cell showing little or no facilitation will display a value close to 1.0 according to this index, and cells with increasing degrees of binocular facilitation will display successively larger values.

In order to provide a measure of the degree to which the unit's firing could be modulated up or down by stimuli of different disparities, a measure caled the dynamic range was derived for each unit. This index represents the difference between the maximum and

minimum response observed over the 7 disparities tested, and was calculated by taking a ratio of the indices of binocular facilitation and inhibition described above (figure 2-3). As before, this was calculated separately for in-phase and antiphase stimulation. Thus, a cell showing substantial binocular facilitation (with a value of 4.0) and no inhibition (a value of 1.0) will achieve a dynamic range of 4.0, minus 1.0 for a total of 3.0. Likewise, a cell which lacks binocular facilitation (a value of 1.0) but displays marked inhibition (a value of .25) will also achieve a dynamic range of 3.0 , as will a cell which displays a moderate degree of both facilitation (a value of 2.0) and inhibition (a value of .5). The distribution of <u>combined</u> binocular facilitation (figure 2-4), binocular inhibition (figure 2-5) and dynamic range (figure 2-6) represents the minimum (inhibition) and maximum (facilitation) value obtained on these indices across the two movement conditions on these indices, and their ratio.

These measures are applied to the responses of a unit with very large binocular interactions in figure 2. In this figure, the 7 post-stimulus time histograms along the top show responses to different stimulus disparities tested with in-phase movement, and to their right, the summary histogram indicates the number of spikes elicited at each disparity. Beneath these, the monocular responses for each eye to the same direction of movement are also shown. To determine the degree of binocular facilitation, the maximum response, 214, was divided by the sum of the monocular responses, 28, to achieve an in-phase facilitatory value of 7.6. Binocular inhibition was calculated by dividing the minimum response, 6, again by the sum of the monocular responses, 28, for an in-phase inhibitory index of .21,

which was rounded to .2. In-phase dynamic range was determined by dividing 7.6 by .2 (max/min) leading to a value of 38, minus one, for a total of 37. In the second row of figure 2, the responses of the same unit to stimulation with antiphase motion at the same seven disparities as above are shown. For this cell, the degree of binocular interaction is less pronounced with antiphase motion than for in-phase motion. The value of the antiphase facilitatory index is 5.1, that for the antiphase inhibitory index is 1.7 and the antiphase dynamic range has a value of 3.0, minus 1, for a total of 2.0. To calculate the combined dynamic range for this unit, the larger of the two facilitatory values were divided by the smaller of the two inhibitory values for the cell. Since in this cell, these indices are both larger for in-phase motion than for antiphase motion, the combined dynamic range is equal in value (37) to the in-phase dynamic range.

RESULTS

I. Qualitative results in normal cats

In experiments on 10 normally-reared cats, 309 units with receptive fields along the 17/18 border were studied with qualitative methods. In 6 of these 10 animals, binocular interactions were examined quantitatively in 158 neurons. Electrode penetrations were perpendicular, or approximately so, to the cortical surface, and were confined to the region outlined in figure 9.' This area encompasses Horsely-Clarke stereotaxic coordinates, anterior 3.0 to posterior 3.0 and lateral 1.5 to 4.0 (Otsuka and Hassler, 1962). Most penetrations were made near AP 0.0, lateral 2-3, as previous experiments had shown that this region marked the 17/18 border. At the end of some representative penetrations, small electrolytic lesions were made (3 microamps for 3 sec, electrode negative) for histological reconstruction of electrode tracks.

Quantitatively studied units had receptive fields which were usually located within 3^{o} of the vertical meridian and generally $5\text{-}10^{o}$ into the lower visual fields. In some penetrations, the response characteristics of the cells were similiar to those of area 18 units. Their receptive fields were relatively large ($5\text{-}8^{o}$), they responded with only a transient burst of impulses to a flashed stimulus, and they preferred very high stimulus velocities-frequently having no apparent high-end velocity cut off (Orban, 1977; Tretter, Cynader and Singer, 1975). Other units were more reminiscent of cells found in area 17, having smaller receptive fields, showing sustained responses to flashed stimuli and a preference for low stimulus velocities. Most

frequently however, penetrations near the 17/18 border contained units which showed a wide range of response characteristics. Some cells preferred low stimulus velocities, others very fast velocities, with a complement of sustained and transient responses to brief stimuli. Monocular receptive field sizes generally ranged between 2 and 5^{o} (86% of all units), while units with very small receptive fields (less than 1^{o}) such as those found often in the area centralis of area 17, and units with large receptive fields ($6-10^{o}$) were relatively uncommon (3% and 11% respectively). All six cell types described in the methods were represented in this sample. Nearly all cells recorded displayed orientation selectivity while 88% of this units showed direction selectivity or at least a directional preference. Many cells were binocularly driven as shown in the normal cat ocular dominance distribution of figure 8A.

Quantitative analysis of binocular interactions in normal cats

As described by previous investigtors, responses of cortical visual neurons to binocularly-presented stimuli vary with the disparity of the stimulus. Some units show binocular facilitation, others binocular inhibition, while others respond with facilitation at certain disparities and inhibition at others. In figure 3, a variety of such responses are shown. The response elicited at each of the 7 different disparities is illustrated for both in-phase (solid line) and antiphase (dotted line) movement, and can be compared with the 'predicted' binocular response (sum of monocular responses, arrow) for the two movement conditions. For reference, the value of the dynamic range index for each condition is indicated next to the graph.

FIGURE THREE Disparity tuning curves in normal cats. These disparity tuning curves illustrate the variety of binocular interactions seen among visual neurons of normal cats. Responses to both in-phase (solid line) and antiphase (broken line) stimulus movement are shown, and the arrows indicate the sum of the monocular responses appropriate to each stimulating condition. The responses of different units were characterized by binocular facilitation (A-in, D-in, E-an, F-an), binocular inhibition (F-in, G-in, H-in and an) or showed inhibition at particular disparities, and facilitation at others (B-in, D-an). Some units were insensitive to variations in stimulus disparity (A-an, C-in and an, G-an). As these tuning curves indicate, interactions to in-phase and antiphase stimulus movement could be similiar (B, C, D), different (A, E, G) or opposite in sign (F). The response characteristics of each of the units were as follows: (A) OD 6, direction selective, unclassified (B) OD 6, direction selective, simple (C) OD 4, direction selective, complex (D) OD 6, direction selective, on/off (E) binocular only, direction selective (F) OD 1, unclassified (G) OD 6, directionally preferential, complex (H) OD 5, direction selective, simple. The values of the in-phase, antiphase and combined dynamic range indices are noted to the right of each tuning curve.

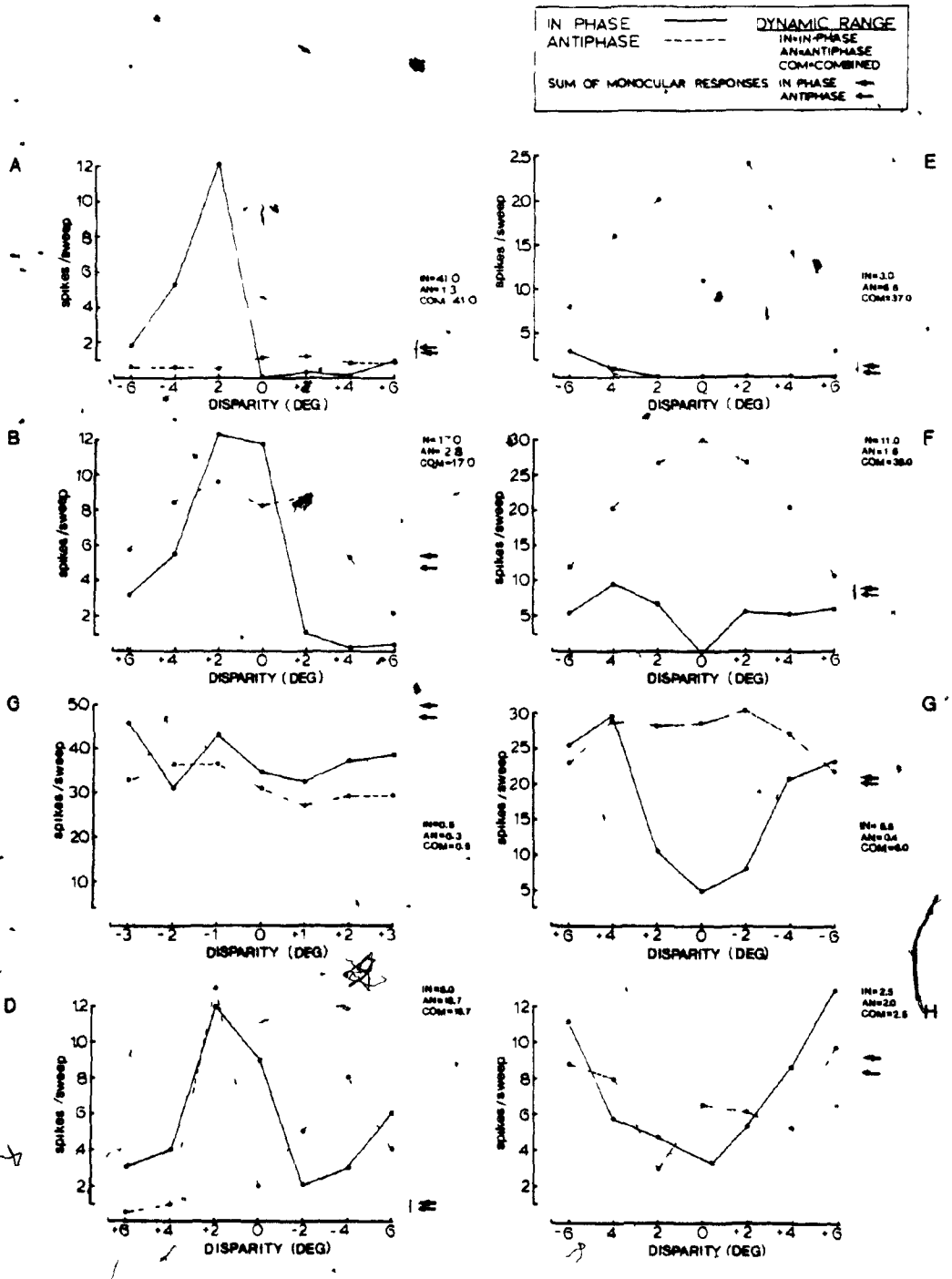


Figure 3 illustrates the responses of eight units located near the area 17/18 border of normal cats to stimuli of varied disparity. These units were, with the exception of unit 3C, rather sensitive to variations in stimulus disparity. Comparison of their dynamic ranges with that of the overall population (Figure 11) shows that most of these units are examples of cells which display relatively large binocular interactions. Figure 3 illustrates the richness and variety of this binocular selectivity in cortical responses. Selectivity could be achieved primarily by binocular facilitation (3A, 3E), binocular inhibition (3G, 3H) or by both mechanisms acting in concert (3B, 3D, 3F). Binocular facilitation could be observed in response to either in-phase or antiphase stimulation (3A, 3E, 3F) as could binocular inhibition (3B, 3D, 3E, 3H). Some cells modulated their firing in a similiar manner as a function of stimulus disparity regardless of the direction of depth motion (3B, 3D, 3H) while in other cells, increased responses for antiphase motion at one disparity were reflected by deep inhibition for in-phase motion (3F). Not uncommonly, disparity specific interactions were found only for in-phase (3A, 3G) or antiphase stimulation (3E) in particular cells, with little modulation of the firing rate of the same cell by the other type of depth motion, regardless of variations in stimulus disparity.

When a unit was found which displayed large binocular interactions, it was often the case that the next 2 or 3 units tested (100-300 micra apart) would also show large interactions. The sign of the interaction however, facilitatory or inhibitory, could be opposite to that of the surrounding units. As described previously, (Cynader and Regan, 1978) some 'clustering' of units with strong binocular

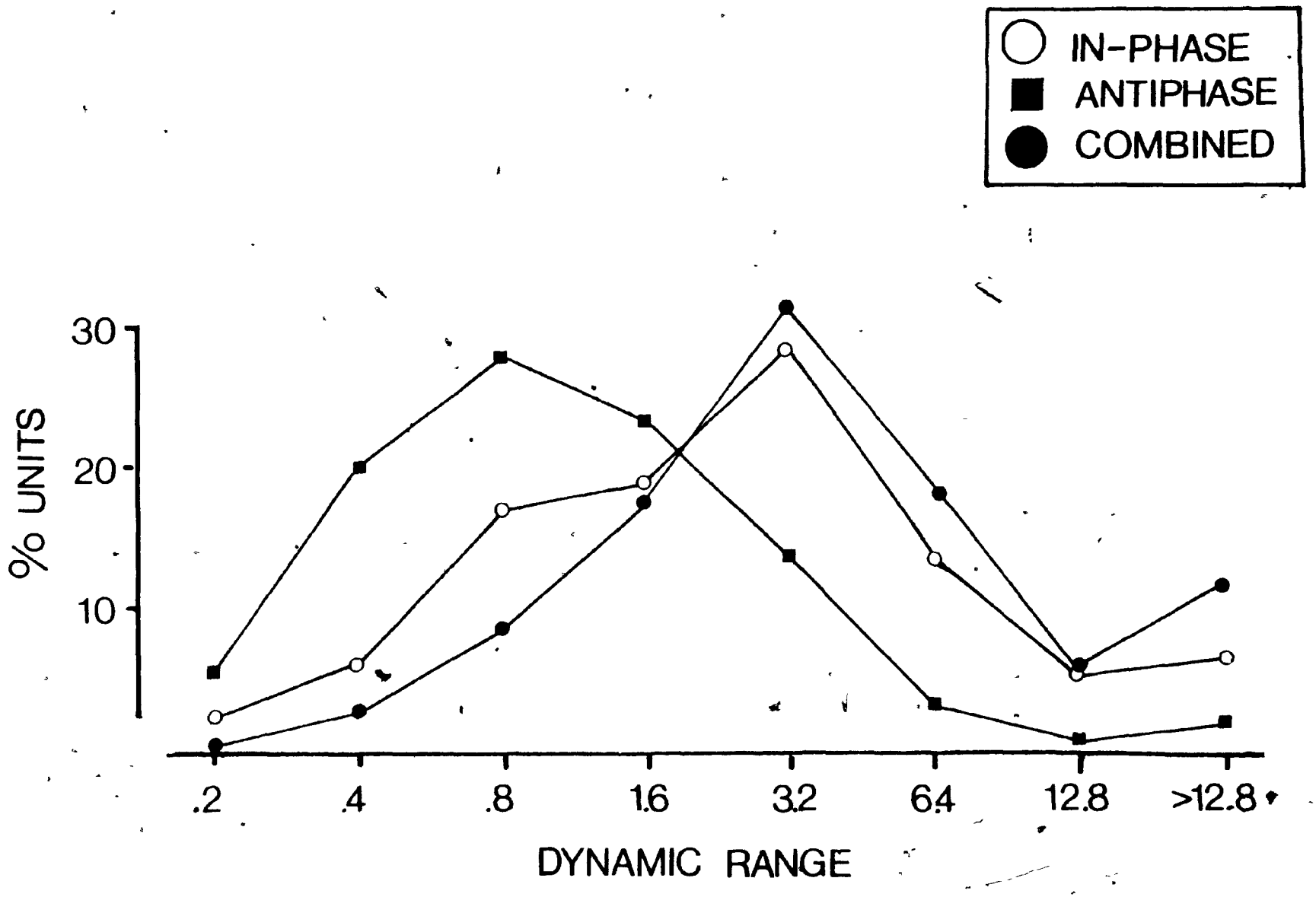
interactions for antiphase stimulation was observed. Although the frequency with which units with large interactions for antiphase motion were encountered was not high, when found, 2 or 3 of these cells were often recorded consecutively.

Dynamic range

Overall, in-phase binocular interactions were larger than antiphase interactions. These data are summarized in figure 4, which shows the value of the dynamic range index for in-phase (o), antiphase (■) and in-phase and antiphase motion combined (●) for the entire population of cells examined. For purposes of comparison, units with a dynamic range of 6.4 or greater were considered to have large binocular interactions while those with dynamic ranges of 0.8 or lower were deemed to be relatively insensitive to stimulus disparity. The peak of the in-phase distribution was centered around the intermediate ratio of 3.2, with about 27% of the cells showing large binocular interactions and around 26% appearing unselective for stimulus disparity. Antiphase interactions, on the other hand, peaked at a value of 0.8, with 54% of the population seeming insensitive to stimulus disparity. Only a small proportion of the units displayed large antiphase interactions (8%). Since 73% of the units displayed larger binocular interactions with in-phase than with antiphase movement, the distribution of the combined dynamic range index was quite similiar to the dynamic range index for in-phase interactions.

In an effort to determine the components of the binocular response which were responsible for the differences between the in-phase and antiphase selectivity, the indices of binocular inhibition

FIGURE FOUR Dynamic range of binocular interactions in normal cats. Strong direction selective inhibition in the preferred direction of motion resulted in a clear distinction between responses to in-phase and antiphase stimulus movement. Binocular interactions to stimuli moving in-phase were substantially larger than those to stimuli moving antiphase. The distribution of the combined dynamic range index was thus very similiar to the distribution of in-phase interactions. Very few units showed large binocular responses (dynamic range 6.4 or greater) and many appeared unselective for stimulus disparity (dynamic range 2.0 or below) when activated with antiphase stimulus motion. Nonetheless, although antiphase responses in general did not display the large binocular interactions, relatively common with in-phase stimuli, almost one half of the units encountered showed evidence of some sensitivity to binocular disparity when activated with motion-in-depth stimuli.

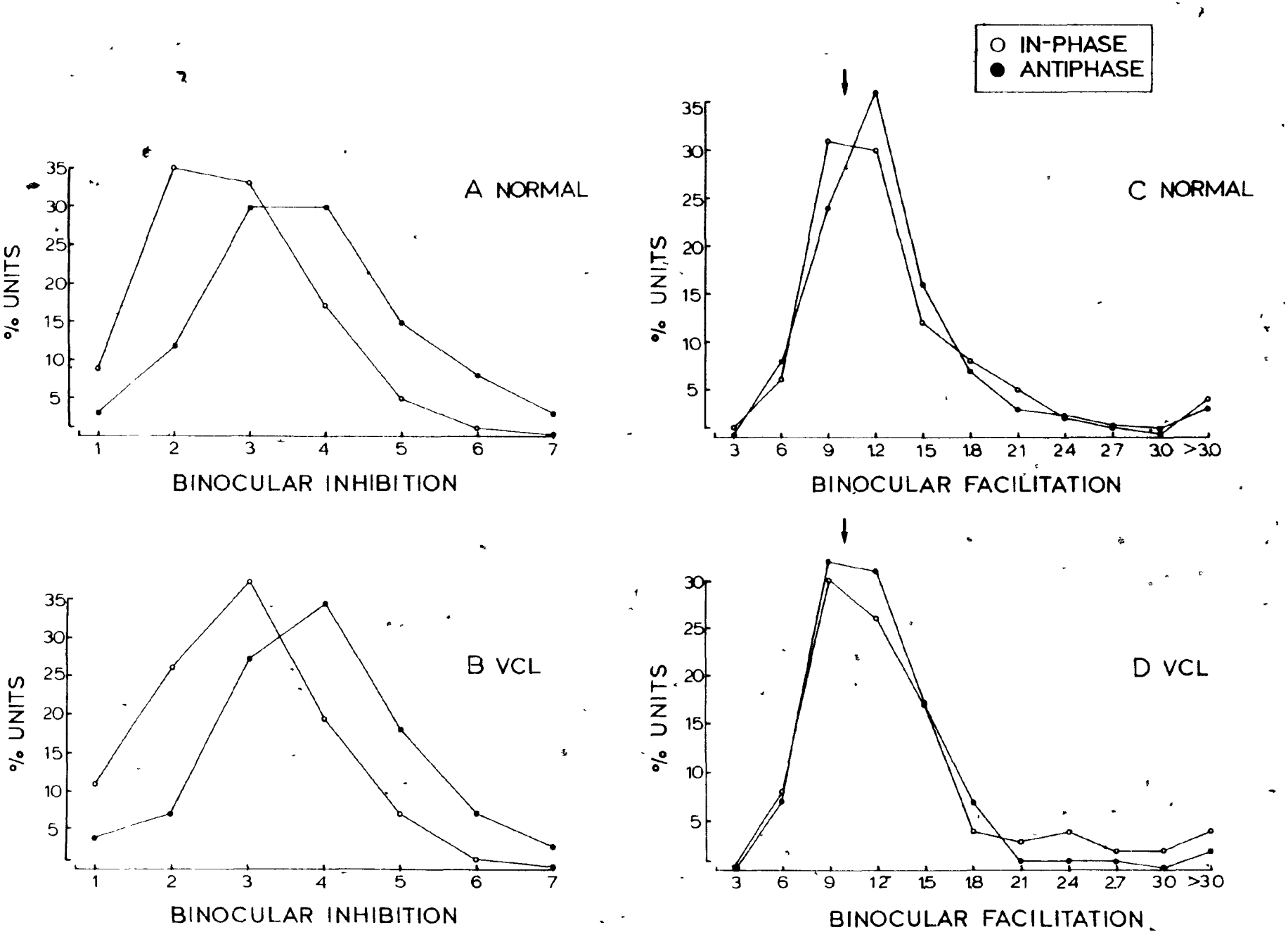

IN-PHASE
ANTIPHASE
COMBINED
30
20
10
% UNITS
.2
.4
.8
1.6
3.2
6.4
12.8
>12.8
DYNAMIC RANGE

(minimum response) and binocular facilitation (maximum response) were compared across the two movement conditions. These data, illustrated the unper two graphs of figure 5, show the distribution of binocular inhibition (left) and facilitation (right) for both inphase (o) and antiphase (•) responses. The two inhibitory distributions were similiar in general shape, range and variance, but there was significantly (t-test, $p>.01$)more inhibition with in-phase than with antiphase movement. Likewise, the characteristics of the two facilitatory distributions were also similiar, but in striking contrast to the inhibitory case, there was no difference in the degree of binocular facilitation across the two movement conditions. These data showed clearly that the larger binocular interactions for in-phase than for antiphase movement reflected a difference in the degree of binocular inhibition across the two movement conditions. Binocular facilitation was similiar for in-phase and antiphase movement, but binocular inhibition was clearly stronger for in-phase stimulus motion.

Characteristics of disparity sensitive cells

In order to identify characteristics which distinguished cells with high from those with low disparity sensitivity, a comparison was made between units with dynamic ranges in the top and bottom quartile of the combined dynamic range distribution of binocular interactions (greater than 5.7 and less than 2.4 respectively). Differences were seen between the two groups on the following measures: 1. cortical location 2. ocular dominance 3. direction selectivity and 4. cell type.

FIGURE FIVE Binocular inhibition and facilitation in normal cats and in cats with unilateral lesions of the visual cortex. Since binocular interactions were substantially larger to in-phase than to antiphase stimulus movement, it was remarkable to find that responses across these two movement conditions differed only in the strength of binocular inhibition. In both normal and decorticate cats, the distributions of in-phase and antiphase binocular facilitation were strikingly similiar. The degree of facilitation was centered around a ratio of 1.0 (representing the sum of the monocular responses, arrow), and when compared to the peaks of the inhibitory distributions, indicated that nonlinearities in response rates were far more common with inhibitory than with facilitatory binocular interactions.


O IN-PHASE
● ANTIPHASE
A NORMAL
% UNITS
BINOCULAR INHIBITION
C NORMAL
% UNITS
BINOCULAR FACILITATION
B VCL
% UNITS
BINOCULAR INHIBITION
D VCL
% UNITS
BINOCULAR FACILITATION

Cortical location

Although units of all types were found throughout the cortex, cells with large binocular interactions were more frequently encountered in the upper cortical layers, while those exhibiting little binocular interaction tended to be found in the lower layers of the cortex. Seventy-four percent of the units with strong binocular interactions were found above a depth of 1100 micra, while only 33% of the relatively unselective cells were found in this region. For a more comprehensive view of binocular interactions as a function of cortical location the average combined dynamic range was examined in units recorded at specific depths from the cortical surface. These data are illustrated in figure 6, which plots the mean value of the combined dynamic range index for the subpopulation of units recorded at each depth (ordinate), against the location of units relative to the cortical surface (abscissa). Since in some cats, the number of units found at the beginning and end of a penetration was quite small, units recorded at the very top and bottom of the cortex were grouped together as one point at the low and high end of the scale.

The data of figure 6 show that, on average, binocular interactions are larger in the upper than the lower half of the cortex. The mean value for the dynamic range index was quite high at the top of the cortex, peaked at a depth of 800-900 micra, was minimal around 1200 micra, then rose and remained fairly constant below 1500 micra. Although the mean dynamic range of units encountered immediately below the cortical surface was somewhat less than that of slightly deeper neighboring cells, this difference can be attributed to prolonged exposure of the dura, and successive penetrations , which were found to depress the binocular responses of units located

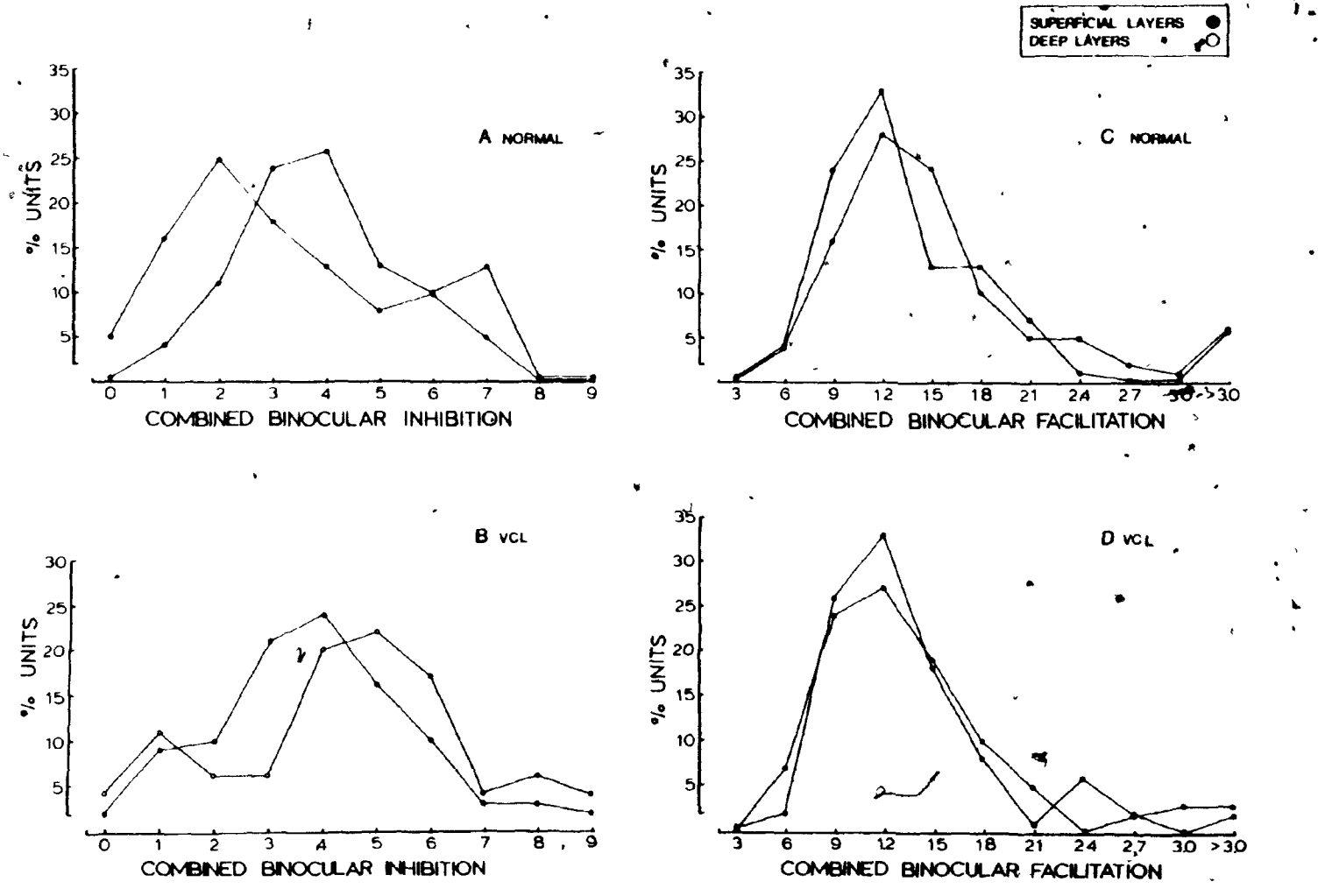
FIGURE SIX Average dynamic range as a function of depth in the cortex in normal and decorticate cats. The effects of unilateral decortications appeared restricted to particular cortical regions, regions which corresponded well with known termination zones of callosal projections. Differences between normal and lesioned cats were seen in two principle zones; one in and around layer III and/or upper layer IV, and the second was at the very bottom of the cortex, around layer VI. A large effect was observed in the superficial cortical layers, where decorticate animals showed a substantial drop in dynamic range in a region extending from about 700 to 1100 micra, and a second, although considerably smaller effect was seen at the very bottom of the cortex, at and below a depth of 1700 micra. As the data of figure 10 suggest, the reduced mean dynamic range seen in decorticate cats at these depths probably reflects an increase in the number of disparity insensitive cells recorded at these cortical locations. Dispite the variance noted above, curves from the two preparations shared a number of common features.

COMBINED DYNAMIC RANGE
2
4
6
8
<3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
>18
DEPTH IN CORTEX (100μm)
NORMAL
VCL

immediately below the cortical surface. When the cortex was in optimal condition, units with large interactions were quite consistently encountered very near the cortical surface. In the middle cortical layers, a number of units found at a depth of around 1200 micra were either insensitive to stimulus disparity or showed very small binocular interactions. This appeared in figure 6 as a region extending for 200-300 micra with a relatively low mean dynamic range. On the basis of the location of these unselective cells relative to the cortical surface, and with respect to the depth at which geniculate fibers were encountered, it is probable that these units were located in the lower portion of layer IV or upper layer V.

To determine the characteristics of the binocular response which were responsible for the larger dynamic range of units in the superficial cortical layers the degree of binocular inhibition and facilitation were compared in cells encountered above and below a depth of 1100 micra from the cortical surface. The distribution of inhibitory binocular interactions across in-phase and antiphase motion (combined minimum and maximum response) was tabulated for the two groups of cells and is shown in the upper left graph of figure 7. Facilitatory interactions are similarly represented in the upper right-hand graph. As these data show, there was only a small difference between the superficial and deep layer cells in maximum, or facilitatory interactions, but there was a clear difference in minimum, or inhibitory interactions. Units in the superficial cortical layers had a larger combined dynamic range than units in the deep layers, primarily because they showed stronger binocular inhibition.

FIGURE SEVEN Binocular inhibition and facilitation in the superficial and deep layers of normal and decorticate cats. The larger dynamic range of units in the superficial cortical layers was principally due to binocular inhibition. In both normal and lesioned cats, binocular inhibition was clearly stronger in the superficial than in the deep cortical layers. Relative to normal cats, decorticate cats showed a substantial reduction in binocular inhibition throughout the cortex and a very slight decrease in the extent of binocular facilitation in the superficial layers only.

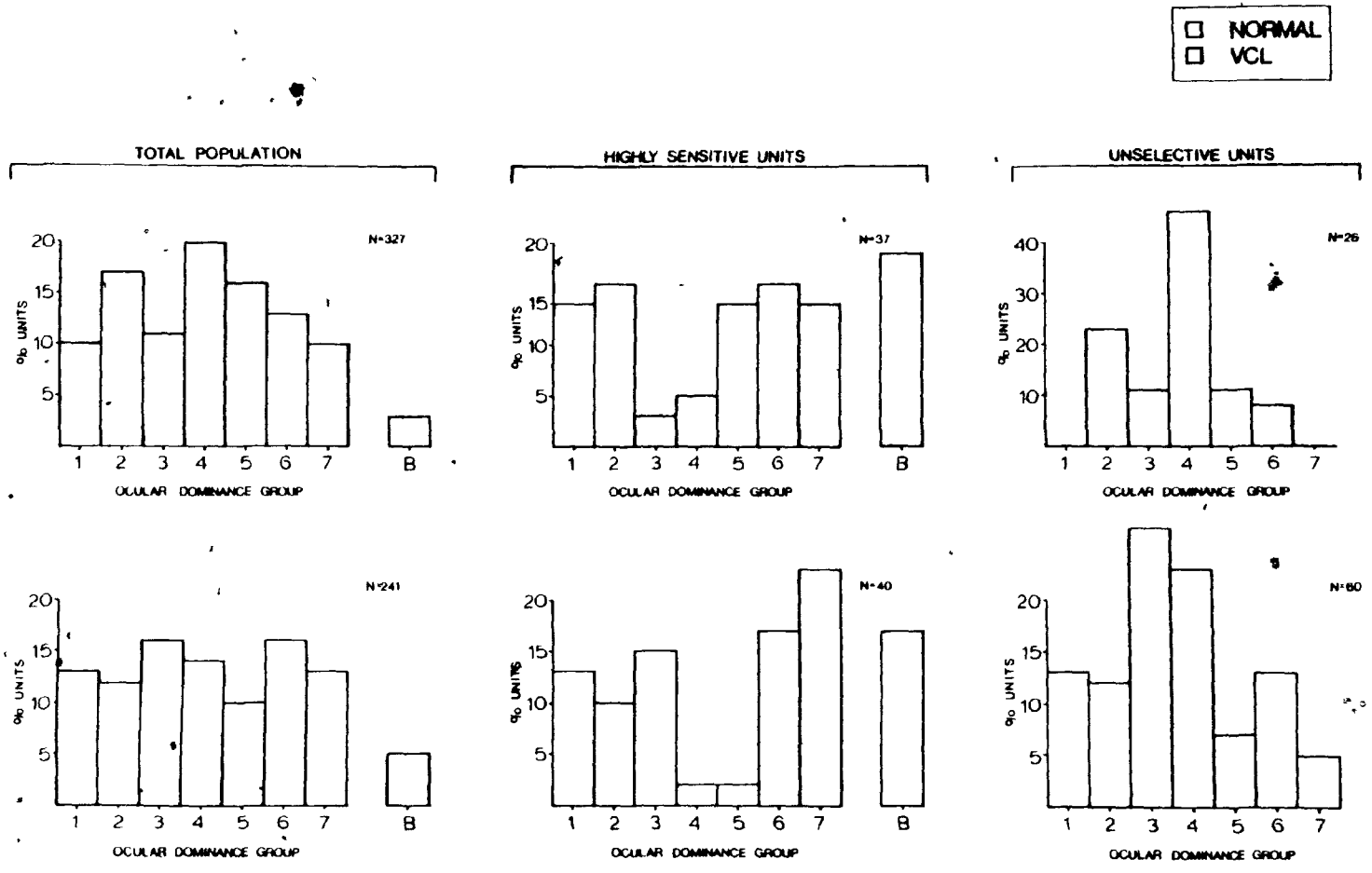

SUPERFICIAL LAYERS
DEEP LAYERS
A NORMAL
C NORMAL
B VCL
D VCL
% UNITS
COMBINED BINOCULAR INHIBITION
COMBINED BINOCULAR FACILITATION
0 1 2 3 4 5 6 7 8 9
3 6 9 12 15 18 21 24 27 30 >30
5 10 15 20 25 30 35

Ocular dominance and direction selectivity

The relationship between the magnitude of a unit's binocular interactions and its ocular dominance was a clear and consistent one. Except for the special case of the binocular only cells, the more biased a cell to one eye, the larger were its binocular interactions. This relationship held for both facilitatory and inhibitory binocular interactions. The binocular only cells had the highest mean combined dynamic range (23.6), followed by cells in ocular dominance groups 1 & 7, 2 & 6, 3 & 5 and 4, with mean combined dynamic ranges of 9.7, 5.0, 3.3 and 2.0 respectively. Of the units in the upper quartile for binocular interactions, 77% were either driven well through only one eye or failed to respond to monocular stimulation of either eye alone (OD groups 1, 2, 6, 7 and binocular only). Of the units in the lowest quartile for binocular interactions, only 32% were strongly dominated by one eye. The top three histograms of figure 8 show the ocular dominance distribution of the entire population of units (histogram on left), units exhibiting substantial binocular interactions (top 25% of the population, center) and units little binocular interaction (bottom 25% of the population, right). As the histograms representing the 2 subpopulations of cells show, units with large binocular interactions and those with little binocular interaction were respectively more "monocular" and "binocular" than the population as whole.

Units which were strongly dominated by one eye (OD groups 1 & 7) also tended to be more direction selective. About 80% of these "monocular" cells were strongly direction selective, compared with 56% for the population as a whole. As indicated in table 1, the mean of

FIGURE EIGHT Ocular dominance of disparity sensitive and disparity insensitive units in normal and decorticate cats. In normal cats, units highly sensitive to stimulus disparity were dominated unequally by the two eyes, or driven poorly to stimulation of either eye alone. Units unselective for stimulus disparity tended to be driven well through either eye. Data from normal cats are shown in the top three histograms, data from decorticate cats below. Although there were no large differences in the ocular dominance (OD) of cells found in the two preparations, lesioned animals showed a slight increase in units which received excitatory input from only one eye (OD groups 1 and 7). This difference was not obvious when the population of units was considered as a whole (histograms on left) but became much more apparent with a comparison of the 2 groups of unselective cells, shown on the right. Since in normal cats, units in OD groups 1 and 7 are rarely disparity-insensitive, these data indicate that an effect of the cortical lesion was to generate truely monocular cells which were insensitive to stimulus disparity. Likewise, since there were no differences between the two preparations in the response characteristics of highly sensitive cells, these data suggest that units rendered unselective by the cortical lesion were not drawn from that population of neurons which show substantial disparity specific responses.



the combined dynamic range index was largest for directional units, somewhat less for units which showed a directional preference and was lowest in non-directional cells. As would be expected, units showing large binocular interactions were more likely to show direction selectivity than cells which were relatively insensitive to stimulus disparity.

Other properties

Also examined was the relationship between orientation preference, cell type and the degree of disparity selectivity amongst visual cortical cells. No effect of orientation was observed. Cells of any orientation, even horizontal, could show substantial variations in strength of response when stimulus disparity was varied. Since stimulus disparity was always varied in a direction perpendicular to the preferred orientation of the cell, in this latter case, these alterations represented changes in vertical rather than horizontal disparity. The relationship between cell type and binocular interctions was not pursued in detail since only qualitative procedures for classifying units were employed. Differences were seen however, in the frequency of cell types seen in the groups of low and highly sensitive cells. With only one one exception, each of the six cell types was represented in each group, yet there were clearly more simple cells among the highly selective units (48% vs 26% among the unselective cells) and more complex cells among units with low binocular interactions (65% vs 23% in the highly selective group.

TABLE ONE Mean combined dynamic range and frequency of direction selective, non-directional and directionally preferential units in normal and decorticate cats. In both normal and decorticate cats, a consistent relationship was seen between a unit's binocular interactions and its directional properties. A unit was considered to be direction selective if it responded with 4 times as many spikes to one direction of stimulus motion than to the opposite direction. Directionally preferential cells responded with twice the number of spikes to one direction of stimulus movement. In both normal and decorticate cats, non-directional and direction selective units respectively had the smallest and largest mean dynamic range. Across the two preparations, there was very little difference in either the dynamic range of direction selective units or in the frequency with which they were encountered. Decorticate cats however, had a greater number of non-directional cells and fewer units which showed a directional preference. These data suggest that a group of units which formerly showed a directional preference were rendered non-directional by the cortical lesion.

	NON-DIRECTIONAL	PREFERENTIAL	DIRECTIONAL
	DYNAMIC RANGE		
NORMAL	3.1	4.3	6.9
VCL	2.8	3.2	7.1
	FREQUENCY		
NORMAL	11%	32%	56%
VCL	22%	22%	56%

Summary

In normal cats, fully 85% of the units along the 17/18 border displayed clear binocular interactions and 78% of these cells showed sensitivity to the retinal disparity to binocularly-presented stimuli moving in the same (in-phase) and/or in opposite (antiphase) directions on the two retinae. The modulation in firing rate (dynamic range) seen in these cells was greater for stimuli moving in-phase than in antiphase. There was no difference in the degree of binocular facilitation between the two movement conditions but binocular inhibition was significantly stronger with in-phase stimulus motion. Binocular interactions were more pronounced for units in the superficial than in the deep cortical layers: this effect could be attributed to a difference in the strength of binocular inhibition. Units showing strong binocular interactions were most frequently found in the superficial cortical layers. These cells were often strongly dominated by one eye and were frequently direction selective.

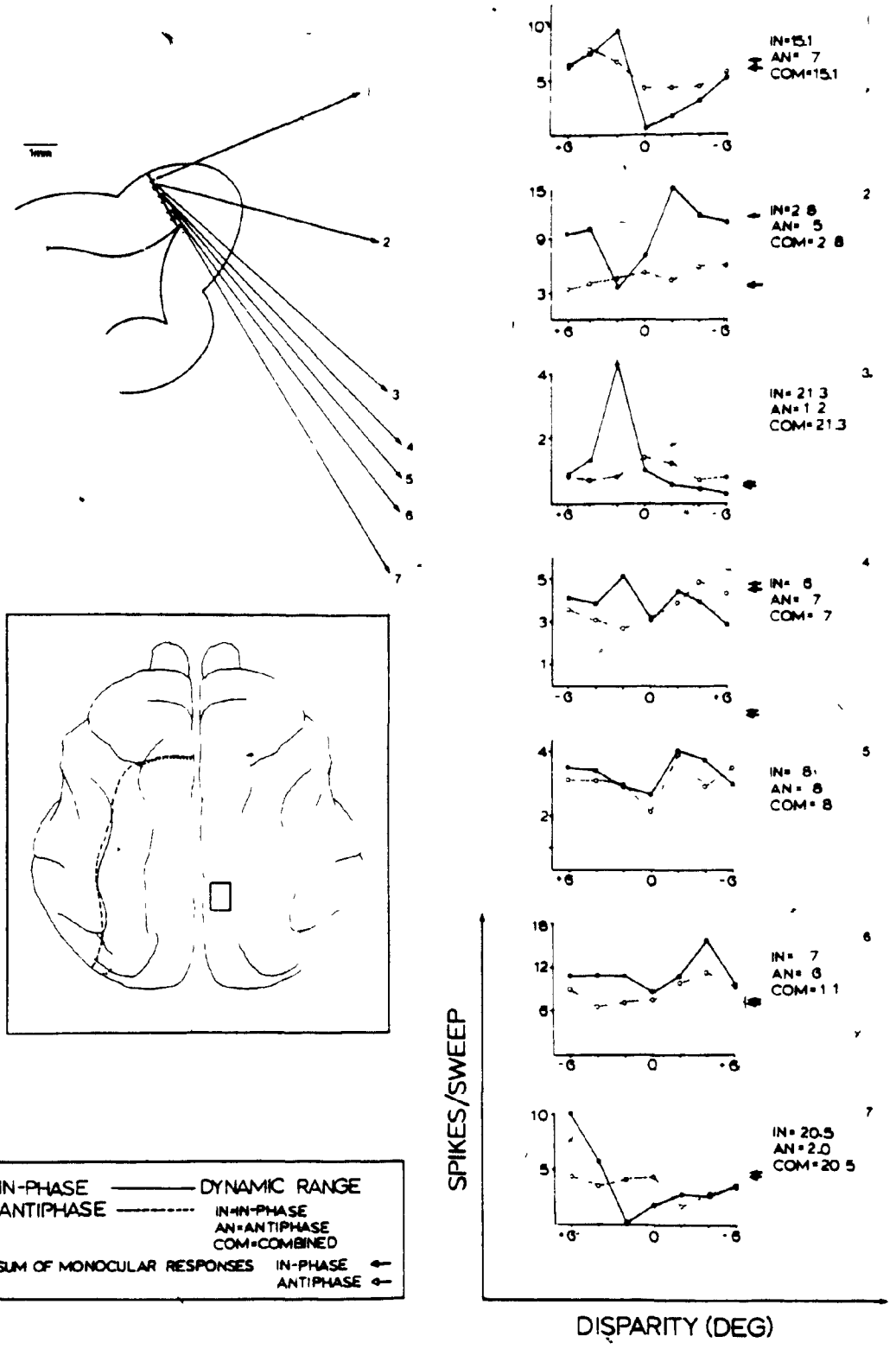
SECTION II

Visual responses in cats with unilateral lesions of the visual cortex

Unilateral ablations of the left visual cortex were performed by supial aspiration in 5 normally-reared adult cats. The lesions were large, including all of areas 17,18 and 19 of the visual cortex, the suprasylvian visual area and invaded the complex of visual areas which have been called the Clare Bishop area (Palmer, Rosenquist and Tusa, 1978). They extended anteriorward as far as the bregma, posteriorally to the tentorium and included most of the marginal gyrus. A reconstruction of the lesions in the 3 cats which were studied with quantitative methods is shown in figure 9. Lesions in two cats were identical (broken line) while that sustained by the third animal (dotted line) was slightly smaller in its lateral extent. It is likely however, that destruction of fibers in this third animal resulted in a functionally similiar lesion to those of the other cats. No differences were seen among the data obtained from the three animals.

Two hundred and thirty units were recorded from 5 unilaterally decorticate cats, and 162 cells in 3 animals were studied quantitatively. The approximate location of eletrode penetrations can be estimated from figure 9. As in normal cat experiments, the angle of the electrode was usually within 10^{o} of perpendicular to the cortical surface. In almost all penetrations receptive fields were located in the lower visual fields, about 5- 10^{o} below the area centralis and within 3^{o} of the vertical meridian. (Stereotaxic coordinates were near AP 0.0, lateral 1-2.) In operated cats, units

FIGURE NINE Electrode penetration in a unilaterally decorticate cat. In lesioned animals, responses were brisk and units showed a variety of binocular interactions, similiar to those seen in normal cats. Some cells showed responses chacterized primarily by either binocular facilitation (#3) or inhibition (#5), while others showed facilitation at some disparities and inhibition at others (#1, 2 and 7). In both normal and decorticate cats, binocular interactions were larger to in-phase (solid line) than to antiphase (broken line) movement. The ocular dominance, cell type, directional charateristics and recording location (depth relative to the cortical surface), of the 7 units shown above were as follows: (1) OD 6, complex, direction selective, 310 micra (2) OD 5, unclassified, direction selective, 493 micra (3) binocular only, direction selective, 548 micra (4) OD 2, complex, direction selective, 815 micra (5) OD 4, complex, non-directional, 1060 micra (6) OD 7, simple, direction selective, 1351 micra (7) OD 7, simple, direction selective, 1520 micra. As illustrated in the insert on the left of the above figure, the lesions in these animals were large, encompassing all of areas 17, 18 and 19 of the visual corex, the suprasylvian visual area and invading the complex of the Clare Bishop area. In this insert, the broken line represents the extent of the ablations in 2 cats and the dotted line, the lesion in the 3rd animal. All electrode penetrations were taken from the region outlined by the solid rectangle in the hemisphere opposite the cortical ablation.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IN-PHASE ——— DYNAMIC RANGE
ANTIPHASE ---------
IN=IN-PHASE
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SUM OF MONOCULAR RESPONSES IN-PHASE
ANTIPHASE
SPIKES/SWEEP
DISPARITY (DEG)

with receptive fields on the vertical meridian were located more medially in the cortex than in normal animals, suggesting mechanical factors had caused the intact hemisphere to shift slightly toward the space vacated by the removed visual cortex.

With qualitative evaluation, responses in unilaterally decorticate cats appeared normal in almost all respects. Units gave brisk responses, displayed orientation and direction selectivity, and their spontaneous and stimulus-locked rates of firing were not obviously different from normal. As shown in table one, the percentage of units displaying strong direction selectivity was the same in both normal and in operated cats (56%). There were however, approximately twice as many non-direction selective cells in decorticate cats (22%) as in normal cats (11%). Thus, there were fewer cells of the "preferential" category in lesioned cats. The ocular dominance histograms for normal and operated cats (figure 8A and 8B) were similiar although decorticate cats showed a slight increase (8%) in cells of OD groups 1 and 7 and a slight decrease (6%) in OD group 4 units. There was no change in the percentage of units in OD groups 2 & 6 or 3 & 5.

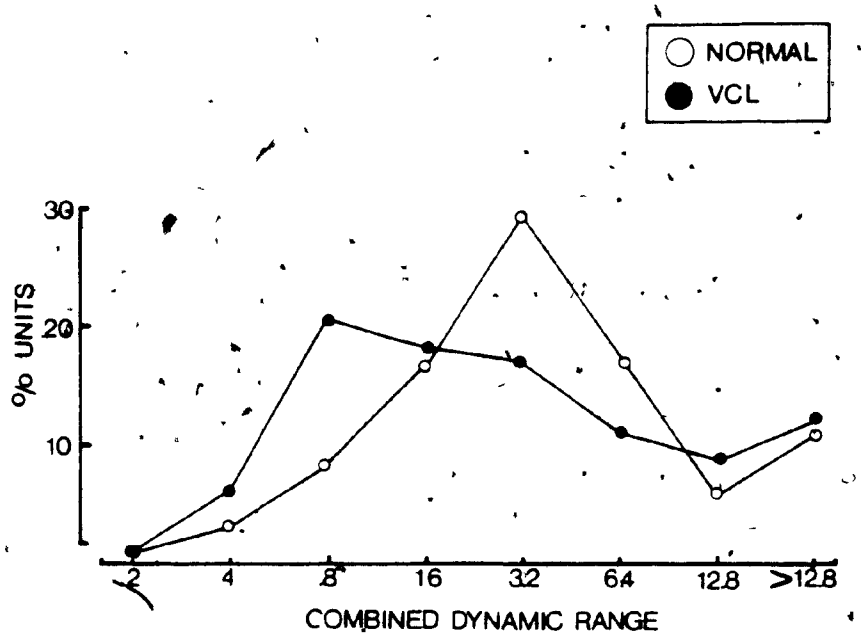
The cortices of all unilaterally decorticate animals appeared to be in excellent condition and many units showed large binocular interactions. A representative penetration through the 17/18 border zone in an operated cat is illustrated in figure 9. On the left is an outline tracing of a coronal section through the cortex showing the reconstructed electrode track. The graphs on the right hand side of this figure show the in-phase and antiphase disparity tuning of 7 of the 14 cells recorded at various depths during this penetration.

Units in the most superficial layers (cells #1-3 of figure 9) showed substantial binocular interactions, with both inhibitory and facilitatory properties. For this penetration, alterations in response rate in most cells were more pronounced for in-phase than for antiphase motion in most cells. In the central layers of the cortex (cells #4-6 of figure 9) binocular interactions were weak, and in general, the firing rate of cells was only slightly modulated by stimuli of varied disparity to either in-phase or antiphase motion. In the deeper layers of the cortex, represented by unit 7 in figure 9, large disparity-specific binocular interactions were again observed.

Dynamic Range

Although many of the units from cats with unilateral lesions showed large binocular interactions, the overall population of cells from these animals showed reduced specificity for stimulus disparity relative to normal cats. A summary of the binocular interactions seen in normal (o) and decorticate (•) cats is shown in figure 10. The three graphs represent the distributions of the dynamic range index for in-phase movement (10B), antiphase movement (10C) and the two movement conditions combined (10A). The combined dynamic range index was the most comprehensive measure of binocular interactions, and it is here that the largest effect was seen. The difference between normal and decorticate cats on this index was significant when the population was considered as a whole (chi square, $p>.01$) or when units found above 1100 micra were analyzed separately (chi square, $p>.01$). There were no significant differences on this index for units found below 1100 micra considered as a group. When the population was

FIGURE TEN Dynamic range of binocular interactions in normal and decorticate cats. The dynamic range index represents the extent to which a unit's firing rate was modulated by stimuli of varying disparity. A dynamic range of 12.8 or greater indicated a very high sensitivity to stimulus disparity while a dynamic range of .8 or less represented a unit which was relatively unselective for the stimulating disparities. These three graphs show the magnitude of the binocular interactions observed in normal (o) and decorticate (●) cats to in-phase (B) and antiphase (C) stimulus motion and across the two movement conditions combined (A). In both preparations, units displayed larger binocular interactions with in-phase than with antiphase movement. On all measures, binocular interactions were less substantial in decorticate cats than in normal cats. This difference reflected a decrease in lesioned cats in the number of cells which showed moderate binocular interactions and a dynamic range index around 3.2, and an increase in the number of units which were unselective for stimulus disparity. When the population was considered as a whole, there were significant differences between the two preparations on the combined dynamic range index (chi square $p>.01$) but not on the indices of in-phase and antiphase dynamic range. There was no real difference between the two preparations in the proportion of units with very large binocular interactions, and the slightly greater number of such units seen in later recorded decorticate cats was attributed to methodlogical improvements in the craniotomy (see methods).


NORMAL
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COMBINED DYNAMIC RANGE

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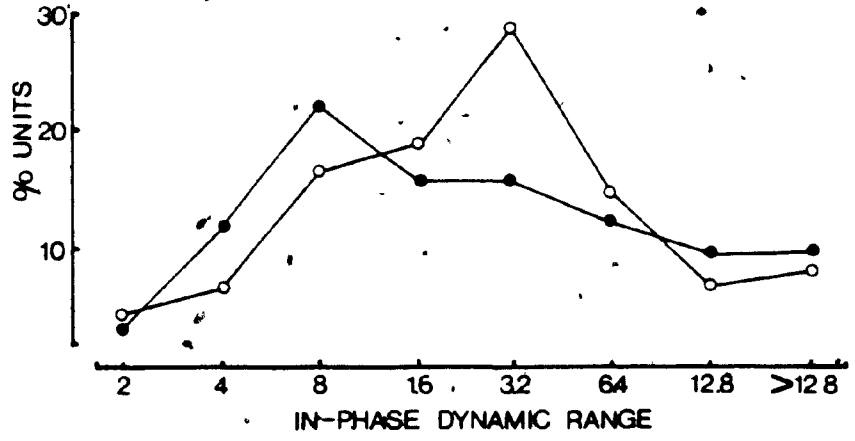
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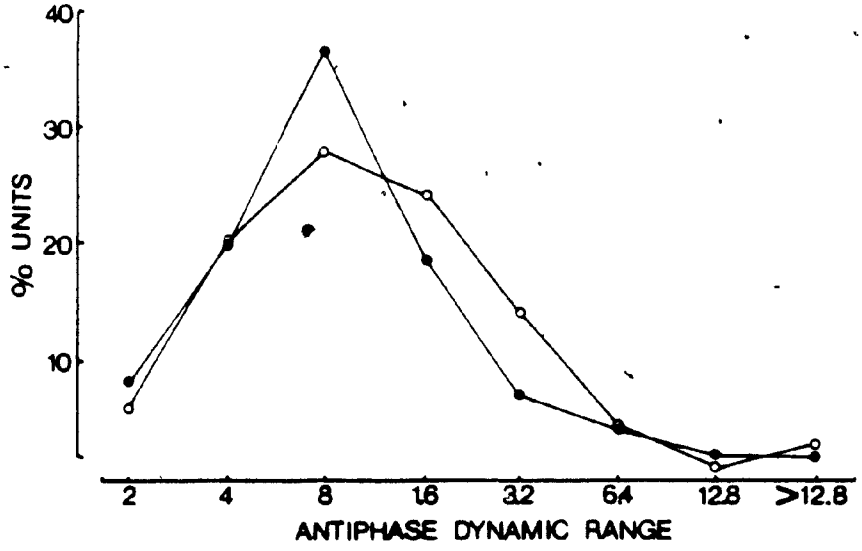
IN-PHASE DYNAMIC RANGE

B.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ANTIPHASE DYNAMIC RANGE

C.

considered as a whole, there were no significant differences between normals and operated cats on either in-phase or antiphase dynamic range. When data from the superficial and deep layers were analyzed separatedly however, a distinct difference was seen between the two praparations in the superficial layers only (figure 11). The in-phase dynamic range of units in the upper cortical layers was significantly (chi square $p>.02$) lower in decorticate cats than in normal animals .

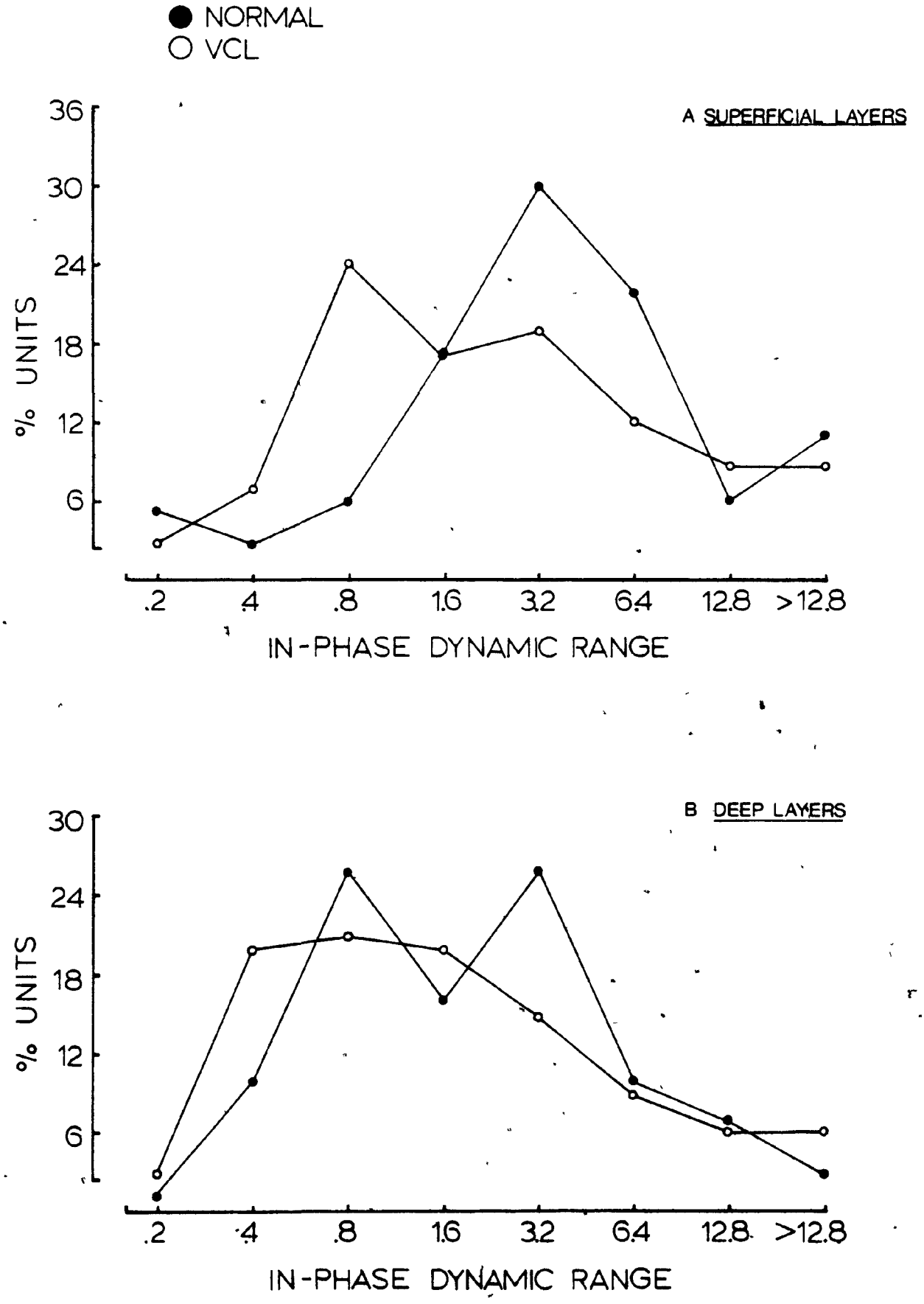
In figure 10A, which shows the combined dynamic range for normal and decorticate cats, three subpopulations of cells could be distinguished: cells with low (less than or equal to .8), moderate (around 3.2) and substantial (greater than or equal to 12.8) binocular interactions. The distribution for decorticate cats peaked at a dynamic range index of .8, a value which represented units showing very little or no binocular interctions. The normal cat population peaked at a combined dynamic range of 3.2, showing many cells with moderate binocular interactions. Both preparations displayed a similar proportion of units with large binocular interactions and a dynamic range index greater than or equal to 12.8. These data suggest that the lesions produced the greatest effet on cells which would have displayed moderate binocular interactions. Decorticate cats showed no change in the proportion of cells with very large binocular interactions, a clear reduction in the number of cells with a moderate dynamic range index and an increase in the number of cells which were insensi[redacted] to stimulus disparity.

As shown in figure 10C, the distribution of the antiphase dynamic range index, in both normal and decorticate cats, peaked at a value of 0.8, indicting that many cells were relatively insensitive to stimulus

disparity when presented with antiphase motion. There was very little difference between the two preparations on this index. In decorticate animals, the distributions of both the in-phase and the combined dynamic range index also peaked at a value of 0.8, showing that many more unselective cells appeared in operated cats than in normal cats. In the superficial layers of normal cats (figure 11A) very few unselective cells were found, and many units displayed moderate levels of binocular interactions. Interestingly, the in-phase dynamic range index for deep layer normal cat units (figure 11B) showed a bimodal distribution. There were two distinct groups of units, those with minimal and those with moderate binocular interactions. Although there was no significant difference between the two preparations amongst deep layer cells, the variation in the shape of the two curves of figure 11B illustrate a consistent trend in the data: that the effects of the lesion were seen throughout the cortex, although these effects were considerably larger in the superficial cortical layers (see also figure 7).

Since units with a combined dynamic range index around 0.8 were relatively insensitive to stimulus disparity, the data presented in figures 10 and 11 indicate that the number of cells with little or no binocular interaction was increased following unilateral ablation of the visual cortex. They also indicate that this effect was considerably larger in the superficial cortical layers. Since both afferent and efferent callosal fibers are known to be more heavily distributed in the superficial cortical layers the occurrence of these unselective cells was examined for layer specificity. Using normal cat data to predict the percentge of unselective units (combined dynamic

FIGURE ELEVEN In-phase dynamic range in the superficial and deep layers of normal and decorticate cats. Differences between the binocular interactions of normal and decorticate cats were more outstanding when units of the superficial and deep cortical layers were analyzed separately. There were no significant differences between the two preparations among deep layer cells on any of the dynamic range indices. For superficially located units, significant differences were seen in both the combined (chi square $p>.01$) and the in-phase (chi square $p>.02$) dynamic range index. The upper graph illustrates that decorticate cats showed a decrease in the proportion of units with moderate binocular interactions (dynamic range 3.2 and 6.4) and an increase in units which were insensitive to stimulus disparity (dynamic range 1.0 or below). In normal cats, the distribution of binocular interactions was bimodal , distinguishing a group of disparity-insensitive units from units with moderate binocular interactions. In the deep layers of lesioned cats, this distribution was shifted toward the low end of the dynamic range index, reflecting a pattern of change similiar to that seen in the superficial cortical layers. Although the differences in the deep layers of normal and decorticate cats were not significant (chi square), the trend seen on this and other measures indicates that the effects of the lesions could be detected throughout the cortex even though they were considerably larger in the superficial cortical layers.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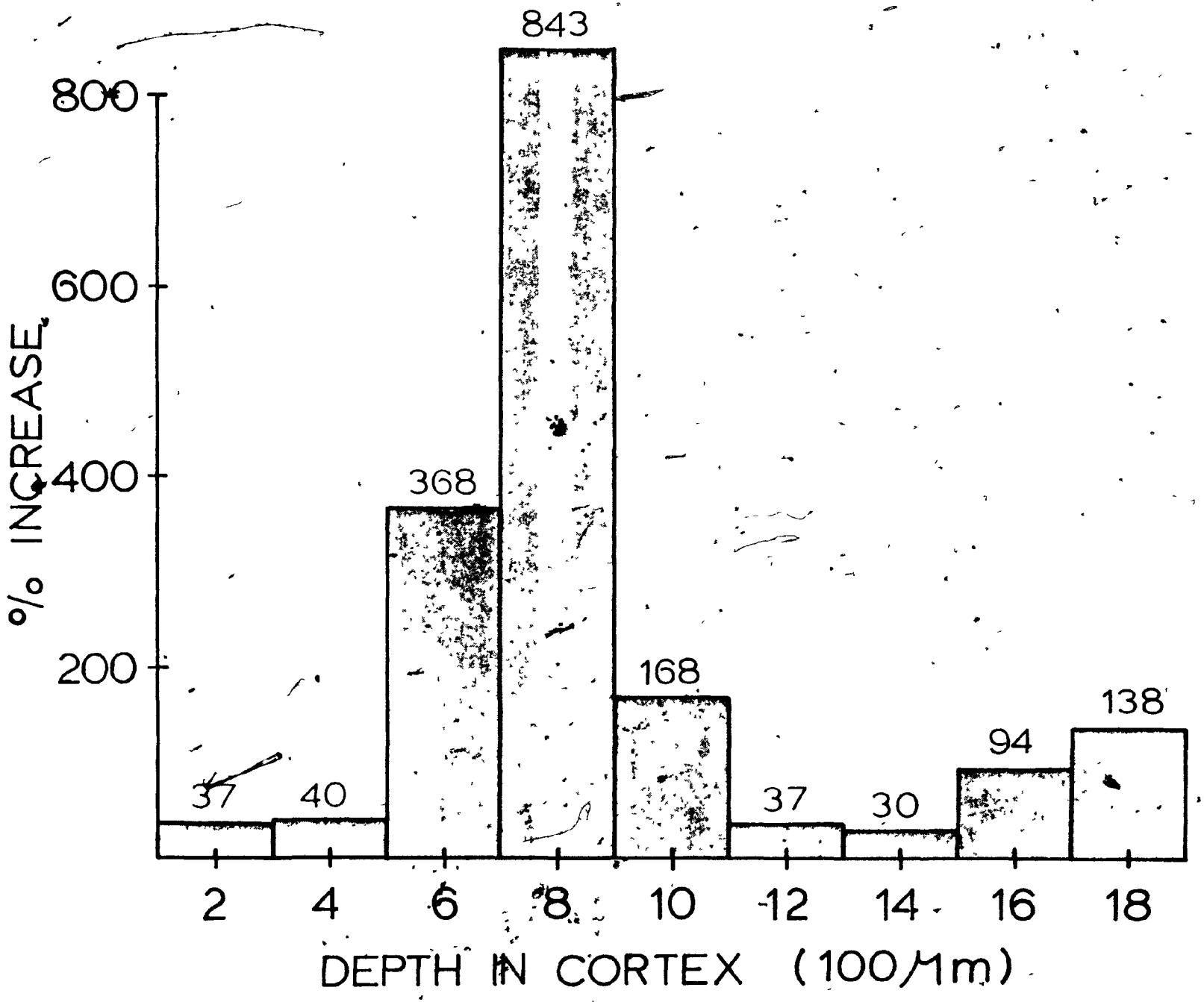
range less than 2.0) which one would expect to find at any particular cortical depth, the % increase in unselective cells in decorticate cats was calculated from the frequency with which such cells were encountered at specific depths in normal cats. These data are shown in figure 10, where the % increase in unselective cells seen in decorticate cats is plotted against depth in the cortex (hundred micra) relative to the cortical surface (zero). Judging from the location of geniculate afferents encountered electrode penetrations and the position of units relative to the surface of the cortex and the white matter, it was estimated that a depth of 800 micra from the cortical surface represented layer III. Figure 12 dramatically illustrates that at this depth, decorticate cats showed a large increase in the proportion of units which were unselective for stimulus disparity. The region where the largest effect was seen extended for about 400 micra, from a depth of 600 to 1000 micra below the cortical surface. There was little change in the proportion of unselective cells at the very top or in the middle of the cortex. Some increase in unselective cells was seen at the bottom of the cortex (1600 micra and below) but this effect was small relative to the effect seen in the superficial cortical layers.

Binocular inhibition and facilitation

In decorticate cats, binocular inhibition was clearly stronger to stimuli moving in-phase than in antiphase, and there were no differences seen between the two preparations on the index of binocular facilitation. This is illustrated in figure 5, which shows the distributions of the in-phase and antiphase indices of binocular inhibition (5B) and facilitation (5D) in normal (upper graphs) and

FIGURE TWELVE Increase (%) in decorticate cats in cells insensitive to stimulus disparity as a function of cortical depth. At particular depths in the cortex, decorticate cats showed a substantial increase in the number of cells which were insensitive to stimulus disparity. The magnitude of these effects corresponded well with the density of known callosal projections. The large effect seen around 600-1000 micra is estimated to encompass layer III and upper layer IV, while the smaller effect at the bottom of the cortex appeared around layer VI.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DEPTH IN CORTEX (100/1m)

decorticate (lower graphs) animals. Each pair of distributions, regardless of preparation or movement condition, were similiar in shape, range and variance. The two facilitatory distributions were clearly overlapping, but the mean of the in-phase inhibitory distribution was distinctly lower than that of the antiphase inhibitory distribution-a relationship which was seen in both normal and decorticate animals. Differences between the two preparations on this index and on the combined index of inhibition and facilitation were not significant. These indices however, suggested that the reduction in combined dynamic range seen in decorticate cats was due principally to a reduction in the strength of binocular inhibition.

Characteristics of disparity sensitive cells

In decorticate cats, units with large binocular interactions (combined dynamic range greater than 6.5) were in all respects similiar to those cells seen in normal cats. In addition to being found more frequently in the superficial cortical layers, they were usually driven unequally by the two eyes and they were strongly direction selective. Units showing little binocular interaction (combined dynamic range less than 2.0) however, differed in two respects from those observed in normal cats: their cortical location and their ocular dominance. In lesioned cats, cells insensitive to stimulus disparity were less often driven equally by the two eyes than were such cells in normal cats. Also in contrast to normal cats, where most unselective cells were found in the lower half of the cortex, decorticate cats showed a large concentration of unselective cells in the superficial cortical layers (see figure 12).

Cortical location

Of the units displaying high sensitivity to stimulus disparity, 74% were found above a depth of 1100 micra from the cortical surface. A number of these cells were seen at the very top of the cortex as the data of figure 6 suggest. As previously described, figure 6 shows the average combined dynamic range of units recorded at specific cortical depths, in both normal and decorticate cats. In both preparations, average dynamic range was high near the surface of the cortex and then dropped to a low value at a depth of 1100-1300 micra below the cortical surface. At the very top of the cortex, binocular interactions in decorticate cats were actually larger than in normal cats. This difference however, is probably not due to the lesion but to methodological improvements in the craniotomy (see methods) which resulted in less damage to the cortical surface of the later-recorded decorticate cats. Despite some variability however, certain regularities can be seen in the data from the two preparations. In both normal and decorticate cats, average combined dynamic range was high within the first 600 micra, dropped off at a depth of 1200 micra and than rose again to a moderate level around a depth of 1500 micra in the deep cortical layers. In contrast to normal cats however, decorticate animals showed a distinct decrease in mean dynamic range at two depths. A large difference between the two preparations was seen in a region extending from about 600-1100 micra, and again at the very bottom of the cortex, around 1600-1800 micra, a second, although considerably smaller effect appeared. As table 2 indicates, the reduced binocular interactions in decorticate cats ment that , unlike normal cats, these animals showed no difference between the dynamic

range of units in the superficial and deep layers. Since lesions were not made after every electrode penetration, some uncertainty is associated with the identification of each depth with a given cortical layer. Nevertheless, by noting the location at which geniculate afferents were encountered during electrode penetrations, and taking advantage of the fact that all penetrations were made in a uniform manner, perpendicular to the cortical surface, it is highly likely that this 600-1100 micra zone represents cortical layer III and upper layer IV. In normal cats, this region is the site of the heaviest termination of callosal fibers . The site of the smaller effect seen at the bottom of the cortex also corresponds to known callosal projections (Jocobson and Marcus, 1970; Shatz, 1977; Innocenti, 1980), for fibers of the corpus callosum project to layer VI of the opposite visual cortex, terminating less densely in this region than in the superficial cortical layers.

Ocular dominance

In both normal and decorticate cats, units which were highly sensitive to stimulus disparity were generally either strongly dominated by one eye (OD groups 1,2,6 and 7) or were driven poorly with stimulation through either eye alone (binocular only). Figure 8 shows the ocular dominance distribution of highly sensitive cells (combined dynamic range greater than 6.1) for the 17/18 border of normal cats and cats with unilateral decortications. The two distributions are similar in that they both show that relatively few highly sensitive cells were driven equally by the two eyes. In normal cats, only 20% of the units were in OD groups 3,4 and 5 and in

decorticate cats, only 23% of the cells were similarly classified. Units which were insensitive to stimulus disparity (combined dynamic range less than 2.0) however, tended to be activated well through either eye. Sixty-eight percent of the unselective cells in normal cats were from OD groups 3,4 and 5, as were 57% of the unselective cells in decorticate cats. Nevertheless, a distinct difference between the two preparations was seen in the number of "monocular" cells which were found to be insensitive to stimulus disparity. In normal cats, units in OD groups 1 and 7 all showed some sensitivity to stimulus disparity, whereas in decorticate cats, fully 18% of the unselective cells were classified as OD group 1 or 7.

In normal cats, cells in OD groups 1 and 7 generally showed large binocular interactions. This can be seen in figure 13, where the eight histograms represent the combined dynamic range index for normal (upper histograms) and decorticate cats (lower histograms) as a function of ocular dominance. Dynamic range is plotted on the abscissa, while the number of units is shown on the ordinate. From left to right the histograms represent units in OD groups 1 & 7, 2 & 6, 3 & 5 and 4. As the data indicate decorticate cats showed an increase in the number of units which were insensitive to stimulus disparity; an increase (20%) which was seen in cells of all ocular dominance groups. There was no change in any OD category in the proportion of cells which showed very large binocular interactions. In table 2, the average combined dynamic range index is shown for normal and decorticate cats as a function of ocular dominance group and cortical location. Ocular dominance groups 1 & 7, 2 & 6, 3 & 5 and 4 are as represented on the left side of this table, and distinctions between the two preparations and cortical locations are

FIGURE THIRTEEN Combined dynamic range in normal and decorticate cats as a function of ocular dominance. In both normal and decorticate cats, there was a consistent and orderly relationship between the magnitude of a unit's binocular interactions and its ocular dominance (OD). The more biased a unit was toward one eye, the stronger were its binocular interactions. Units which were largely dominated by one eye, OD groups 1 & 7, showed the most substantial interactions, followed by units in OD groups 2 & 6, 3 & 5 and then OD 4. Across all ocular dominance groups, decorticate cats showed an increase in the number of units which were insensitive to stimulus disparity (combined dynamic range less than 2.0) , and very little difference in the proportion of units which displayed very large interactions (combined dynamic range greater than 10.0). Although units in all OD groups were effected by the cortical lesions, the appearance of a large number of disparity-insensitive units among cells of OD groups 1 & 7 was particularly striking, for in normal cats, these neurons reliably show substantial disparity-sensitive binocular interactions.

TABLE TWO Mean combined dynamic range as a function of ocular dominance group and cortical region. In normal cats, units in the superficial cortical layers showed more substantial binocular interactions than units in deep layers; in both regions, a direct relationship was seen between a unit's ocular dominance and the magnitude of its dynamic range. The more strongly biased a unit was toward one eye, the larger were its binocular interactions. Differences between normal and lesioned cats were minimal in the deep layers and quite substantial in the superficial cortical layers. In decorticate cats, superficially located cells showed a decrease in mean dynamic range across all ocular dominance groups, with the greatest drop seen among the "monocular" cells of OD groups 1 and 7. In contrast to normal cats, decorticate animals had a similiar mean dynamic range in both superficial and deep layer cells, lesioned cats did however show the normal relationship between dynamic range and ocular dominance.

	SUPERFICIAL LAYERS		DEEP LAYERS.	
OD GROUP.	NORMAL	VCL	NORMAL	VCL
1 AND 7	11.2	5.4	5.2	5.3
2 AND 6	6.2	3.2	4.9	4.0
3 AND 5	4.1	3,2	3.1	2.8
4	3.2	1.1	1.3	1.1

as indicated on top. These data show that, in normal cats: 1) binocular interactions were larger in the superficial than in the deep cortical layers and that 2) the more "monocular" cells displayed the largest binocular interactions. They further illustrate that the differences in combined dynamic range of normal and decorticate cats were 1) larger in the superficial than in the deep layers and that 2) effects were seen in units of all OD groups. Nonetheless, it was certainly the case that the drop in combined dynamic range was most dramatic in cells of OD groups 1 and 7. This does not imply however, that these "monocular" units were most strongly affected by the decortication, but rather, reflects that in normal animals, cells of OD groups 1 and 7 were rarely unselective for stimulus disparity. In decorticate cats, units in OD groups 1 and 7 which were disparity-insensitive were most striking, for they represented a distinct subset of monocular cells, a type of unit rarely encountered along the 17/18 border of normal cats.

Direction selectivity and cell type

As in normal cats, units in decorticate cats which were highly sensitive to stimulus disparity also showed strong direction selectivity. Of the group of cells with large binocular interactions (top 25% of the population), 73% were directionally selective and only 17% were non-directional. Thirty-one percent of the relatively insensitive cells (bottom 25% of the population) were direction selective and 35% were non-directional. Units which were direction selective also displayed a larger combined dynamic range. This can be

seen in table 1, which shows the average combined dynamic range for units which were directionally selective, non-directional and for those with a directional preference, in both normal and decorticate cats. The bottom two rows of table 1 indicate the frequency with which each type of unit was found in the two populations. The data show very little difference in directionally selective units of normal and decorticate cats, either in their frequency or their mean dynamic range. In operated cats, there appeared to be a decrease in the proportion of units with a directional preference and an increase in non-directional cells. Correspondingly, the largest drop in mean dynamic range in operated cats was seen in the population of directionally-preferential cells.

The relationship between cell type and binocular interactions in decorticate cats was also similar to that seen in normal cats. Although all cell types were represented in each group, more simple cells were seen among the units showing large interactions and more complex cells among the units with little binocular interaction. Of units in the upper quartile of the combined dynamic range index, 34% were simple cells and 25% were complex cells. Of the group with small binocular interactions, 14% were simple cells and 81% were complex cells. The large number of complex cells among the group of unselective units suggests that these cells were most strongly affected by the cortical lesions.

Summary

Binocular interactions in cats with unilateral lesions of the visual cortex were reduced relative to those in normal cats. The differences seen in combined and in-phase dynamic range between the two preparations were significant only in cells found in the superficial cortical layers. No significant changes were seen among deep layer cells. Although no one component-inhibition or excitation-of the binocular response was exclusively responsible for these changes, the data suggested that binocular inhibition was more strongly affected by the decortication than was binocular facilitation.

The principle effect of the lesion was to produce an increase in number of cells encountered which were insensitive to stimulus disparity. These cells appeared primarily in two cortical locations. A large increase in the proportion of unselective cells occurred around layer III and upper layer IV and a small increase was seen at the bottom of the cortex, around layer VI. These regions correspond well to the known terminations of callosal fibers. These unselective cells were found in all ocular dominance groups but their appearance was most striking among cells of OD groups 1 and 7, for in normal cats, these cells generally show very large binocular interactions. Decorticate cats also showed a decrease in the number of cells which displayed moderate binocular interactions, a type of interaction which characterizes complex cells more so than simple cells, and cells driven nearly equally by the two eyes (OD groups 3-5) more so than cells strongly dominated by one eye. Decorticate cats also showed a decrease in the proportion of cells which displayed a directional

preference although there was no change among cells showing strong direction selectivity. The data thus suggest that the type of unit most likely to have been affected by the unilateral decortication were complex cells in the superficial cortical layers, which showed a directional preference, and exhibited moderately large binocular interactions.

DISCUSSION

Disparity specific interactions in normal cats

The role of facilitation vs inhibition in the generation of in-phase and antiphase selectivity near the border of area 17 and area 18

In normal cats, fully 80% of the units encountered along the 17/18 border displayed sensitivity to the retinal disparity of binocularly-presented visual stimuli. This high level of sensitivity, which is comparable to that observed in the striate cortex of the awake, behaving monkey (Poggio and Fischer, 1978; Poggio and Talbot, 1981), suggests that disparity processing is a major activity of visual cortical neurons and is consistent with recent behavioral findings indicating that one of the most clear-cut consequences of visual cortex removal in the cat is a loss of stereoscopic capacities (Kaye, Mitchell and Cynader, 1981).

The characteristics of the disparity sensitive responses observed in individual neurons were rich and varied. Some cells displayed large facilitation or deep inhibition only when activated with sideways moving stimuli (in-phase motion), while showing little or no binocular interaction for stimuli moving in depth (antiphase movement). Other cells responded in the opposite fashion, or exhibited clear disparity-specific interactions in both movement conditions. Some units gave a response which was dominated primarily by either binocular facilitation or inhibition while others displayed complex interactions, showing facilitation at some disparities and inhibition at others. A wide variety of "symmetric" and "asymmetric" and complex tuning curves were seen in both movement conditions including each of

the 4 types described by Poggio and coworkers in the monkey (1978,1981) and Fischer and Kruger (1978) and Ferester (1981) in the cat.

Overall, binocular interactions were more common to stimuli moving sideways at different disparities than to stimuli moving in depth. This difference between in-phase and antiphase responses has also been observed in the monkey (Poggio and Talbot, 1981). Whereas 18% of the units encountered in this study displayed large interactions with in-phase stimuli, only 4% showed comparably large interactions with antiphase stimuli. Nonetheless, although the number of units showing substantial antiphase interactions was not high, many cells did display clear sensitivity to retinal disparity when activated with stimuli moving either toward or away from the animal. For the most part though, this to-fro stimulus motion evoked only moderate levels of modulation in firing rate.

In the present experiment, the frequency with which units were encountered which showed at least some degree of antiphase disparity sensitivity was higher than in the monkey striate cortex (Poggio and Talbot (1981). It is possible however, that a greater degree of antiphase disparity tuning was revealed simply because the present procedures employed a wider range of stimulus disparities . Since the disparity tuning of cat visual cells is broader than that of the monkey, responses here were examined over a range of plus/minus 6^{o}; whereas the range used in the monkey was usually around plus/minus 1^{o}. Since in both cat and monkey, antiphase responses exhibit a broader tuning profile than in-phase responses, it could be that by using a wide range of stimulus disparities indvidual units showed evidence of

antiphase tuning that would show very little disparity-specificity over a range of only a few degrees. This conclusion is consistent with a possible function of such a motion-in-depth system and with evidence from human psychophysics (Regan, Beverly and Cynader, 1979). If the antiphase system serves to alert the organism to the possibility of an impending collision with the stimulus, then it need not necessarily provide extremely precise information about the location of the stimulus in depth. In fact, there is good (psychophysical) evidence that sensitivity to the direction of stimulus motion occurs even with very large stimulus disparities, well outside the range of fine stereopsis. The use of a broad range of stimulus disparities for testing may thus have enabled the identification of a larger population of antiphase-selective neurons than would be found with tests restricted to a narrow range of disparities.

Despite these considerations, it was clearly the case that sensitivity to stimulus disparity was much more pronounced when tested with in-phase than with antiphase stimulus motion. Whereas, even over the broad range of disparities examined, almost half of the cells in normal cat appeared to be relatively unselective for stimuli presented with antiphase movement, only 20% of the units failed to show some sensitivity to in-phase stimulus disparities. The most striking of the disparity sensitive units was that group of cells which responded with very large facilitations and inhibition over a limited range of in-phase disparities. These units were dramatic in their appearance and have been the object of attention of many others (Nikara, Bishop and Pettigrew, 1968; Joshua and Bishop, 1970; Hubel and Wiesel, 1970; von der Heydt, Adorjani, Hanny and Baumgartner, 1978). Units showing

extremely large binocular interactions to antiphase stimulation were however, only rarely encountered (an example is shown in Fig 3D) and thus it was somewhat surprising to find, after detailed analysis, that the only difference between binocular interactions to in-phase and to antiphase stimuli was in the strength of binocular inhibition. Whereas the chance of evoking the maximum response from a unit was the same for both in-phase and antiphase motion, it was highly likely (85% of the time) that the minimum response would be evoked by sideways motion at a given disparity rather than with antiphase motion. In-phase and antiphase binocular interactions were thus distinguished by deep, direction selective inhibition seen in the preferred direction of motion.

The above data emphasize the role played by binocular inhibition in determining the disparity sensitive response of normal cat visual neurons, and suggest that inhibitory binocular interactions are important in the processing of disparity specific visual information. This notion has recently received support from both human psychophysical studies (Ruddock and Wigley, 1976; Ruddock, Waterfield and Wigley, 1979), and from a previous study of binocular interactions in strabismic cats (Cynader, Gardner and Mustari, 1979). These cats, made strabismic early in life, have been shown to have stereoscopic capacities which are much reduced (Kaye, Mitchell and Cynader, 1982). Studies of cortical area 18 in such animals revealed that binocular interactions in normal and strabismic cats differ only in the strength of binocular inhibition with little or no change in levels of binocular facilitation. These data indicate that in the determination of disparity specific responses, it is binocular

inhibition which is the crucial process. Since a unit's selectivity for stimulus disparity can be modified by early experience (Skeler, 1971; Gardner, 1979) the above observations suggest a significant role for inhibitory neurotransmitters in both the developing and normal visual cortex.

The location and properties of disparity sensitive cells

In normal cats, large binocular interactions were consistently found in the superficial cortical layers, often among units located directly below the cortical surface. When responses from the superficial and deep layers were compared, the binocular interactions of superficially located cells were consistently found to be larger. Although this difference could not be attributed solely to one component of the binocular response, the major distinction between superficial and deep layer responses was seen in the strength of binocular inhibition. In the middle layers of the cortex, at a depth of about 1100-1300 micra, a number of units were found which were relatively insensitive to stimulus disparity. In the deeper cortical layers, below 1500 micra, units were again encountered which showed substantial binocular interactions. These cells with large disparity interactions were often found at the very bottom of the penetration--not uncommonly being the last cells in the pass. In contrast to many of the surrounding units, these units clearly distinguished themselves as being disparity sensitive. Since there is known to be a projection from cortical layer VI, back to the LGNd, it is possible that these cells play a role in a cortico-geniculate feedback loop which modulates the transmission of disparity specific information through

the LGNd to the visual cortex (Schmielau and Singer, 1977). In this context it is interesting to note that recent evidence indicates that cortico-geniculate projection neurons of layer 6 send a recurrent collateral back to geniculo-recipient cells in layer IV (Baughman and Gilbert, 1980). Accordingly, layer 6 cells may be involved in the generation of binocular inhibition and facilitation which is seen at the level of the LGNd (Suzuki and Kato,1966; Singer, 1970; Sanderson, Bishop and Darian-Smith, 1971) and/or it may provide disparity specific information which causes the first-order cortical cells of layer 4 to be binocularly tuned. Since almost all of the units which were insensitive to stimulus disparity were also driven well by either eye (OD groups 3,4 and 5), it seems unlikely that they represented first order cells of layer IV, as these neurons are known to be highly monocular with conventional testing (Shatz and Stryker, 1976). Indeed, in normal cats, very few of the unselective cells came from OD groups 1 and 7. This observation points to the possibility that the first-order cortical cell of layer IV might show sensitivity to binocular retinal disparities. Detailed studies involving electrical stimulation of the LGN would be required to establish this point, but the present data as well as that of Poggio and Fischer (1978) and Poggio and Talbot (1981) who found few unselective units in monkey striate cortex are consistent with the notion that these layer 4 geniculo-recipient cells do in fact, show disparity specific tuning. The question of disparity specificity in first-order cortical neurons has received little attention and is a problem which clearly warrants further study.

One of the most consistent and orderly relationships observed in normal cats was that between a unit's degree of binocular excitatory

convergence and the magnitude of it's binocular interactions. In short, the more biased a unit appeared toward one eye, the more substantial were it's binocular interactions. This was true for units whose interactions were characterized by binocular inhibition as well as units whose primary binocular component was facilitatory. It is interesting to note that neurons which would be considered to be "monocular" with conventional testing procedures, are the very cells which show the largest binocular interactions. These data are in direct contradiction to the notion that "highly binocular cells" such as those in ocular dominance groups 3-5 are for "seeing with 2 eyes" while those in OD groups 1 and 7 are for monocular viewing. Clearly cells of all OD groups must play a role in binocular vision.

How units in different ocular dominance groups relate to one another in contributing to the sensation of depth is not clear at this time. However, the observation that such a clear and consistent relationship has been found between ocular dominance and binocular interactions suggests that the mechanism for stereoscopic depth perception has an anatomical substrate in the ocular dominance columns of Hubel and Weisel. It may be, for instance, that the cells showing the strongest binocular interactions are located at the center of ocular dominance columns of one eye or the other, while cells less concerned with disparity processing occur at the borders. The notion that disparity systems are reflected in the ocular dominance columns of cat visual cortex, is also consistent with the formulation of Gardner (1977) and Cynader, Gardner and Douglas (1978) and the organization of a proposed time based mechanism for stereoscopic depth perception. This formulation, as well as the present data, emphasize

the role of direction selectivity in the determination of disparity-sensitive responses and have led to the prediction that stereoscopic capacities in strobe-reared cats, animals which lack direction selectivity (Cynader and Chernenko, 1976), should be significantly degraded.

Comparison with other studies

Although the sensitivity to stimulus disparity observed among cells in the present study was comparable to that seen in the primate (Poggio and Fischer, 1977; Poggio and Talbot, 1981), a substantially greater degree of selectivity was seen here than in two other recent studies of binocular interactions in cat visual cortex (von der Heydt, Adorjani, Hanny and Baumgartner, 1978; Ferester, 1981). In contrast to the present study where 78% of the units showed at least some sensitivity to stimulus disparity, von der Heydt et al. (1978) found that only 10-20% of the units, and Ferester (1981), that only 37% of the units encountered were selective for stimulus disparity. Although the reason for these discrepencies is unclear, possible sources of variabilty include, differences in the cortical areas studied, procedures and/or criteria. This study was conducted on the 17/18 border whereas the previous studies involved area 17 (von der Heydt et al, 1978; Ferester, 1981) or area 18 (Ferester, 1981). We have found (Gardner and Cynader, 1980) that binocular interations are more substantial along the 17/18 border than in area 18 although a comparison has not yet been made between the 17/18 border and area 17. In the present analysis, nonlinear responses, both inhibitory and excitatory were considered in the calculation of binocular

interactions . A unit was considered to be disparity-sensitive if its tuning curve showed an orderly modulation in firing rate across the disparities tested. Since, in almost all cases, units with a dynamic range of 2.0 or above fulfilled this criteria, this value was taken as a cut-off in categorizing unselective cells. In the studies of von der Heydt (1978) and Ferester (1981) the proportion of disparity-sensitive cells was calculated on the basis of a unit's tuning curve profile and based on a measure of binocular facilitation only. In contrast to the approach used here, these authors would have considered units showing only inhibitory interactions to be disparity-insensitive. Additionally, in the experiments of both von der Heydt (1978) and Ferrester (1981) stimuli were presented in an uninterleaved manner which was considerably more time consuming than the procedures used in the present experiment. In the present study stimuli were always presented in an interleaved fashion and a unit's disparity profile could be generated within 3-15 minutes, in contrast to, for example, 2-3 hours (Ferester, 1981). It is possible that the procedures used in the present study helped to reduce variability in the data and to reveal small interactions which otherwise would not have been apparent.

A second discrepancy between the present results and those of recent studies (Fischer and Kruger, 1979; Ferester, 1981) involves the reported relationship between a unit's ocular dominance and the shape of it's disparity tuning curve. These studies claimed that units with "unbalanced ocularity" (OD groups 1,2,6 and 7) had tuning curves which were asymmetric around zero disparity, and were thus "tuned" for either crossed or uncrossed, non-zero disparities (Ferester, 1981;

Fischer and Kruger, 1978) Units with balanced ocular input (OD groups 3,4,5 and binocular only cells) were said to be symmetric about, and thus tuned to around zero disparity. In the present study, a variety of disparity tuning curves were observed in units of all ocular dominance groups, a finding in agreement with that recently seen in the monkey (Poggio and Talbot, 1981).

The fact that moving stimuli were used for disparity measurements, and that cells were not tested for their sensitivity to interocular delay makes it impossible to say whether units which were strongly dominated by one eye had tuning curves which were offset from zero disparity. In previous experiments which utilized flashed, stationary stimuli, we have found that cat visual neurons are sensitive to both the spatial and temporal characteristics of binocular stimuli (Gardner and Cynader, 1977; Cynader, Gardner and Douglas, 1978, Gardner 1979). Cells were shown to be sensitive to interocular delays as small as 1 millisecond, indicating a level of temporal sensitivity on the order of what has been shown for neurons in the auditory system (Kitzes, 1978). Response latencies of units strongly dominated by one eye were different through the 2 eyes, and the latency through the dominant eye was consisently shorter. Cells driven equally through the two eyes had equal response latencies through each eye. Since the strongest response is elicited from a cell when the input from both eyes reaches the cortical cell at the <u>same</u> time the use of moving stimuli in the calculation of binocular spatial disparities confounds the variables of space and time, and can make a temporally based response appear as an apparent spatial disparity. Since cells most strongly biased toward one eye have been shown to have the largest interocular latency differences, a confound

of space/time variables would have the effect of selectively shifting the tuning curves of the "ocular unbalanced" cells away from zero, while having no effect on the tuning curve of a unit driven equally by the two eyes. In this situation data similar to those described by Fischer and Kruger (1978) and Ferester (1981) would be predicted. At this time therefore, it must be concluded that the question of whether units strongly dominated by one eye display tuning curves which are off-set from zero, remains unanswered. However, in previous studies of temporal tuning in cat cortical cells, we have found that units strongly dominated by one eye do respond best at a particular non-zero interocular delay and on this basis have proposed (Gardner and Cynader, 1977; Cynader, Gardner and Douglas, 1978) that these cells code specific non-zero temporal disparities. On a theoretical basis therefore, our ideas as to the function of cells strongly dominated by one eye are in alignment with those of both Fischer and Kruger (1978) and Ferester (1981).

Binocular Interactions after unilateral decortications

Cats with unilateral lesions of the visual cortex showed a clear reduction in disparity specific binocular interactions in neurons of the 17/18 border of the opposite visual hemisphere. These data indicate that the corpus callosum contributes significantly to the binocular responses of visual cells and support the findings of previous investigators (Choudhury, Whitteridge and Wilson, 1965; Berlucchi and Rizzolatti, 1968; Cynader, Dobbins, Gardner, Lepore and Guillemot, 1979) that this commissural pathway is an effective route for the transfer of visual information across the two sides of the brain.

In decorticate cats, unit reponses were brisk and in almost all respects reminiscent of responses in normal cats. Comparing normal and lesioned cats, no differences were seen among units which showed very large binocular interactions. These cells were generally encountered in the superficial cortical layers, were strongly dominated by one eye and usually direction selective. In both preparations these units represented about 20% of the cells and were characterized by strong disparity sensitive responses, often with deep inhibition and/or facilitations. Thus, their presence in decorticate cats was unmistakable, particularly by contrast with the sparcity of cells with "moderate" binocular interactions. These latter cells appeared to be the ones most strongly effected by the lesion. In normal cat, these units are more frequently complex cells than simple cells and as a group, tend to be non-direction selective or to show a directional preference rather than strong direction selectivity. Across the normal and decorticate cat preparations there was no change in the proportion of units which were directionally selective but the number of units with a directional preference was decreased, coupled with an increase in nondirectional cells. These data raise the possibility that units which formerly showed a directional preference were rendered nondirectional by the cortical lesion. Given that changes were observed primarily in the superficial cortical layers, the data suggested that the type of unit most likely to have been affected by the lesion was a superficially located Cx cell, with moderate binocular interactions and a preference for one direction of stimulus motion.

The primary effect of the cortical lesions was the generation of a large number of cells which were insensitive to stimulus disparity. These units were found mostly in the superficial cortical layers, around the border between layers III and layer IV, and a small number appeared at the very bottom of the cortex, around layer VI. The location of these cells and the relative size of the two effects very nicely mimicked the location and density of the known callosal projections in cat visual cortex. This projection undoubtedly exerts a powerful influence on the binocular responses of neurons along the 17/18 border for although only a relatively small proportion of units appeared altered by the lesions (20%), these differences were significant even when the population was considered as a whole. Whereas in normal cats, binocular interactions were substantially larger in the superficial cortical layers, interactions in decorticate cats were of similar magnitude in both the superficial and deep layers. There were however, no significant effects found in the deeper layers, although consistent trends in the data suggested that at least small changes occurred throughout all cortical layers. Although no one component of the binocular response showed significantly large changes, the data suggested that in decorticate cats, binocular inhibition was more strongly effected than binocular facilitation. This probably reflects the fact that in normal cats, inhibitory binocular interactions play a very large role in determining the disparity sensitive response. The action of the corpus callosum need not be inhibitory in and of itself, but may function to activate local inhibitory circuits within the visual cortex.

Although the type of neuron which sends its axon across the corpus callosum has recently been characterized (Harvey, 1980; Hornung

and Garey, 1980; Innocenti, 1980) much less is known about the callosal recipient cells. In the visual cortex, callosal projection cells are found along the border of layers III and IV, have been identified as being pyramidal in shape and frequently complex in type. Given the location and the characteristics of units effected by the decortications the data suggest that callosal neurons have a strong influence on homotypical cell types in homotopical locations in the opposite visual cortex. The view that the callosal recipient cells are also likely to be complex in type is one which has recently been expressed by Innocenti (1980). Interestingly, in observations which are consistent with the findings of the present study, he has concluded that these post-callosal complex neurons have properties which are similar to those predicated for inhibitory interneurons of area 17.

In principle, the data of the present experiment agree with the findings of Payne, Elberger, Berman and Murphy (1980) and Zeki and Fries (1980), that the corpus callosum lends "binocularity" to cat visual neurons. However, in contrast to these studies, it was found that removal of the callosal pathway substantally influenced the binocularity of visual cells only when responses were measured under conditions of binocular stimulation and not when the response from each eye was tested separately. Unlike the very large increase in "monocular "cells (OD groups 1 and 7) which appear after callosal sections, a relatively small increase (8%) in the units of OD groups 1 and 7 was observed after unilateral decortications. There were however, an abnormally large number of units in decorticate cats which received input from only one eye (OD 1 and 7) and which proved to be

insensitive to stimulus disparity. Since in normal cats, units in OD groups 1 and 7 generally show very large binocular interactions and are only rarely unselective for stimulus disparity, the presence of these unusual cells in decorticate cats was unmistakable. Although in decorticate cats, there was a similar increase in the proportion of unselective cells (20%) across all ocular dominance groups, the relative change in the number of unselective cells among units in OD groups 1 and 7 characterized these units as a functionally distinct subgroup of monocular cells which were insensitive to stimulus disparity.

In monkey, Poggio and cowofkers found a large proportion (45%) of cells (tuned excitatory) which gave a poor response when activated through each eye separately but responded with substantial facilitation under conditions of binocular stimulation. These cells were tuned to very small stimulus disparities and were thought to provide the substrate for a system of fine stereopsis. A much smaller proportion (3%) of these cells was encountered here, in the paralyzed cat, than in the monkey. It is not possible to say whether this was due to procedural differences or whether this represents a real difference between the two species. It might be that more of these facilitatory units can be found in alert preparations or that they are more numerous immediately around the fovea or <u>area centralis</u> rather than the regions of the lower visual fields, where the present recordings were made. Nevertheless, a fairly large (20%) proportion of the units which were considered to be in the "highly sensitive" group were binocular-only cells or units which would have been classified as tuned excitatory or inhibitory cells according to the sharpness of their disparity tuning curves. Thus, many of the units

which were considered to be "highly sensitive" in the present classification were similar to the units which Poggio and coworkers consider to underlie fine stereopsis in the monkey striate cortex. Certainly, the very dramatic facilitations and inhibition observed in these cells in the cat make them appear as if they would play a very fundamental role in stereoscopic function.

The finding that units with the very largest binocular interactions were spared by the cortical lesions is consistent with the notion of Bishop and Henry (1971): that fine stereopsis is mediated by fibers of the nasotemporal overlap. Virtually no changes were seen in the proportion units showing substantial nonlinear interactions in cells of any ocular dominance group. This group of highly sensitive cells contained a large number of direction selective simple cells. Since the breath of the disparity tuning in individual cells is directly related to receptive field size (Fer ester, 1981) it would seen that simple cells, with their relatively small receptive fields and precise stimulus specificities would be well suited for a system of fine stereopsis and central fusion. Complex cells, on the other hand, with their larger receptive fields, would seem more appropriate for a system of coarse than fine stereopsis. The mean dynamic range of complex cells, indicated that these units commonly showed only moderate binocular interactions. It was this type of cell, showing moderate binocular interactions and broader disparity tuning which was most strongly affected by the lesion. Since complex cells have been associated with oculmotor structures (eg the cortico-tecal projection), the notion that the corpus callosum is involved with the mediation of vergence eye movements is consistent with the

apparent dominance of this cell type in the callosal system.

Although it would seem likely , that no one visual area works independently in the genetation of all phases of stereoscopic function and vergence eye movements, it would appear that fine stereopsis and central fusion are a function of the primary visual cortex, for the limits of stereoacuity have been found to parallel the limits of visual acuity (Bishop, 1980) and it is in the fovea/area centralis of area 17 where the smallest cortical visual receptive fields have been found. That the area centralis of the cat (Albus, 1975) contains a large proportion of monocularly-driven cells is consistent with the results of the present study indicating that these cells play a critical role in stereoscopic function.

If the neural substrate for fine stereopsis is localized in the primary visual cortex, might we not then ask if the mechanisms for coarse stereopsis and vergence may not also originate here? Although very dissimilar and very disparate stimuli do not immediately seem to be optimal stimuli for cells in the visual cortex, this point has never really been examined. The possibility does exist therefore that under dynamic and optimal stimulating conditions, response characteristics of cells in the visual cortex may manifest a considerable transformation from those observed under conventional testing procedures (Hammond, 1979; Frost, 1978). We have found for example, that under conditions of binocular stimulation, in which both the spatial and temporal characteristics of the stimuli were varied, that the size of apparent visual receptive fields could be dramatically larger (100-300%) than they were when plotted monocularly. These data emphasize the limitations of any two-dimensional analysis of visual response-properties, and for the

present time, discourage sweeping conclusions concerning the information processing capacities of cells in the visual cortex.

It does seem however, that cells in the extrastriate visual areas, which have large receptive fields and lack the precise stimulus requirements of units in the visual cortex, could well be responsible for the initiation of vergence eye movements evoked with different and very disparate (Westheimer and Mitchell, 1969) stimuli. In area 19, for example, electrical stimulation will evoke both accommodation and vergence movements (Janpel, 1964). It has also been shown (Sanides, 1978) that, in addition to having an extensive representation of the ipsilateral visual field achieved by the retinal-thalamo projection, the LSVA, as well as area 19, receives an extensive callosal projection. The extent of the visual field represented in the corpus callosum does not appear to be uniform throughout the visual cortex but increases in width from area 17 through areas 18 and 19, possibly extending further in the LSVA. The function of the extrastriate visual areas in the generation of stereopsis and vergence eye movements is is a question which would demand a series of controlled lesion studies, but it is one whose answer would lend much to our understanding of the organization of disparity-sensitive neuronal systems.

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