Burns, Sheila

THE AVIAN ACCESSORY OPTIC SYSTEM: NEUROPHYSIOLOGY, DEVELOPMENT AND OCULOMOTOR FUNCTION

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THE AVIAN ACCESSORY OPTIC SYSTEM: NEUROPHYSIOLOGY, DEVELOPMENT AND OCULOMOTOR FUNCTION

by

SHEILA BURNS

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date

Chairman of Examining Committee
Joshua Wallman, City College

15 April 1985
date

Executive Officer
Peter Chabora

READER ONLY
Nicholas Brecha, CURE

Michael Engber, Mathematics, City College

Olivia McKenna, City College

Joseph Osinchak, City College

Sheryl A. Scott, SUNY at Stony Brook

Supervisory Committee

The City University of New York

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CHAPTER 1

INTRODUCTION

One way of relating brain function to behavior is to study simple neural systems that are associated with simple behaviors. Among vertebrates, stabilizing eye movements are one of the less complex forms of behavior. These stereotypic eye movements have been studied extensively and they can be systematically correlated with specific visual stimuli (Carpenter, 1977). A study of the neural systems underlying this behavior would contribute to our understanding of brain function because of the possibility of relating neuronal characteristics to specific known sensory inputs and motor outputs. It is of interest, therefore, to identify the neural systems responsible for stabilizing eye movements, and also to learn how these visual and oculomotor systems code and process sensory information.

The neural systems responsible for stabilizing eye movements have only recently begun to be identified and studied. There is physiological evidence from work in mammals that the accessory optic system (AOS)[1] constitutes part of this neural system (Maekawa and Simpson,

[1]Abbreviations used in the text are listed in the Appendix.

1972, 1973; Collewijn, 1975a,b; Simpson et al., 1979). It is in birds, however, that the anatomy of the AOS has been most throughly studied and one complete pathway from sensory input to motor output has been identified. There is a specific population of retinal ganglion cells,the displaced retinal ganglion cells (DRGCs), which carry the afferent information (Karten et al., 1977; Reiner et al., 1979). These fibers compose the basal optic root (BOR), which terminates in the nucleus of the basal optic root (nBOR) in the midbrain. There is a direct projection from nBOR to oculomotor neurons (Brecha and Karten, 1979). The AOS in birds is thus part of a very short pathway involving the visual control of eye movements. It also provides input through polysynaptic pathways to other areas of the brain known to be involved in oculomotor function (Brauth and Karten, 1977; Brecha et al., 1980).

The purpose of this research is to investigate the functional role of the AOS in stabilizing eye movements in birds by electrophysiological recording from single units in nBOR and by electrically stimulating the nBOR. A second purpose is to investigate the postnatal development of nBOR by electrophysiological recording.

BACKGROUND

Stabilizing Eye Movements

Stabilizing eye movements are found throughout the animal kingdom (Carpenter, 1977). They serve to compensate for retinal slip (movement of the visual world across the retina due to an animal's own motion or to motion of the world) by stabilizing the retinal image, thereby providing a clear view of the world. There are two major inputs to stabilizing eye movements, one via the visual system which produces optokinetic nystagmus (OKN) and one via the vestibular system which produces the vestibulo-ocular reflex (VOR). The visual system detects retinal slip, which, in turn, provides a signal for the generation of eye movements in the same direction and at approximately the same velocity as the moving object, thus stabilizing the retinal image. The vestibular system detects movement of the head, via stimulation of the semicircular canals. Head movement results in movement of the eyes in the opposite direction to, but at approximately the same velocity as, the head, thus compensating for the apparent movement of the world. In natural circumstances of locomotion, there is an interaction between these two systems such that very effective stabilizing eye movements occur over a large range of velocities of head movement (Baarsma and Collewijn, 1974; Batini et al.,1979).

There is strong evidence that the optokinetic system is a closed-loop system. Under normal low velocity stimulus conditions (closed loop) the gain (ratio of eye velocity/stimulus velocity) approaches one. The loop can be opened by immobilizing one eye, which views the visual stimulus, and measuring the movements of the other eye, which is covered. Under these open-loop conditions the gain of OKN increases well beyond one (Collewijn, 1969, 1972; Erickson and

Barmack, 1980), indicating that a visual negative feedback system normally functions in regulating the gain of OKN so that it is compensatory. The vestibulo-ocular system, in contrast, is an open-loop system, since the output (eye movement) cannot directly influence the input (semicircular canal stimulation). The gain (ratio of eye velocity/head velocity) can, however, show adaptive plastic modification guided by input from the visual system, if, in fact, the gain is not compensatory. The most spectacular demonstration of this is in humans. Subjects wearing dove prism goggles which reverse the visual world in the horizontal plane experience the VOR as anti-compensatory, since it increases rather than decreases retinal slip (Gonshor and Melvill Jones, 1976a,b). Reduction in gain and changes of phase of the VOR, however, result in an approximate functional reversal of the reflex. This has the effect of compensating for reversal of the visual world. A reduction in gain also occurs in monkeys, cats and chickens when the visual world is reversed (Miles and Fuller, 1974; Robinson, 1975; Wallman et al., 1982). It is also possible for the gain of the VOR to show an increase under experimental conditions in which retinal image slip is increased, rendering the normal gain too low to be compensatory. This has been shown in humans (Gauthier and Robinson, 1975), monkeys (Miles and Eighmy, 1980; Miles and Fuller, 1974), and chickens (Wallman et al., 1982).

Neural Systems Regulating Stabilizing Eye Movements

The neural substrate for OKN includes the pretectal nucleus of the optic tract (NOT) and the AOS. There is substantial evidence that the NOT in mammals has an important role in horizontal OKN. Electrical stimulation of NOT in rabbits generates horizontal OKN and lesioning it eliminates horizontal OKN (Collewijn, 1975a). Electrophysiological recording in NOT shows that these cells have very large receptive fields (up to 40 x 150 deg.), respond best to large random patterns, are velocity tuned (range of 0.01-20 deg./sec.) and are directionally selective, preferring movement in the temporal to nasal direction (Collewijn, 1975b). This is exactly the stimulus direction which is best in eliciting OKN in the horizontal plane. Similar results have been obtained from recording from single units in the NOT in cats (Hoffmann and Schoppmann, 1975; Hoffmann, Behrend and Schoppmann, 1976), which showed that neurons respond best to large, richly contoured patterns, are directionally selective, preferring movement in the temporal to nasal direction and respond to stimulus velocities ranging at least from 0.1 to 50 deg./sec. In addition, electrical stimulation of the NOT produces temporal-to-nasal OKN (Hoffmann and Huber, 1983).

In birds a pretectal nucleus, the lentiform nucleus of the mesencephalon (LM), considered analogous to the NOT (Kuhlenbeck, 1939), also has a role in horizontal OKN. Metabolic mapping studies show labeling in LM in response to full-field horizontal OKN stimuli (McKenna and Wallman, 1981) and single unit recordings show that most

neurons respond best to large visual stimuli moving in the temporal-to-nasal direction (Winterson and Brauth, 1981). Lesions of LM produce severe deficits in horizontal OKN (Gioanni et al., 1983a).

The AOS in rabbits also contains cells whose projections and properties indicate that it is involved in OKN (Walley, 1967; Maekawa and Simpson 1972,1973; Simpson et al., 1979). In rabbits the AOS contains three terminal nuclei: medial terminal nucleus (MTN), dorsal terminal nucleus (DTN) and lateral terminal nucleus (LTN). Cells respond best to large, highly textured patterns, have large receptive fields (40 x 60 deg. average), are velocity tuned (0.1-1 deg./sec.) and are directionally selective (Simpson et al., 1979). Cells in the DTN, like those in NOT, respond best to horizontal movement in the temporal-to-nasal direction, while cells in MTN and LTN prefer movement up and posterior and down and posterior, respectively. The velocity tuning of cells in the AOS (Simpson et al., 1979) is similar to the stimulus velocity (1 deg./sec.) which elicits OKN in the rabbit (Collewijn, 1972). The AOS receives a direct retinal projection (Giolli, 1961; Giolli and Guthrie, 1969), probably from a class of ganglion cells--the on-directionally selective cells--whose velocity tuning is also about 1 deg./sec. (Oyster et al., 1972; Simpson et al., 1979).

The AOS in cats also contains cells whose properties suggest that it is involved in OKN. Neurons in the MTN of cats have large receptive fields (approximately 60 x 40 deg.), respond to large but not small stimuli, prefer low stimulus velocities of approximately 0.8 deg./sec. and are directionally selective primarily for downward

vertical motion (Grasse and Cynader, 1982). Neurons in LTN are directionally selective for either upward or downward motion and respond best to stimulus velocities between 0.8 and 12.8 deg./sec. Those in DNT respond best to temporal-to-nasal stimulus motion at velocities between 6.4 and 12.8 deg./sec. (Grasse and Cynader, 1984).

The AOS in birds is known mainly from anatomical work and has been studied much more thoroughly than in mammals. Afferent and efferent projections have been extensively described. The terminal nuclear complex, which has three divisions: nBOR proper, a dorsal division (nBORd) and a lateral division (nBORl), receives afferents from the DRGCs of the contralateral eye (Karten et al., 1977; Reiner et al., 1979), from the contralateral nBOR (Brecha et al., 1980) and from the visual Wulst (analog of the visual cortex) (Rio et al.,1983). The nBOR projects directly to the oculomotor nucleus, sparsely to the trochlear nucleus, to the inferior olive, to the vestibulocerebellum via mossy fibers, to the interstitial nucleus of Cajal (INC), to the lentiform nucleus of the mesencephalon pars magnocellularis (Brauth and Karten, 1977; Brecha and Karten, 1979; Brecha et al., 1980) and to the vestibular nuclei (Wold, 1979). These projections clearly implicate the AOS in oculomotor function, specifically with respect to vertical eye movements, since the projection to the oculomotor nucleus is to the dorsolateral and ventral divisions only (Brecha and Karten, 1979; Brecha et al., 1980), and these areas project to the inferior rectus and to the superior rectus and inferior oblique, respectively (Heaton and Wayne, 1983). Furthermore, the INC in mammals has been implicated in the control of vertical eye and head movements (Hyde and

Eason, 1959; Hyde and Toczek, 1962; Carpenter et al., 1970; Fukushima et al., 1978; Anderson, 1981; King, 1981).

The inferior olive is the source of the climbing fiber input to the vestibulocerebellum and both structures are thought to have a role in stabilizing eye movements. In rabbits, the inferior olive receives afferents from the AOS (Maekawa and Simpson, 1972, 1973) and the NOT (Mizuuo et al., 1973). There are cells in both the inferior olive (Maekawa and Simpson, 1972, 1973; Simpson and Alley, 1974; Barmack and Hess, 1980a) and vestibulocerebellum (Simpson and Hess, 1977) with visual responses similar to those of cells in the AOS and NOT. Lesions of the dorsal cap of the inferior olive modify horizontal OKN (Barmack and Simpson, 1980) and electrical stimulation evokes horizontal nystagmus (Barmack and Hess, 1980). In cats, the inferior olive also receives afferents from the NOT (Hoffmann et al., 1976). Although lesions of the inferior olive in cats do not affect OKN, they prevent the adaptive changes in VOR which normally occur in response to reversal of the visual world (Haddad et al., 1980). Thus, there is evidence that the inferior olive and vestibulocerebellum have a role in OKN and in visual-vestibular interactions.

Neuronal responses to horizontal optokinetic stimuli in the vestibular nuclei have been described in several species (Dichgans et al., 1973; Waespe and Henn, 1977; Keller and Precht, 1979; Cazin et al., 1980). In rats, the visual input to the vestibular nuclei is from the NOT via a pontine nucleus, the nucleus reticularis tegmenti pontis (NRTP) (Precht, 1981); lesions of NRTP strongly impair or abolish horizontal OKN (Precht, 1981), suggesting that the pathway for

horizontal OKN in the rat includes the vestibular nuclei. Horizontal OKN in monkeys (Cohen et al., 1973) and rabbits (Collewijn, 1976) is modified by bilateral labyrinthectomies. This is probably due to removal of tonic input from the vestibular neurons to the vestibular nuclei, since it has been shown that plugging of the semicircular canals does not affect OKN (Barmack and Erickson, 1981). It is unknown whether the pathway for horizontal OKN in the monkey or rabbit includes the vestibular nuclei. The MTN in rabbits and rats projects to the vestibular nuclei (Blanks et al., 1982), but the functional role of this projection has not been identified.

In summary, all of the efferent projections of the avian AOS are to areas of the brain implicated in the regulation of stabilizing eye movements. Although most of these areas have been studied in mammals, rather than in birds, it is likely that their functions are to some extent comparable. Thus, it is of interest to investigate the role of the avian nBOR to determine whether its physiological function is similar to that of the analogous nuclei in the AOS of mammals.

CHAPTER 2

METHODS

1.) SINGLE UNIT RECORDING EXPERIMENTS

General procedures

The experimental animals were white Leghorn chickens. Twenty-six animals were five to seven weeks old and 13 were neonates, two to six days old. They were anesthetized with 40% urethane (2g./kg. of body weight, injected intraperitoneally), but were not paralyzed. To assess the eye movements which occur under this anesthetic, a laser beam was reflected off a mirror attached to the eye of one animal. It was found that the eye stayed most of the time within a circle of 5 min. of arc over 10 min. This stability is comparable to that obtained with gallamine in awake monkeys (Pease, 1973) over 1.5 hrs., the chicken's eye stayed within a circle of 0.3 degs. in diameter. The movements seen were slow drifts, small saccades and slow circular movements associated with respiration. Older animals were not ventilated, but neonates were ventilated by forcing humidified air to

enter the respiratory systen unidirectionally through a cannula inserted in the posterior air sac at the approximate rate of 100 ml./min. (Burger and Lorenz, 1959).

The bird was placed in a Kopf cat stereotaxic instrument modified so that the bird's visual field was minimally obstructed. These modifications consisted of the beak bar coming up from below and the ear bars being at the open end of the frame with a horizontal offset so that the bird's eyes were out of the frame. The lower eyelid was held open with collodion, and silicone fluid was applied to the cornea as needed to keep it moist. In early experiments, the eyes were refracted by streak retinoscopy and found to be always within two diopters of correct refraction for the distance to the screen. Consequently, refraction was discontinued in later experiments. The electrode was lowered from the dorsal surface of the brain with a hydraulic microdrive. Stereotaxic coordinates with reference to the ear-bars were approximately A 3.9, L 2.0, D 1.25 for older birds and A 2.2, L 1.5, D 1.4 for the neonates. The head was held so that the line between the proximal angle of the beak and the auditory meatus was 25 deg. to the horizontal.

Recording Methods

Tungsten electrodes (F. Haer and Co.; Bak Electronics, Inc.) with impedances at 1 kHz between 1 and 12 megaohms were used for recording. Recording methods were largely conventional, and for quantification relied mostly on counting spikes by means of a spike

height discriminator. Recordings were confirmed to be from single units by triggering the sweep of an oscilloscope by the spike analyzer output pulse while feeding the input signal through a home-built analog delay line, which permitted viewing the complete waveform of the spikes counted. This technique also made apparent any spikes that occurred within one refractory period of the counted spikes, indicating inadequate isolation of a single unit.

Visual Stimuli

Two technically different, but essentially similar, methods of presenting stimuli were employed. In the earlier experiments, visual stimuli were projected from a slide onto a galvanometer-driven front-surface mirror, through a dove prism, to a second mirror and onto a tangent screen. The pupillary axis of the left eye was centered on, and perpendicular to, the rear projection tangent screen which was 57 cm from the eye. This alignment was done by placing a telescope with an attached marker light behind the tangent screen so that the marker light was normal to and centered on the screen. The screen was then lifted and the bird was moved so that the corneal reflection of the marker light was centered in the pupil, which was constricted by a second brighter light.

During these early experiments, the nBOR was located using as a searching stimulus a sinusoidally-moving projected black and white random pattern covering the tangent screen, which subtended 60 deg. horizontally and 45 deg. vertically. Once a unit was isolated and

its best velocity roughly determined, its directional selectivity was systematically explored with constant velocity stimuli in eight directions at intervals of 45 deg., repeating each direction four times. Next, the velocity tuning curves for the excitatory and inhibitory directions were determined by varying the stimulus velocity in approximately logarithmic steps centered on the best velocity. The sweep duration was 4.85 sec., except above 10 deg./sec., where it was reduced. For all of the above measurements the random pattern stimulus covered the entire tangent screen. Subsequently, an attempt was usually made to map receptive fields using small light and dark stationary and moving spots or by masking areas of the tangent screen. Responses to room lights being turned on and off and to strobe flashes were also recorded.

In the later experiments a more elaborate method of stimulus presentation was employed, using a 60 x 60 cm tangent screen which was moveable and, therefore, permitted more extensive exploration of the animal's visual field. The projection optics were mounted behind and moved with the screen. Because of its unusual design, this equipment will be described in some detail. The optics and projection screen are part of a pantograph-type arm as shown in Fig. 1. This apparatus can be rotated horizontally and vertically around the animal. When the screen is at eye level it lies in a vertical plane; when it is moved above or below this level it tilts so that it always remains 57 cm from the birds eye and tangent to an imaginary sphere centered on the left eye. The optics were mounted behind the screen so that they moved with it, insuring that the image filled the screen and remained

centered on it. Linear image movement was produced by a closed-loop galvanometer motor (General Scanning G-300PD) connected to a thin flexible cable which moved the slide at variable velocities back and forth along tracks as shown in Fig. 2. Rotation of the slide was accomplished by using a stepping motor to rotate the plate on which the slide and galvanometer motor were mounted. This made it possible to present stimuli in any orientation. The slide was projected through a 25 mm lens, onto a mirror and then onto the screen. To accommodate the projection screen apparatus, the stereotoxic apparatus was placed on a cantilivered platform made of a heavy stone slab balanced on two columns of cement. Transmission of vibration to the platform was reduced by tennis balls, immobilized in wooden frames, and by pieces of felt placed between the platform and the cement blocks. When using this moveable tangent screen the nBOR was located by slowly moving the screen, on which was projected a black and white random pattern, throughout the visual field. Once a unit was isolated, its best receptive field was located and the stimulus presented in that position. The remainder of the methods were the same as those used with the stationary screen, except the sweep duration of the stimulus at all velocities was 5 sec.

Tangent screens are not suitable for measuring velocity tuning unless the distance from the animal to the front of the screen is equivalent to the distance from the slide to the back of the screen. This is because a gradient of velocities is present across the screen. If the animal is closer than the slide to the screen, motion at the edges of the screen is seen to be slower than motion at the center.

Conversely, if the animal is further from the screen, motion at the edge is seen as faster than motion at the center. In the apparatus used here the optics were approximately the same distance behind the screen as the animal was in front, thereby compensating for the gradient of velocities on the screen.

Use of the moveable tangent screen permitted the analysis of the receptive field location of units, which could not be analyzed using the stationary screen because of the large size of the receptive fields. Consequently, data presented in the results section are based on varying numbers of units. Furthermore, because of the general difficulty in holding cells not all data were collected for all units.

Corrections for Head Tilt

Because the animal's head in the stereotaxic apparatus was tilted downward 20 deg. below its usual position, as estimated by two observers, and relative to the natural coordinate system of the stimulus apparatus, corrections for directional preferences and receptive field locations were necessary.

As explained above, stimuli were presented on a moveable screen which was 57 cm from the animal's eye and tangent to an imaginary sphere centered on the eye. The natural spherical coordinate system for the position of the tangent screen in the horizontal dimension was azimuth 0 to 180 deg. where 0 is the midsaggital line in front of the animal and 180 the midsaggital line behind the animal; 90 is on the interaural line. In the vertical dimension 0 deg. is at the level of

the ear and eye, with +90 deg. being the highest elevation and -90 deg. the lowest depression. Fig. 3A illustrates the coordinate system. The screen could be moved horizontally along any parallel of latitude and vertically along any meridian. A few parallels and meridians are shown in Fig. 3A.

If the animal's head in the stereotaxic apparatus were in its usual position rather than tilted 20 deg., the coordinate system of the stimulus apparatus would be coincident with the coordinate system of the animal's visual world when its head is in its customary position. Regardless of the mechanisms that may exist for perceptual compensation of head tilt, it is assumed that no such compensation exists at the level of nBOR, since there are no known otolithic inputs to this nucleus. The bird's coordinate system is shown in Fig. 3B. It can be seen that the sphere is rotated by 20 deg. relative to the sphere shown in Fig. 3A.

During experiments both receptive field locations and preferred directions of stimulus motion were defined in terms of the coordinate system of the stimulus apparatus. To describe these parameters in a more functionally relevant way, they have to be redescribed in terms of the bird's coordinate system. As can be seen by a comparison of Figs. 3A and B, although the tangent screen is in the same absolute position in both figures, it is in a different position in each of the two coordinate systems. Since the receptive field location as defined in this paper refers to the azimuth and elevation of the center of the tangent screen, it is clear that receptive field locations with respect to the visual world of the bird differ from receptive field

locations with respect to the coordinate system of the stimulus apparatus. Also, it is necessary to make corrections in identifying preferred directions of stimulus motion. For example, stimulus motion along the vertical meridian at 90 deg. azimuth is exactly vertical in the coordinate system of the stimulus apparatus as shown in Fig. 3A. However, the same absolute motion would be perceived by the bird as off vertical.

Now, at first view, it may seem that the corrections simply require a rotation of 20 deg. This is not, however, the case. Consider first preferred directions of vertical motion. In contrast to the example of vertical stimulus motion presented along the meridian at 90 deg. azimuth described in the previous paragraph, vertical stimulus motion presented directly in front of the animal is always vertical regardless of whether the head is tilted or not. Furthermore, as will be illustrated below, directions of motion along meridians other than the one at 0 deg. azimuth have to be corrected by increasing amounts depending not only upon the distance of the azimuth from 0 deg., but also upon the elevation.

The corrections for receptive field locations differ somewhat from the corrections for directional preference. In this case, a correction is required directly in front of the animal, at 0 deg. azimuth; the correction decreases with distance from that azimuth, with no correction required exactly on the interaural line. Like the corrections for directional preference, however, corrections for receptive field locations also increase with elevation.

The corrections for receptive field locations and directional preferences were made using spherical trigonometry. Fig. 4 (which essentially represents Fig. 3A superimposed on Fig. 3B) shows a portion of a sphere with arrows indicating three receptive field positions: #1 is at azimuth 30, elevation 20(of the apparatus coordinate system), #2 azimuth 60, elevation 20, #3 azimuth 60, elevation 60. Spherical triangles are formed by the meridian on the coordinate system of the apparatus (solid arc), the meridian on the coordinate system of the bird (dashed arc) and the arc of 20 degree rotation. By comparing receptive field position #1 and #2 it can be seen that x, the angle of rotation, increases as azimuth nears 90 deg. (the interaural line). By comparing receptive field position #2 and #3, it can be seen that x increases as elevation increases. In the inset the spherical triangle for receptive field position #3 is shown again. The angle labeled az represents the original azimuth of the receptive field position; the arc labeled 90-elev represents the original elevation subtacted from 90 deg. The arc X and the angle y are, respectively, the corrected elevation subtracted from 90 deg. and corrected azimuth subtracted from 180 deg. of the receptive field position. (The subtraction of arcs and angles is necessary simply to solve the triangles, as can be seen from a consideration of Fig. 4.) The angle x is the amount by which directional tuning plots are rotated. The triangles are solved for x, X and y using the law of cosines for sides and the law of sines for spherical triangles:

1) $\cos(X) = \cos 20 \sin(\text{elev}) + \sin 20 \cos(\text{elev})$

2) $\sin(x) = \sin 20 \sin(az)/\sin(X)$

In summary, receptive field locations have been rotated counterclockwise from the point of view of the left eye so that they are referenced to the normal head position of the bird. The further the receptive field from the interaural line (around which the bird's head was tilted) in terms of either elevation or azimuth, the greater the correction. No correction was necessary for receptive fields exactly on the interaural line. All data on receptive field locations incorporate these corrections.

In addition, directional tuning plots have been rotated taking into account the azimuth and elevation of the tangent screen during presentation of the visual stimulus. As mentioned above, for 0 deg. of original elevation the corrections range from zero at 0 deg. azimuth to 20 deg. at 90 deg. azimuth. The correction is also zero for all elevations at 0 deg. azimuth; i.e., there is no change in direction in spite of the 20 deg. rotation when the stimulus is presented directly in front of the animal. The greatest change occurs at 90 deg. azimuth and 90 deg. elevation, where the 20 deg. of head tilt requires a correction of 90 deg. (Stimuli were never actually presented at this extreme.) This may seem surprising, but Fig.4 illustrates that angles of rotation (x) increase as elevation increases and near the poles where distances are small, rotation results in large changes. Consequently, at 90 deg. azimuth, the correction ranged from 20 deg. at 0 deg. elevation to 90 deg. at 90 deg. elevation. All data on directional tuning preferences incorporate these corrections.

Measurement of Position of Pecten and Optic Axis

In order to relate the observed spatial distribution of unit characteristics to retinal location, I measured the location of the optic axis and of the pecten with respect to the experimental coordinate system. The bird was anesthetized with urethane and placed in the stereotaxic instrument in the position used for single unit recording. A transparent hemisphere nine inches in radius was positioned one inch from the bird's midline and centered as accurately as possible on the left ear. The pecten was observed through the hemisphere using an ophthalmoscope. The position of the light beam was marked on the surface of the hemisphere as the pecten was traced from its tip until it was no longer visible due to the presence of the eyelid. The position of the pupillary axis was determined by centering the corneal reflection of the ophthalmoscope light beam in the pupil and marking the position of the beam on the surface of the hemisphere. The azimuth and elevation of the image of the pecten and the pupillary axis were measured with reference to the vertical and horizontal meridians of the hemisphere using a protractor.

To compensate for the fact that the edge of the hemisphere was one inch lateral to the bird's midline, rather than on the midline, these azimuths and elevations were corrected using conventional trigonometry to calculate their corresponding positions on a hemisphere ten inches in radius. Subsequently, these coordinates were corrected to compensate for head tilt in the manner described earlier.

Measurement of the position of the pecten and pupillary axis was made on two birds, five and six weeks of age. Given the inherent limitations of the measurement system and the data published by others (Miles, 1972a; Ehrlich, 1981; Wallman and Velez, 1985), it is estimated that the measurement is accurate within ten degrees. The position of the pecten was also measured on one three-day-old bird. This animal was sacrificed prior to the procedure since the eyelid had to be removed to permit viewing of the pecten beyond the tip. Extensive measurements of the pupillary axis in the horizontal plane made on birds of several ages by Joseph Su (see Wallman and Velez, 1985) have shown that the angle of the pupillary axis is the same in newly hatched and six-week-old birds; therefore, I did not measure the axis in younger birds. The pupillary axis will subsequently be referred to as the optic axis since extensive experience in this laboratory has shown that all of the Purkinje images lie within a few degrees of the pupillary axis (J. Wallman, pers. comm.)

Analysis of Directional Tuning of Units

Although units were tested for their responses to movement in eight directions, their excitatory and inhibitory directions were specified to the nearest degree by interpolation. To do this I needed to choose a function to describe the response between data points. Since the stimulus presentation was periodic, i.e., repeated every 360 deg. at 45 deg. intervals, the responses of the units were analyzed using the first seven terms of the Fourier series (Wallman and Velez,

1985). Specifically, the following equation was fit to the data:

$G(a)=K_0 + K_1\cos a + K_2\sin a + K_3\cos 2a + K_4\sin 2a + K_5\cos 3a + K_6\sin 3a$

where K is the average number of spikes, a is the stimulus direction expressed as an angle and G(a) is the calculated number of spikes in a particular direction. Then, the maxima and minima of the fitted function were determined. Fig. 5 illustrates a hypothetical unit the directional tuning of which is exactly fitted by this function since its response is that of a pure sine wave. Some units in nBOR have broad excitatory or inhibitory peak widths and the maxima or minima of the fitted function sometimes falls inappropriately near the edge of the peak (see Fig. 6). To accommodate such cases all units were treated in the following way. The excitatory peak was found by starting at the maximum of the fitted function and then finding the points at which the curve fell to 75% of the difference between the maximum and the minimum. The center of these two points was taken as the maximum. The same method was used to locate the inhibitory valley starting at the maximum of the fitted function and finding the points at which the curve fell to 25% of the difference between the maximum and minimum. The center of these two points was taken as the minimum. For sharply tuned units, the maxima or minima determined by the above methods are virtually identical. For more broadly tuned units, the centers of the 75% and 25% points in general gave a better fit than the absolute maxima and minima. In a few cases the fit of the function to the data points was poor and even the centers of the peaks did not fit the data well, particularly with respect to identifying the

inhibitory direction. In these cases two experienced observers independently and blindly corrected the inhibitory directions. An example is shown in Fig. 7.

Location of Recording Sites

Recording sites were identified using lesions made by passing 5 to 20 μA of current through the electrode (tip positive) for 10 to 15 sec. At the end of an experiment, birds were given an overdose of urethane and perfused transcardially with Heidenhain's solution (without mercuric chloride). Brains were removed and placed first in Heidenhain's solution overnight and then in a 30% sucrose solution for at least 48 hrs. Frozen brains were cut in 25 or 50 μ transverse sections and stained with cresyl violet for identification of lesion sites. Lesion sites were plotted on a standard series of drawings representing transverse sections through nBOR at 150 μ intervals. In some cases recording sites themselves were not lesioned, but a lesion was made elsewhere in the track or occasionally, in a second track. These recording sites were located from stereotaxic coordinates, taking into account shrinkage occurring during histological processing. The amount of shrinkage was assessed by making double lesions in two animals and comparing the distance between lesions measured by stereotaxic coordinates with the distance measured on the histological sections. Shrinkage was approximately 15%. In 2 out of 39 brains lesion sites could not be located. However, data from these two experiments are included since the findings were totally consistent with

those of other experiments.

2.) ELECTRICAL STIMULATION EXPERIMENTS

General Procedures

Experimental animals were white Leghorn chickens four to seven weeks of age. On the day prior to the experiment, monopolar semimicroelectrodes (Rhodes Medical Instruments Inc., SNEX-300) were implanted in nBOR. Birds were anesthetized with 200mg/kg of Ketamine(Ketaset, Bristol Laboratories) and 1ml/kg Chloropent (Ft. Dodge Laboratories), placed in a stereotaxic apparatus and a small opening was made in the skull. As the electrode was lowered into the brain multiunit recordings were made while the birds were presented with appropriate visual stimuli to insure correct electrode placement in nBOR. The electrode was cemented in place with dental acrylic and the birds were allowed to recover. In a few experiments the contralateral nBOR was lesioned in birds at the age of two to two and a half weeks. At the age of four to six weeks, experiments identical to those described for non-lesioned birds were conducted with the intact nBOR. The purpose of the lesions is explained in the Results section.

Electrical Stimulus

Stimuli consisted of monopolar square wave pulses delivered through a constant current unit. The current was monitored by reading the voltage across a 100 kiloohm resistor in series with the stimulating circuit. Many stimulus variables were tried initially and eye movements were obtained with a current range of 50 to 200 μA, frequency range of 80 to 200 Hz, pulse duration of 0.2 msec. and train duration of approximately 5 to 30 sec.

Visual Stimulus

In some experiments nBOR was electrically stimulated while the bird was viewing an optokinetic stimulus through the contralateral eye. This made it possible to assess the relative influence on eye movements of an electrical stimulus compared to a visual stimulus to nBOR. The optokinetic stimulus was either horizontal, vertical or torsional. The horizontal stimulus was a vertically striped cylinder which was rotated around the animal at a constant velocity in either the nasal to temporal or temporal to nasal direction. In most experiments the stimulus velocity was either 20 or 25 deg./sec. and in one experiment was 50 deg./sec. The vertical and torsional stimulus, devised by Wallman and Velez (1985), was a cylinder with horizontal stripes on the side walls and radial stripes on the end wall. A cantilevered platform that extended into the cylinder supported the animal. The cylinder was rotated on a horizontal axis in either a clockwise or counterclockwise direction. Depending upon the position

of the bird in the cylinder, the bird viewed either vertical or torsional movement. That is, with the optic axis facing the side wall, the bird viewed upward or downward moving stripes; with the optic axis centered on the end wall of the cylinder, the bird viewed clockwise or counterclockwise torsion. For most experiments the vertical and torsional stimulus velocity was 15 deg./sec.; in one experiment it was 25 deg./sec. and in another it was 40 deg./sec.

Recording Methods

Eye movements were recorded using the search coil technique (Robinson, 1963, Wallman et al., 1982). On the morning following electrode implantation, the bird was again anesthetized with Ketaset and chloropent or with halothane while the eye was prepared for attachment of the search coil by making a small scalp incision near the dorsal rim of the orbit. Recovery from the anesthesia took about two hours. Xylocaine was applied to wound edges periodically during the experiment. For attachment of the eye coils and during the experiments, the animal was placed in a cylindrical plexiglass container with a cover which allowed the head to protrude, but which restricted head movement. The head was further immobliized by using a beak bar attached to the cylinder. The beak bar could be adjusted so that the animal's head approximated its natural position. The eye coils were approximately 6 mm in diameter and consisted of ten turns of AWG43 magnet wire, made rigid by a thin epoxy coating. In order to simultaneously record horizontal and vertical or torsional eye

movements, two coils were used. A slightly smaller coil was placed inside and at right angles to a slightly larger coil and attached with dental wax. The holder for the coils consisted of a small circle of cellophane or 0.001-inch-thick Lexan to which a short length of 1-mm-diameter glass micropipette tubing was attached with a drop of epoxy. The vertical post and its platform was attached to the exposed globe with a drop of Histoacryl surgical adhesive (Braun Melsungen; distributed by Trihawk International Traders, Montreal). The coils were attached to the post with dental wax so that one coil was horizontal and the other vertical. Care was taken that the placement of the post and the coil did not impede eye movement and the area was kept moist with silicone fluid. Throughout the experiment, the waveform of the bird's saccades were monitored on an oscilloscope to ensure that there were no adhesions restricting eye movements. The search coil technique, which is conventional and widely used, is fully described by Robinson (1963). Briefly, the animal was placed in an alternating magnetic field produced by two 24-inch-diameter coils, 24 inches apart, that were driven by a 25 kHz signal from an oscillator and amplifier. The signals from the eye coils were amplified, sent to phase-sensitive detectors where eye position is derived, and then to a polygraph. In a few experiments an analog differentiator also produced a velocity signal. Signals above 30 Hz were filtered from the differentiated signals both to clip the fast phases and to remove extraneous noise.

Data Analysis

For all experiments, average slow-phase eye velocity was estimated from measurements of position traces on polygraph records. In some experiments in which velocity records were available as well, measurements were made with the aid of a digitizing tablet and, in this case, peak eye velocity of each slow-phase was measured. A comparison of the two methods indicated that peak velocities were one-third higher than these average velocities. All data presented in this paper are from measurements of position traces.

Location of Sites of Stimulating Electrodes and Analysis of Lesions

At the end of an experiment lesions were made by passing 50 or 100 μA of current through the stimulating electrode (tip positive) for 15 or 20 sec. and birds were given an overdose of urethane. The procedures used to identify sites of stimulating electrodes and to verify placement of lesions in the contralateral nBOR were identical with those used to verify sites of recording electrodes.

Fig. 1. Sketch of stimulus apparatus showing moveable projection screen. The bird and stereotaxic instrument are placed on the cantilivered platform shown on the right. The optics are mounted behind the screen and move with it. The screen can be moved horizontally and vertically around the animal. When the screen is moved vertically it tilts, as shown, so that it always remains 57 cm from the bird's eye and tangent to an imaginary sphere centered on the eye.

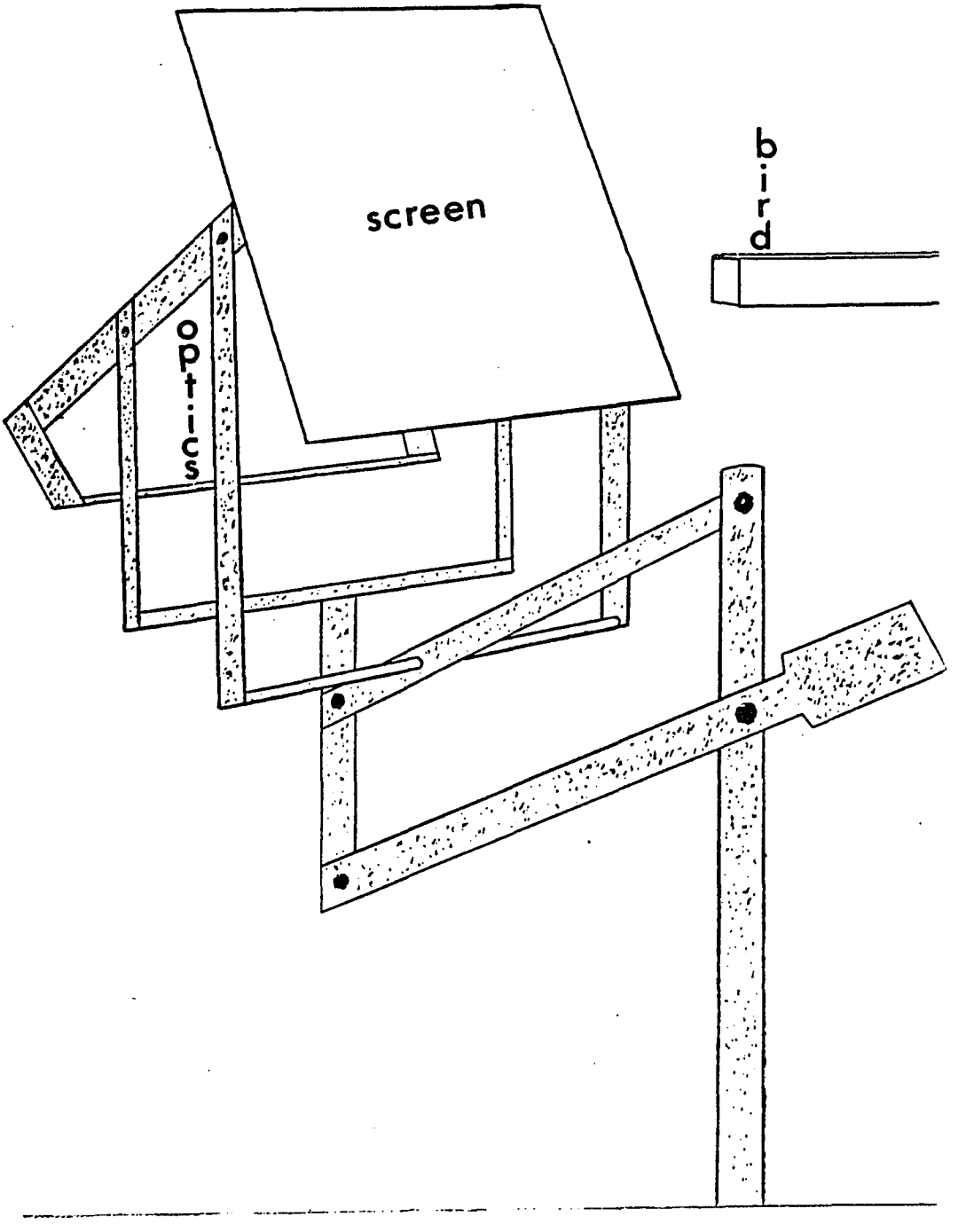

screen
bird
optics

Fig. 2. Sketch of apparatus used to produce image motion. Linear motion was produced by a closed-loop galvanometer motor connected to a thin flexible cable which moved the slide at variable velocities back and forth along the tracks. Rotation of the slide was accomplished by using a stepping motor to rotate the plate on which the slide and galvanometer motor were mounted.

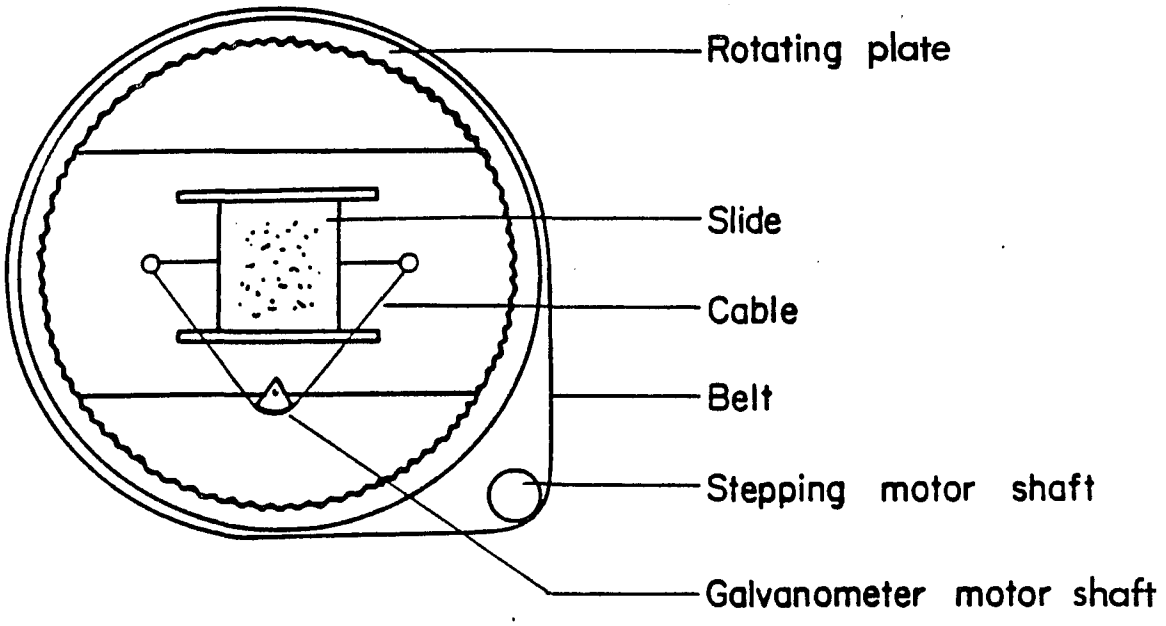
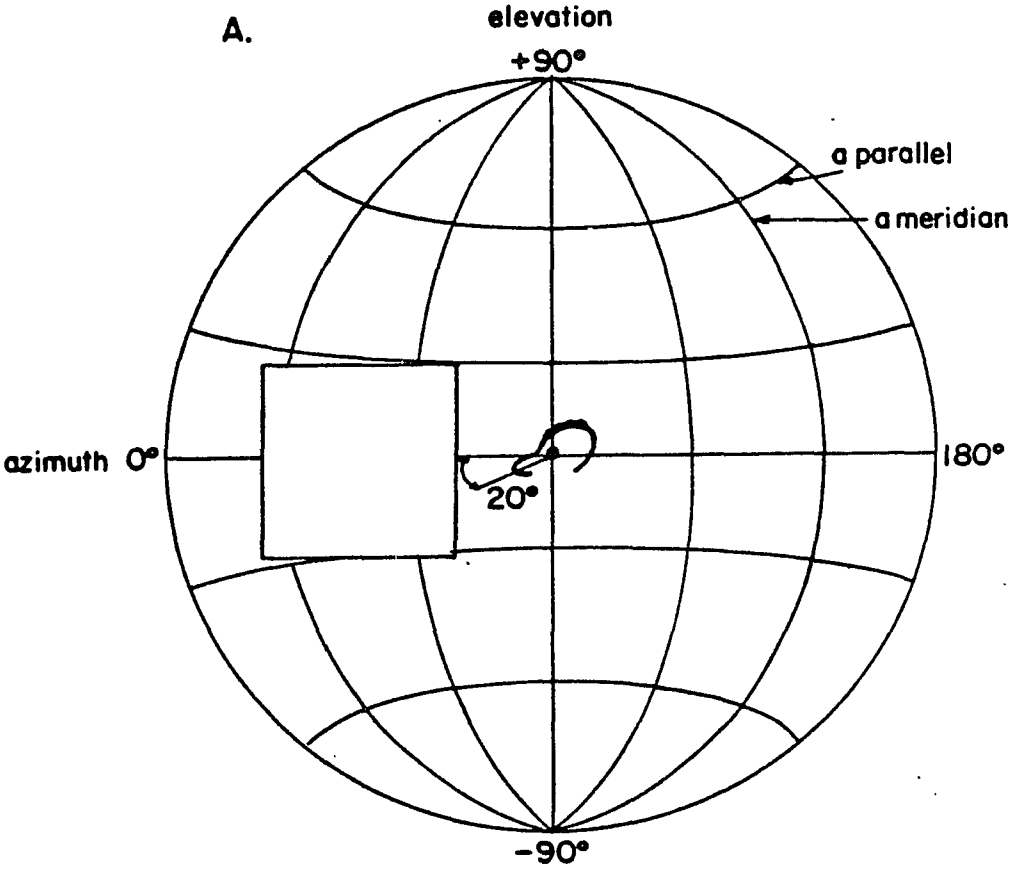

Rotating plate
Slide
Cable
Belt
Stepping motor shaft
Galvanometer motor shaft

Fig. 3. A. Illustration of the spherical coordinate system of the stimulus apparatus used for describing the position of the tangent screen. Zero deg. azimuth is on the midsaggital line in front of the animal and 180 deg. is on the midsaggital line behind the animal; 90 deg. of azimuth is on the interaural line. Zero deg. elevation is at the level of the ear and eye, +90 deg. is directly above the animal's head and -90 deg. is directly below the animal's head. The screen, represented by the square, could be moved along any parallel of latitude and any meridian; a few of these are shown. Also shown is the position of the bird's head, which is tilted downward 20 deg. from its natural position. B. Illustration of the spherical coordinate system referenced to the bird's customary head position. This sphere is rotated 20 deg. in the counterclockwise direction with reference to the sphere in A. The square representing the tangent screen and the bird, however, remain in the same absolute position as in A. The coordinates of the tangent screen have clearly changed. See text for further discussion.


A.
elevation
+90°
a parallel
a meridian
azimuth 0°
180°
20°
-90°

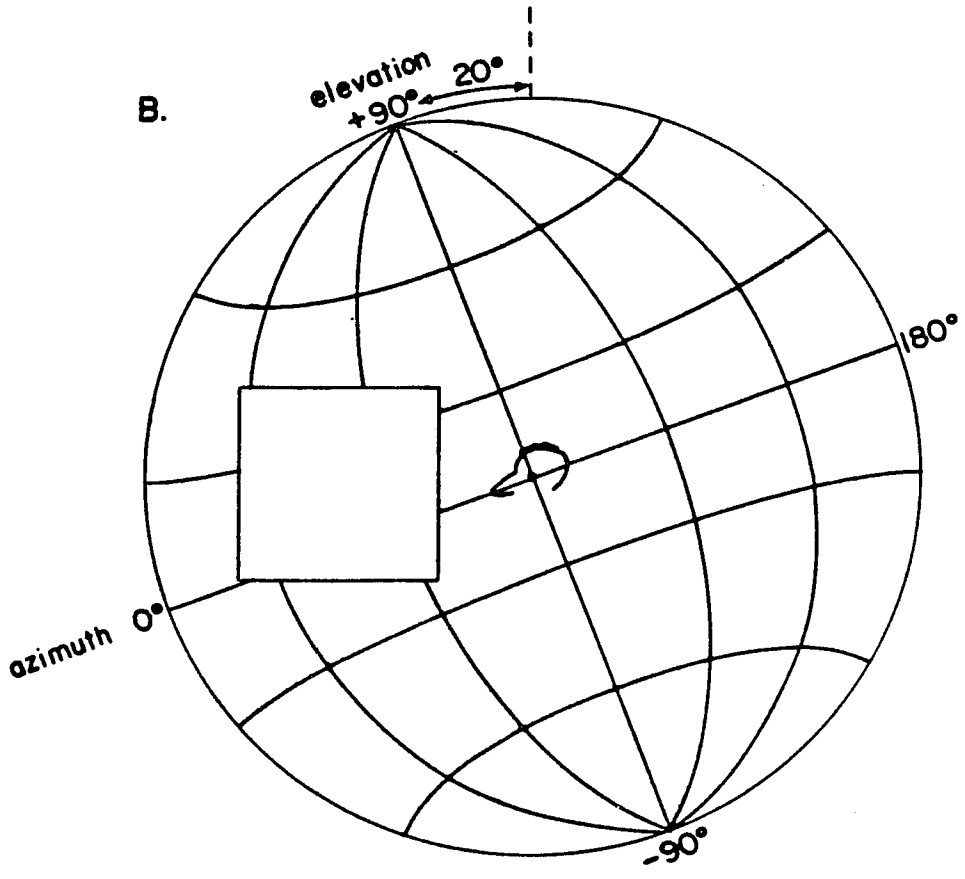
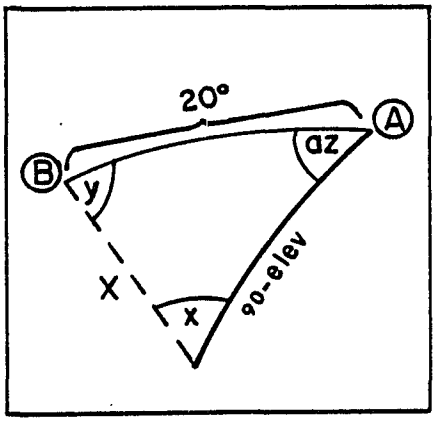

B.
elevation
+90°
20°
180°
azimuth
0°
-90°

Fig. 4. Explanation of method used to redefine receptive field locations and preferred directions of motion. The locations of 3 receptive field positions in the coordinate system of the stimulus apparatus are shown on the sphere: #1 is at azimuth 30, elevation 20, #2 at azimuth 60, elevation 20, #3 at azimuth 60, elevation 60. The positions are transformed into the new coordinate system referenced to the normal position of the bird's head using spherical trigonometry. Spherical triangles are formed by the meridian on the coordinate system of the apparatus (solid arc), the meridian on the coordinate system referenced to the bird (dashed arc) and the arc of 20 deg. rotation. In the inset, the spherical triangle for receptive field position #3 is shown again. The angle labeled az represents the original azimuth of the receptive field position. The arc labeled 90-elev represents the original elevation subtracted from 90 deg. The arc X and the angle y are the new elevation subtracted from 90 deg. and the new azimuth subtracted from 180 deg. respectively. The angle x is the amount by which directional tuning plots are rotated. The triangles are solved for x, X and y using spherical trigonometry. See text for further explanation.



A = pole with reference to stimulus apparatus

B = pole with reference to animal's normal head position

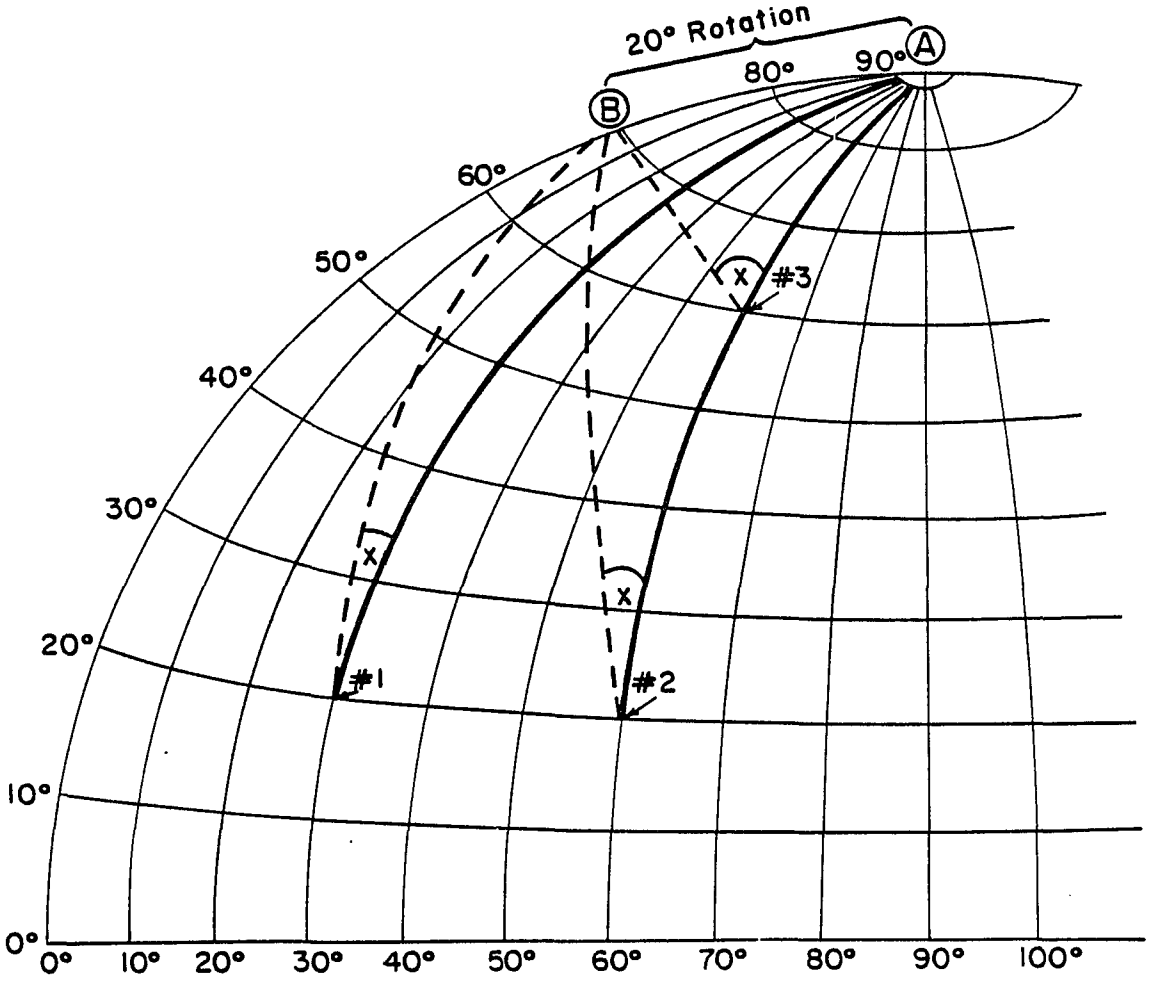


Fig. 5. Result of Fourier analysis of data from a hypothetical unit. Eight data points are plotted in polar coordinates. Radii of dotted arcs connecting data points are interpolations between radii of adjacent data points. Solid curve is fitted function. Within each curve, large ticks mark level of spontaneous firing and small ticks indicate 100 spikes. Maximum is exactly up; minimum is exactly down.

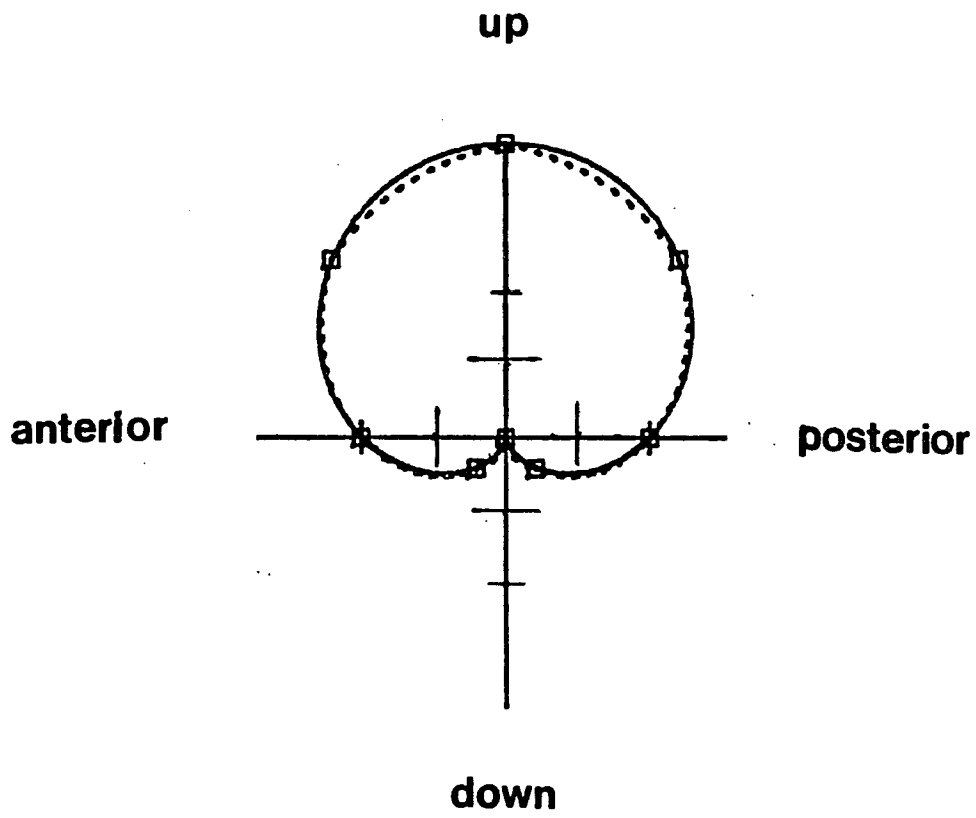

up
anterior
posterior
down

Fig. 6. Result of Fourier analysis of data from a unit in nBOR with a broad excitatory peak width. The solid line indicates the maximum of the fitted function which is inappropriately skewed toward one side of the peak. The dashed line indicates the corrected maximum which is centered between the points at which the curve was 75% of the difference between the maximum and the minimum, as explained in the text.

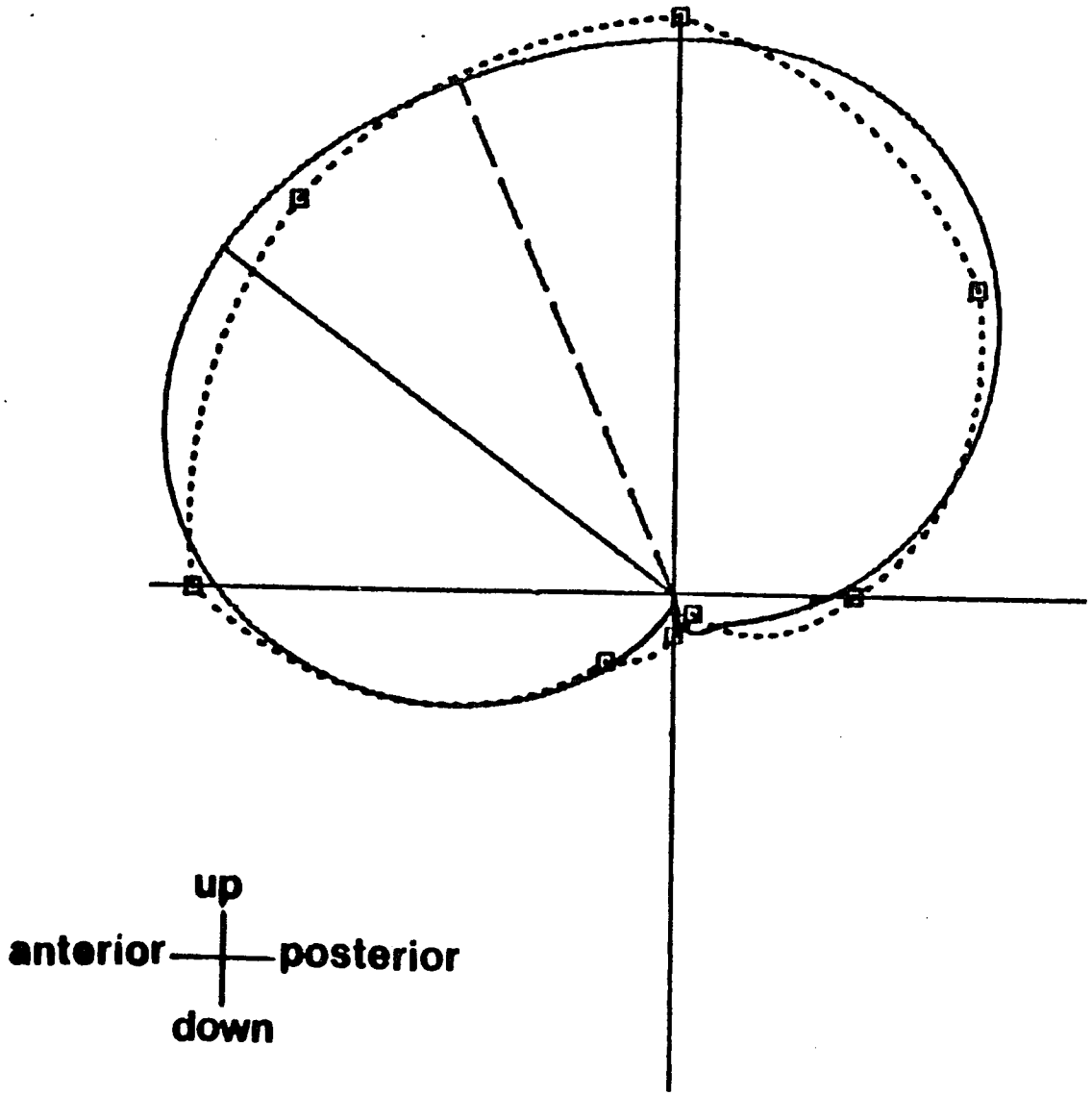
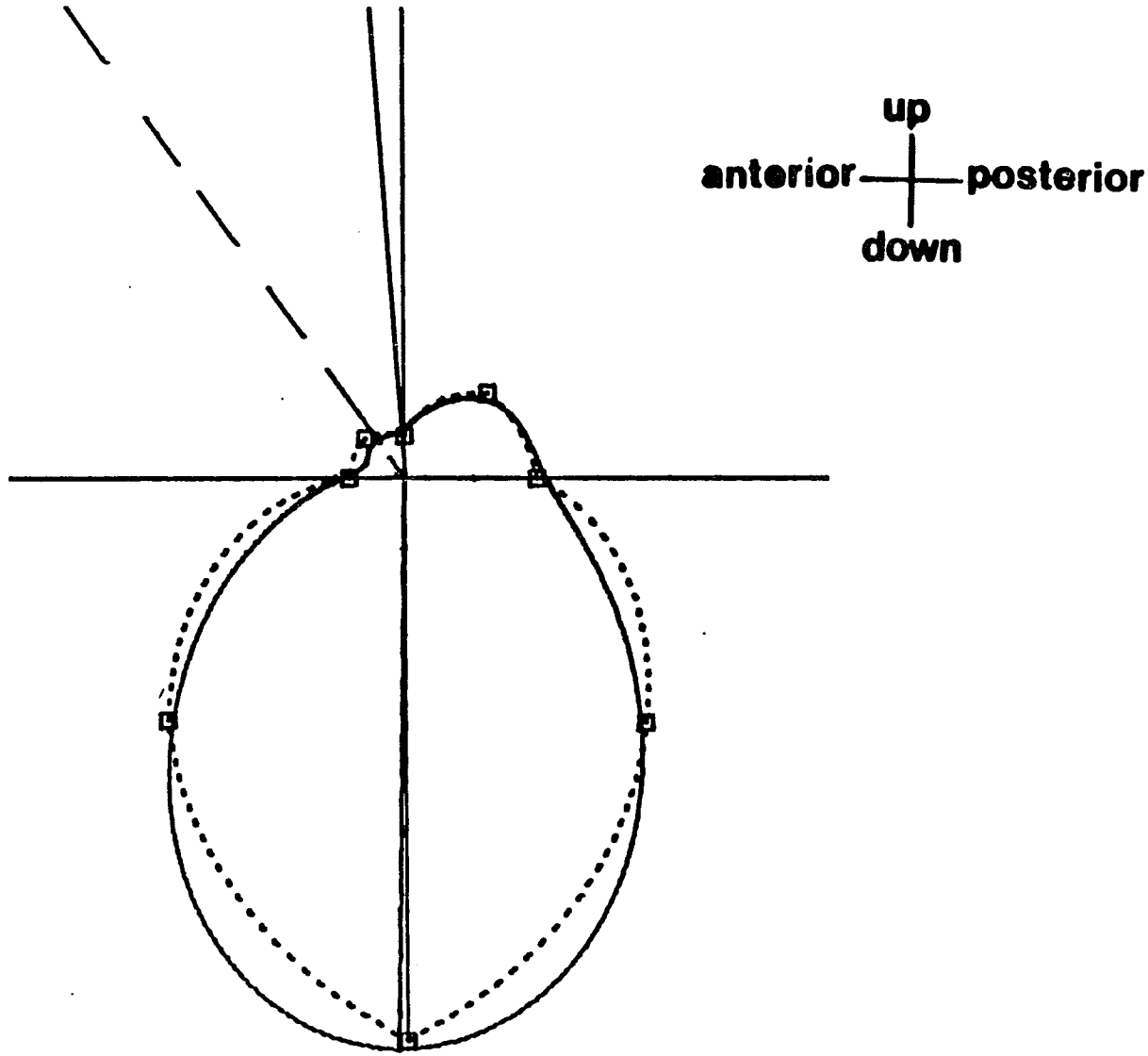

up
anterior
posterior
down

Fig. 7. Result of Fourier analysis of data from a unit in nBOR for which the inhibitory direction (indicated by solid line) was judged to be incorrectly identified using the method for finding the centers of peaks described in the text. The dashed line indicates the observer-corrected inhibitory direction, as explained in the text.


up
anterior
posterior
down

CHAPTER 3

ELECTROPHYSIOLOGY AND FUNCTIONAL ORGANIZATION OF nBOR

RESULTS

General Properties and Receptive Fields

Units in nBOR responded best to a moving, richly contoured random pattern covering the entire screen. They never responded to small stationary spots being turned on or off. Occasional units responded to small spots moved anywhere within the receptive field, but only when moved in the preferred direction.

Units had very large receptive fields, most frequently at least as large as the tangent screen and often larger. As can be seen in Fig. 32, most receptive field centers were in the more peripheral parts of the visual field. The significance of this pattern will be discussed below with the data from neonates.

The on-off properties of units in nBOR vary. Off units were found most frequently, but on and on-off units also occurred. The prevalence of off responses is consistent with findings in the retina

of cat (Nelson et al., 1978) and carp (Famiglietti et al., 1977) that off ganglion cells have their dendritic ramifications in sublamina a of the inner plexiform layer. Displaced ganglion cells of the avian retina, which provide the input to nBOR are also located in this sublamina (Karten et al., 1977; Reiner et al., 1979). The response to lights off occured with a latency of 25 to 30 msec., as shown in Fig. 8A. Some units responded to a flash of strobe light with an inhibition lasting 80 to 200 msec., as shown in Fig. 8B.

Directional Tuning

Most cells in nBOR are highly directionally selective and are best modulated by movement in vertical directions. There are two predominant classes of cells: a group of cells excited by generally upward movement and inhibited by downward movement and a second group excited by generally downward movement and inhibited by upward movement. Out of approximately 770 units recorded either singly (including 30 studied extensively) or in small groups, about 60% were excited by upward movement and 40% by downward movement. As will be discussed below, there was a dramatic tendency for units with similar directional preferences to be found together. This permitted making approximate estimates of directional selectivity from multi-unit as well as single unit recordings.

Directional tuning plots of single units excited by generally upward movement and inhibited by downward movement are shown in Fig. 9A and B. Of the 11 up units, 5 preferred movement up and anterior (Fig.

9A), while 6 preferred movement up and posterior (Fig. 9B) (mean 90 deg., stan. dev. 18 deg.). Units excited by generally downward movement and inhibited by upward movement are shown in Fig. 10A, B and C. Of 14 down units, 11 preferred movement down and anterior (Fig. 10 A and B) and 3 preferred movement down and posterior (Fig. 10C) (mean 265 deg., stan. dev. 13 deg.)

Only three units were best modulated by horizontal movement as is shown in Fig. 11. Two units preferred anterior motion and one preferred posterior motion. Two unusual bi-directional units are shown in Fig. 12. A summary of the excitatory and inhibitory directions of individual units modulated by vertical movement is shown in Fig. 13A and B. Excitatory and inhibitory directions of up units are both anterior and posterior to vertical, but those of down units are more often anterior to vertical.

In a previous report (Burns and Wallman, 1981) it was noted that the angles between excitatory and inhibitory directions of units were not always 180 deg. apart. For up units the median value for this angle was 184 deg. (not significantly different from 180 deg.). However, for down units the median value was 156 deg. (significantly different from 180 deg., Mann-Whitney U test, $p<0.001$). This led to the hypothesis that up units responded to linear motion, while down units responded to curvilinear motion, i.e., along arcs formed by angles less that 180 deg. apart. To continue testing this hypothesis, additional units were studied and the results from all units studied are shown in Fig. 14. The median values for differences in angle between excitatory and inhibitory directions are 180 deg. for up

units and 165 deg. for down units. Although there is a tendency for the angle between the excitatory and inhibitory directions of down units to be less than 180 degrees apart, the difference (Mann-Whitney U test $p<0.19$) is less than previously reported. Clearly the hypothesis needs to be tested directly using a rotatory visual stimulus.

Velocity Tuning

As shown by the examples in Fig. 15, units in nBOR respond best to slowly moving stimuli; for most units the preferred velocities are between 2 and 4 deg./sec. Velocity tuning is generally manifested most strongly by a change in firing in the excitatory direction (Fig. 15A), but occasional cells exhibit a substantial velocity-dependent change in spike rate in both the excitatory and inhibitory directions (Fig. 15B).

Retinotopic Organization of nBOR

There is a partial retinotopic organization in nBOR in which the frontal to lateral visual field is represented in dorsal to ventral nBOR. This is shown in Fig. 16 in which the locations of units recorded in single tracks in nBOR are plotted against the azimuths of their receptive field centers. There is a very strong tendency for units with frontal receptive fields to be located in the more dorsal part of the nucleus and for units with lateral receptive fields to be located in the more ventral part (t test of whether slope of

regression line differs from zero, $t=-5.35$, $df=15$, $p<0.001$). These data are taken from single unit recordings or, in a few cases, from two units recorded together. In addition, this pattern of receptive field centers progressing from frontal to lateral as the electrode was moved ventrally in nBOR was observed qualitatively in many tracks through the nucleus.

To further test these findings, 5 tracks were made in one brain in the rostrocaudal plane and multi-unit recordings from approximately 202 units were taken at 44 loci throughout the dorsoventral extent of nBOR. Responses of units were tested qualitatively by using the audio monitor or quantitatively by taking spike counts when the tangent screen was centered at azimuths of 41 +/- 11 deg., 68 +/-15 deg., and 90 +/- 16 deg. The results confirm that there is a retinotopic organization in nBOR in which frontal visual fields are located more dorsally and lateral visual fields are located more ventrally (Fig. 17). As found here and in many other experiments, most units in nBOR responded best to stimuli centered in one of these two portions of the visual field and fewer responded to stimuli centered at 68 deg., which is close to the optic axis.

To evaluate the retinotopic organization of nBOR more extensively, quantitative data were obtained from brain loci labelled 1, 2 and 3 in Fig. 17. Multi-unit spike counts were taken at the three loci when the tangent screen was centered at each of the 9 locations shown in Fig.18. Contour lines of spike frequency illustrate the progression from frontal to lateral visual fields as the electrode was moved ventrally. Neither in this experiment nor in others was

there evidence of a retinotopic organization of superior and inferior visual fields.

Functional Organization of nBOR

There is a second pattern of organization in nBOR in which units are grouped according to directional preference. In the more rostral portion of nBOR up units tend to be found throughout the entire dorsoventral extent of the nucleus. In the middle and caudal portions of nBOR, up units tend to be located in the dorsal portion of the nucleus and down units tend to be located in the ventral portion. In multi-unit recordings of from 2 to 10 units, it was almost always the case that all units recorded at once had similar directional preferences and that the preferences shifted abruptly. The organization of up and down units in nBOR is illustrated in Fig. 19, which shows the preferred directions and recording sites of approximately 770 units recorded at 155 loci in 33 electrode tracks. The few horizontal units are located in the more medial and lateral parts of nBOR.

Thus, nBOR is organized by directional preference in both the rostrocaudal and dorsoventral dimensions. In the rostrocaudal dimension there is a progression from almost exclusively up units to a combination of up and down units. In addition, in the more caudal part of the nucleus, there is a dorsoventral organization in which up units tend to be dorsal to down units.

It is of interest to compare this organization to the anatomical divisions of nBOR. On the basis of cell size, nBOR has been divided

into a dorsal portion, nBORd, and a larger, more ventral portion, nBOR proper (Repérant, 1973; Brecha and Karten, 1979; Brecha et al., 1980). These are shown in Fig. 20. The nBORd projects to the ventral division of the oculomotor complex, while the nBOR proper projects to the dorsolateral division (Brecha and Karten, 1979; Brecha et al., 1980). The ventral division innervates the superior rectus and the dorsolateral division innervates the inferior rectus (Heaton and Wayne, 1983). The functional organization of up and down units in nBOR described in the present study does not coincide with the anatomical divisions of nBOR, nor with the efferent projections to the oculomotor nucleus. The implications of this finding will be addressed in the discussion section.

Relation Between Retinotopic and Functional Organization of nBOR

There are, then, two notable patterns of organization in nBOR: one retinotopic and the second by directional preference. The relationship between these two patterns, however, is such that both up and down units have receptive fields in both the frontal and lateral visual fields. Frontal fields are represented in the dorsal part of nBOR, while lateral fields are represented in the ventral part. Up units are found throughout the dorsoventral extent of the rostral part of the nucleus, which contains both frontal and lateral fields. In the middle and caudal parts of the nucleus frontal fields and up units are dorsal and lateral fields and down units are ventral. However, these divisions are not exactly aligned, as can be seen in Fig. 17.

The two most caudal tracks contained both up and down units; the line labeled D marks the beginning of the down area. There are down units with frontal visual fields as a result of the overlap rather than coincidence of the dorsoventral division of up and down units and the dorsoventral division of frontal and lateral visual fields. Furthermore, down units with frontal as well as lateral receptive fields were found in single unit recordings from middle and caudal nBOR.

DISCUSSION

Characteristics of nBOR Units in Relation to Stabilizing Eye Movements

The general characteristics of neurons in nBOR strongly implicate them in the control of stabilizing eye movements. For the eyes to remain relatively stable in space despite movements of the head, they must move at approximately the same velocity, but in the opposite direction, as the head. If these head movements are signalled by the semicircular canals, the signal is unambiguous. If, however, the signal comes from the visual system (as it does at low velocities of head movement), only the movement of the whole visual world across the retina (retinal slip) can signal head movement with reliability. Since the resulting stabilizing eye movements (optokinetic responses) are basically reflexive, it is necessary for the visual system neurons providing the input to this system to filter out irrelevant characteristics. Thus, one would expect neurons to have large

receptive fields and to be relatively unresponsive to small stimuli, since, otherwise, every moving object would initiate optokinetic eye movements. Similarly, one would expect neurons to respond to slow stimulus movement since it is only to low velocity movement that optokinetic responses are effective. Since optokinetic responses must be opposite in direction to head movement, one expects directional selectivity.

Cells in nBOR have precisely these characteristics. They have extremely large receptive fields. Most cells do not respond at all to small stationary or moving targets. Although I recorded from occasional units which did respond to small spots moving in the preferred direction, they, like the others, responded best to large fields of stimuli, implying that even a weak retinal slip signal would overwhelm any response to small targets.

Most cells in nBOR are decidedly directional and prefer slow vertical movement; cells preferring horizontal movement are rare. This result is consistent with studies using 2-deoxy-D-glucose that showed an increased metabolic rate in nBOR and nBORd during vertical, but not horizontal, whole-field visual stimulation in chickens (McKenna and Wallman, 1981). Also, lesions of nBOR and nBORd in chickens abolish vertical and torsional OKN, while leaving horizontal OKN unaffected (Wallman et al., 1981). Units in nBOR in pigeons have properties essentially similar to those in chickens. They have large receptive fields, respond only to large stimuli, are directionally selective, particularly for upward motion, and respond best to slow stimulus velocities of 0.5 to 5 deg./sec. (Morgan and Frost, 1981).

In a brief report of a qualitative study of units which could be antidromically activated from the vestibulocerebellum or oculomotor nuclear complex units were reported to have large peripheral receptive fields, to be velocity sensitive and to respond most often to vertical motion (Britto et al., 1981). Although many units were direction selective, the majority were described as being axis specific. These latter units responded to movement in both directions along a particular axis (usually vertical) and showed weaker responses or even inhibition to movement along other axes. Such axis specific units were not found in the more detailed quantitative studies of Morgan and Frost (1981). Taken together, these data indicate that vertical retinal slip signals which provide visual input to stabilizing eye movements in birds are processed in nBORd and nBOR proper. The characteristics of units in the accessory optic system of other vertebrates are also consistent with a role in stabilizing eye movement. In rabbits, units respond best to large stimuli, are directionally selective and prefer slow stimulus velocities of 0.1 to 1 deg./sec. Units in MTN are directionally selective for upward and somewhat posterior motion, those in LTN for downward and somewhat posterior motion, and those in DTN for horizontal motion (Simpson et al.,1979). Neurons in the MTN of cats have large receptive fields (approximately 60 x 40 deg.), respond to large, but not small stimuli, prefer low stimulus velocities of approximately 0.8 deg./sec. and are directionally selective primarily for downward vertical motion, although a minority of units respond best to upward motion (Grasse and Cynader, 1982). Units in LTN respond to either upward or downward

motion and those in DTN respond best to temporal-to-nasal motion. Preferred velocities in LTN are between 0.8 and 12.8 deg./sec. and in DTN between 6.4 and 12.8 deg./sec. Recent studies also show that the nBOR of frogs contains neurons which respond to very large targets moving at slow velocities (less than 5 deg./sec.), and are directionally selective for upward and downward motion and less often for horizontal motion (Cochran et al., 1984). Recordings from the basal optic neuropil in newts also show that most units respond best to vertical motion (Manteuffel, 1982). There is substantial evidence then, for a similar role and pattern of organization of the accessory optic system in all three classes of vertebrates--birds, mammals and amphibians--in which it has been studied.

On the other hand, this particular oculomotor function of the accessory optic system in chickens does not rule out additional functions for nBOR. It is to be noted (Fig. 19) that most recording sites in this study were in the medial half of nBOR. Although this could be due to a sampling bias, the possibility remains that units in the more lateral half have stimulus characteristics which were not discovered in this study nor in the 2-deoxy-D-glucose studies and have, therefore, different functions. In pigeon nBOR all units studied were directionally selective (Morgan and Frost, 1981), but the location of specific recording sites within the nBOR were not described. Grasse and Cynader (1982) report that approximately one-quarter of the units which they studied in the cat accessory optic system were not directionally selective but did respond to changes in levels of background illumination. Transection of BOR in frogs

results in increased latency to fly-catching behavior (Fite et al., 1983), although this could be a secondary effect due to loss of stabilizing eye movements . Lesions of nBOR in birds (Wallman et al.,1981; Gioanni et al., 1983b) definitely result in deficits in OKN, but other behaviors were not tested in these experiments. However, intensity and pattern discrimination showed no significant impairments after lesions of nBOR in pigeons (Hodos and Bonbright, 1975). In monkeys, lesions of the accessory optic system together with the striate cortex resulted in inability to perform a light versus no-light discrimination task, suggesting a possible role for the accessory optic system in discriminating differences in total luminous flux (Pasik and Pasik, 1973). However, lesions of the accessory optic system or striate cortex alone did not result in such impairment and gross behavior was normal; OKN was not studied. Simpson (1984) suggests that these lesions were close to, but not in, the accessory optic system of the monkey since the site of the lesions differs from other anatomical descriptions of the monkey's accessory optic system.

In summary, the present research has provided strong evidence for the role of the avian accessory optic system in stabilizing eye movements based on unit recordings in chickens. These findings are consistent with 2-deoxy-D-glucose and lesion studies in this species. Results from unit recordings and lesions in several other species of vertebrates indicate that the accessory optic system has a similar function in many vertebrates.

Functional Organization of nBOR and Its Relation to Efferent Projections

One of the most striking findings of this study is the pattern of segregation of up and down units in specific portions of nBOR. This functional division within the nucleus differs substantially from the anatomical division, as can be seen in Fig. 19. The functional segregation of units is such that only up units are found in rostral nBOR, whereas both up and down units are found in caudal nBOR. Furthermore, up units are found in the dorsal half and down units in the ventral half of the caudal part of the nucleus. This functional organization does not coincide with the anatomical divisions of the nucleus into nBORd and nBOR proper.

These differences between the functional and anatomical organization of nBOR raise some questions concerning the function of the efferent projections to the oculomotor nuclei. Using anterograde autoradiographic and retrograde horseradish peroxidase techniques, it has been shown that nBORd projects to the ipsilateral ventral division of the oculomotor complex, while nBOR proper projects to the contralateral dorsolateral division (Brecha and Karten,1979; Brecha et al., 1980). The ventral division of the oculomotor complex innervates the contralateral superior rectus and ipsilateral inferior oblique muscles, while the dorsolateral division innervates the ipsilateral inferior rectus muscle (Heaton and Wayne, 1983). Since nBOR detects retinal slip signals that provide the input to vertical OKN, it has been hypothesized by Burns and Wallman (1981) that nBORd

carries excitatory upward retinal slip signals to oculomotor neurons moving the contralateral eye up and that nBOR proper carries excitatory downward retinal slip signals to oculomotor neurons moving the contralateral eye down. However, since the functional organization of nBOR, as shown in the present study differs so markedly from the anatomical divisions, the actual situation may be more complex. Since units in nBORd respond to upward motion, it is likely that the projection to oculomotor neurons moving the eye up do carry excititory signals as hypothesized. However, since units in nBOR proper respond to both upward and downward motion, both excitatory and inhibitory signals may be transmitted to oculomotor neurons which move the eye down. Studies of OKN in chickens in response to vertical visual stimuli show that OKN gain to upward motion is 1.5 times greater than the gain to downward motion (Wallman and Velez, 1985). It is possible that rapid inhibitory signals carried directly to oculomotor neurons moving the eye down may facilitate the stronger OKN response to upward stimuli. On the other hand, neurons in nBOR proper carrying upward retinal slip signals may not project to the oculomotor nuclei, but to other target sites. There is, indeed, evidence for this hypothesis. The efferent projection to oculomotor neurons that move the eye down is predominantly from cells in the caudal region of nBOR proper (Brecha et al., 1980). The position of these cells corresponds well with the location of the down units which I recorded from in nBOR proper. On the other hand, the more rostral cells in nBOR proper project predominantly to other target sites (Brecha et al., 1980). The position of these cells compares with the location of the up units which I

recorded from in nBOR proper.

It should be pointed out that the direct projections from nBOR to the oculomotor nuclei are unlikely to carry sufficient information to produce the OKN response. There are several reasons for this. First, in addition to the oculomotor projection, nBOR also projects directly to other structures implicated in the visual control of stabilizing eye movements: the inferior olive, vestibulocerebellum, interstitial nucleus of Cajal (Brecha et al. 1980), and the vestibular nuclei (Wold, 1979). Furthermore, a simple excitatory connection from nBOR to the oculomotor neurons would be very unlikely to produce optokinetic nystagmus, since a constant velocity stimulus would produce a constant level of activity in nBOR, and hence, in oculomotor neurons. This would simply cause the eye to shift abruptly to a new position and remain there. To transform the steady nBOR output into a constant velocity eye movement would require integrating the nBOR signal to produce a ramp. In addition, the temporal characteristics of OKN, for example, its persistance if the lights are turned off (optokinetic afternystagmus), argues strongly for another stage of integration to provide this velocity storage (Cohen et al., 1977; Raphan et al., 1979). What then is the function of the direct pathway? It is possible that the eyes may act quite sluggishly and require a feedforward velocity signal to function well and this may be provided by excitatory connections in the direct pathway. Such a pathway is included in Collewijn's (1972) model of OKN in the rabbit, and is a common feature of other oculomotor models (Carpenter, 1977). Furthermore, upward OKN responses may be facilitated by a rapid direct

inhibition of downward movement of the eyes.

Retinotopic Organization of nBOR and Its Relation to Functional Organization

In spite of the large receptive fields of units in nBOR, there exists a partial retinotopy within the nucleus. Centers of receptive fields progress from frontal to lateral in the dorsoventral extent of nBOR. A somewhat similar retinotopy has been found using retinal lesion and ganglion cell terminal degeneration methods (Ehrlich and Mark, 1984). That study described inferior temporal (frontal visual field) retinal projections to mediodorsal nBOR, nasal (lateral visual field) projections to the medioventral nBOR and superior retinal projections to lateral nBOR. There is agreement between these results and mine with respect to frontal to lateral visual fields, but I found no retinotopy with respect to inferior to superior visual fields. As noted above, few unit recordings were made in the lateral half of nBOR; however, both inferior and superior visual fields were represented in both the dorsal and ventral portions of the medial half of nBOR. In any case, the chicken is the first species reported to have any retinotopic organization in the accessory optic system. Perhaps this is related to the prominent torsional OKN seen in this lateral-eyed species (Wallman and Velez, 1985). Unlike the visual stimuli for vertical or horizontal OKN, the stimulus for torsional OKN contains dramatically different directions of motion in different parts of the visual field. The detection of the direction of

whole-field torsional motion seems to require a retinotopically organized directionally selective input. Although such an input could come totally from the DRGCs, the limited size of receptive fields of retinal ganglion cells (Miles, 1972a) argues that it does not. Furthermore, there is no evidence that retinal ganglion cells respond to torsional stimuli.

With respect to this proposed function of retinotopy in nBOR, it is of interest to examine the relationship between the retinotopy and the functional organization of up and down units. The relationship is such that cells directionally selective for both upward and downward motion have receptive fields throughout the visual field. Up units with frontal receptive fields are found dorsally throughout the entire rostrocaudal extent of nBOR, but up units with lateral receptive fields are found only in rostral nBOR. Thus, up units in nBOR have receptive fields throughout the visual field. This is also the case with down units, which are found only in caudal nBOR. In this part of the nucleus, although there is a dorsoventral division of up and down units and a dorsoventral division of frontal to lateral receptive fields, these two divisions do not coincide, but overlap in such a way that down units have receptive fields in the frontal as well as middle and lateral visual field.

Do nBOR Neurons Code Retinal Slip in Vestibular Coordinates?

Although OKN, like other eye movements, is usually considered to be organized around horizontal, vertical and torsional movements of the eyes, there have been suggestions that the more natural axes are those of the semicircular canals. The argument is that since VOR requires that the circuitry exist to convert head velocity (in vestibular coordinates) into compensatory eye movements (Suzuki et al. 1964), and since VOR and OKN summate quite linearly (Baarsma and Collewijn 1974; Batini et al. 1979), the visual input, too, may be in vestibular coordinates. This theory, most explicitly stated by Simpson et al (1979), holds that neurons of the accessory optic system respond best to retinal slip along curved rather than linear paths and in directions that would be evoked by head movements maximally stimulating particular canals.

I will consider first the hypothesis that units respond best to stimuli along curved rather than linear paths. As shown in Fig. 14, the excitatory and inhibitory directions for up units are 180 deg. apart, but for down units the excitatory and inhibitory directions are not opposite, but 165 deg. apart. Based on these characteristics it is reasonable to conclude that up units respond best to linear motion and that down units may respond best to a combination of linear and rotational motion. Similar asymmetric units have also been found in the rabbit accessory optic system (Simpson et al. 1979.) Such asymmetry suggests that cells are most strongly modulated by stimulus movement along an arc rather than a linear path. The question arises

as to whether this asymmetry is a property of retinal afferents to nBOR or whether it is found only in neurons within nBOR itself. Cells with asymmetric excitations and inhibitory directions have not been described in studies of avian retinal ganglion cells (Miles, 1972a; Pearlman and Hughes, 1976a). Furthermore, this property does not seem compatible with the mechanisms of directional selectivity which have been extensively analyzed in rabbit retina (Barlow and Levick, 1965; Oyster, 1968; Wyatt and Daw, 1975). It appears, then, that while retinal ganglion cells are best modulated by linear stimulus motion, down units are best modulated by curved stimulus motion and that this transformation takes place within nBOR.

The second prediction of the vestibular coordinate hypothesis is that neurons of the accessory optic system respond best to retinal slip in directions evoked by head movements maximally stimulating particular canals. Fig. 21 summarizes these relationships, using the conventional canal representation, that is, that the anterior and posterior canals on the same side are perpendicular to each other and at 45 deg. to the saggital plane. In lateral-eyed animals, such as the chick, both ipsilateral canals show an excitatory response to head movement that produces upward retinal slip. Therefore, to sum upward and downward retinal slip in one eye with canal signals requires summing with one of the contralateral canals. The optic axis of the chick is approximately 60 deg to the midline. If the animal moves its head downward in such a way as to maximally stimulate the left anterior canal, the optic axis of the left eye would move (if no compensatory eye movements were made) down and slightly posterior along the

arc LA. This would produce retinal slip up and slightly posterior (the opposite direction along arc LA). If the head moves up so as to maximally stimulate the right anterior canal, the optic axis of the left eye would move up and anterior along the arc RA. This would produce retinal slip down and anterior (the opposite direction along arc RA). For the visual and vestibular signals produced by these head movements to summate in the simplest way (i.e., without computation of an axis transformation), the directional selectivities of accessory optic system neurons should be arranged along the same arcs. To say it differently, the accessory optic system and hence the optokinetic behavior system would be composed of subsystems that resolve any direction of retinal slip into the same components as the semicircular canals would resolve the head movement that produced the retinal slip. Since the optic axis in chicks is at approximately 60 deg. to the midline, the subsystem in the accessory optic system associated with the left anterior canal (arc LA) should respond best to stimulus movement along a more linear path, since this canal plane is only 15 deg from the optic axis. The subsystem associated with stimulation of the right anterior (arc RA) should respond best to stimulus movement along a more curved path, since this canal plane is 105 deg from the optic axis of the left eye. Units in nBOR, as shown in Fig. 13, are predominantly of two types: one that may be best modulated by movement up (along arc LA) and one by movement down and anterior (along arc RA), both corresponding to stimulation of anterior canals. These results are similar to those of Simpson et al. (1979) in the rabbit, although those authors account for their results in a slightly

different way. They describe their results in words partly opposite to those used here; for example, they describe some MTN cells that respond best to downward and posterior movement. However, since their stimulus pattern was above the optic axis and in between the two canal axes, this would correspond to the upper part of arc RA in Fig. 21, over this part of the arc, movement down and posterior is part of the same movement path that I call down and anterior. It is of consequence that OKN in chicks is also best in directions that approximately correspond to stimulation of the contralateral anterior canals (Wallman and Velez, 1985). In monkeys (Matsuo et al., 1979), cats (Evinger and Fuchs, 1978) and humans (Jung and Kornhuber, 1964), the gain of upward OKN exceeds that of downward OKN. In these species upward OKN may correspond to stimulation of the anterior canals. In summary, up units in nBOR have symmetric excitatory and inhibitory directions corresponding with preference for stimulus motion along a more linear path and down units have somewhat asymmetric excitatory and inhibitory directions which may correspond with a preference for stimulus motion along a more curved path. The directional preference of units is for movement up or somewhat down and anterior, which may correspond with the directions of motion that best stimulate the anterior semicircular canals. This provides some evidence, then, for the hypothesis that nBOR neurons code retinal slip in vestibular coordinates. A more convincing test of this hypothesis, however, awaits the testing of responses of units in nBOR to curvilinear stimulus motion.

Fig. 8.A. An example showing the short latency of nBOR units to turning room lights off. The arrow indicates the start of the decline in illumination; therefore, the latencies shown overestimate the actual latency. B. Record showing the inhibitory response of one nBOR unit to strobe flash. Before the flash the unit showed spontaneous activity (not shown). After the flash, there was first a long-lasting (80 msec.) inhibition, then a possible rebound excitation, and finally a return to activity comparable to pre-flash levels.

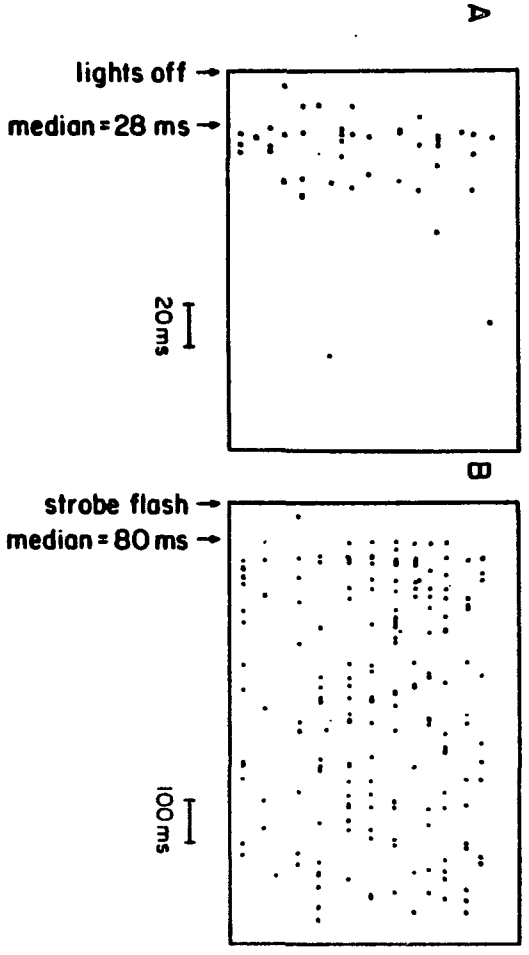
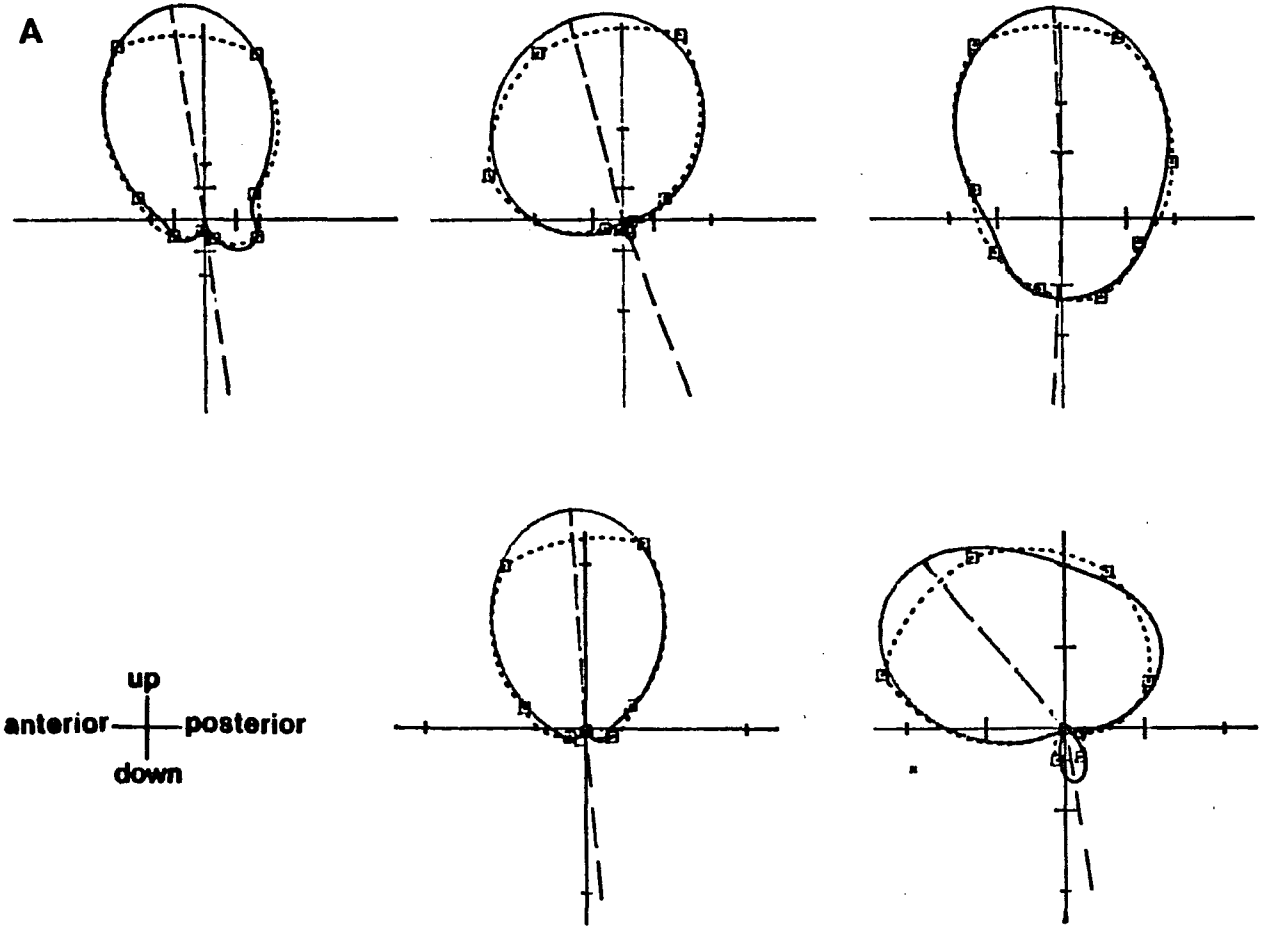

A
lights off
median = 28 ms
20 ms
B
strobe flash
median = 80 ms
100 ms

Fig. 9A and B. Directional tuning plots of units excited by upward movement and inhibited by downward movement. Dashed lines indicate excitatory and inhibitory directions as defined in methods. Occasionally a unit lacked a clear inhibitory direction. Within each curve, the large ticks mark the level of spontaneous firing. Small ticks indicate 100 spikes per total stimulus duration, except in plots marked by an x where they indicate 10 spikes or by a o where they indicate 1000. Occasionally data on spontaneous rates were lacking.


A
up
anterior
posterior
down

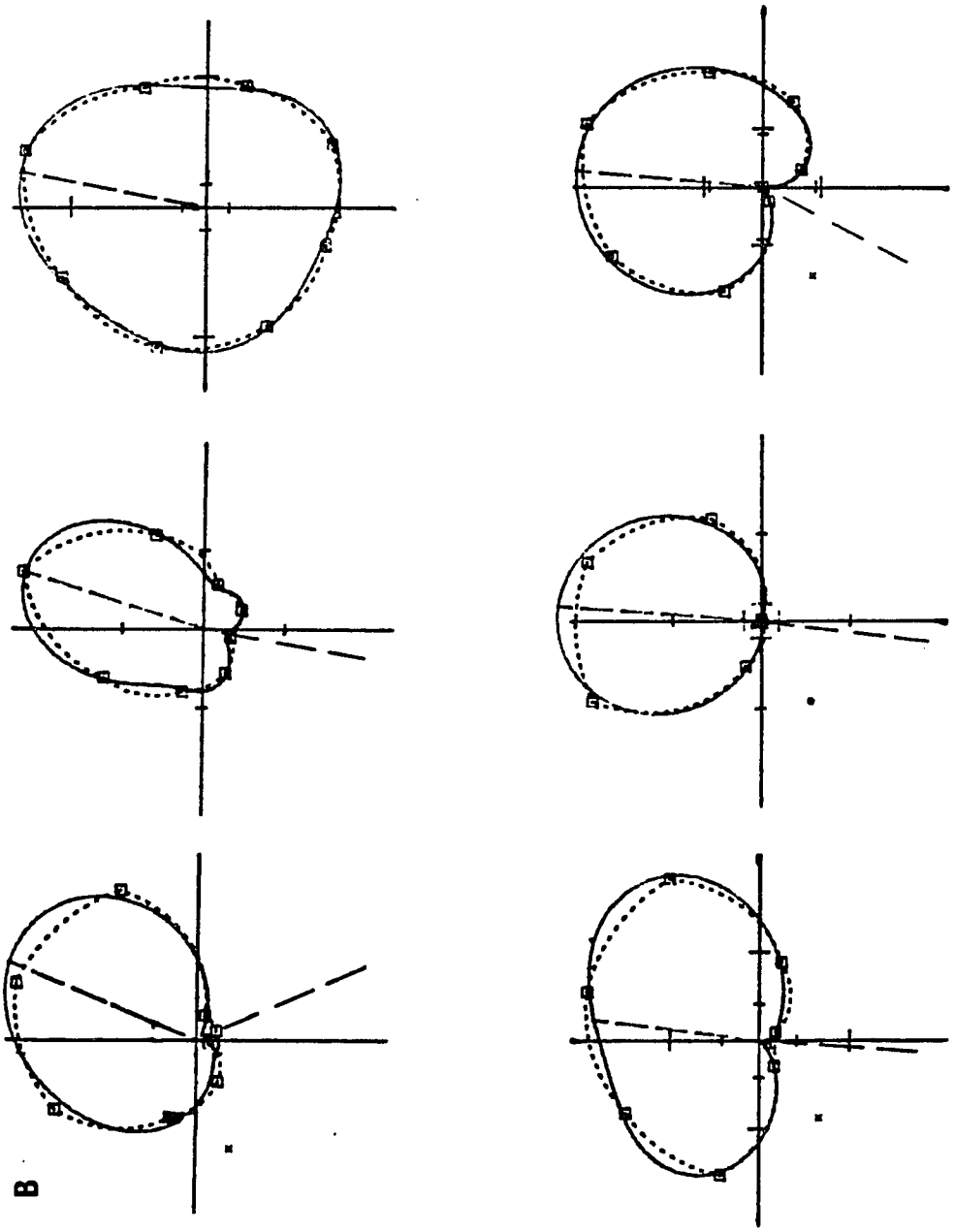
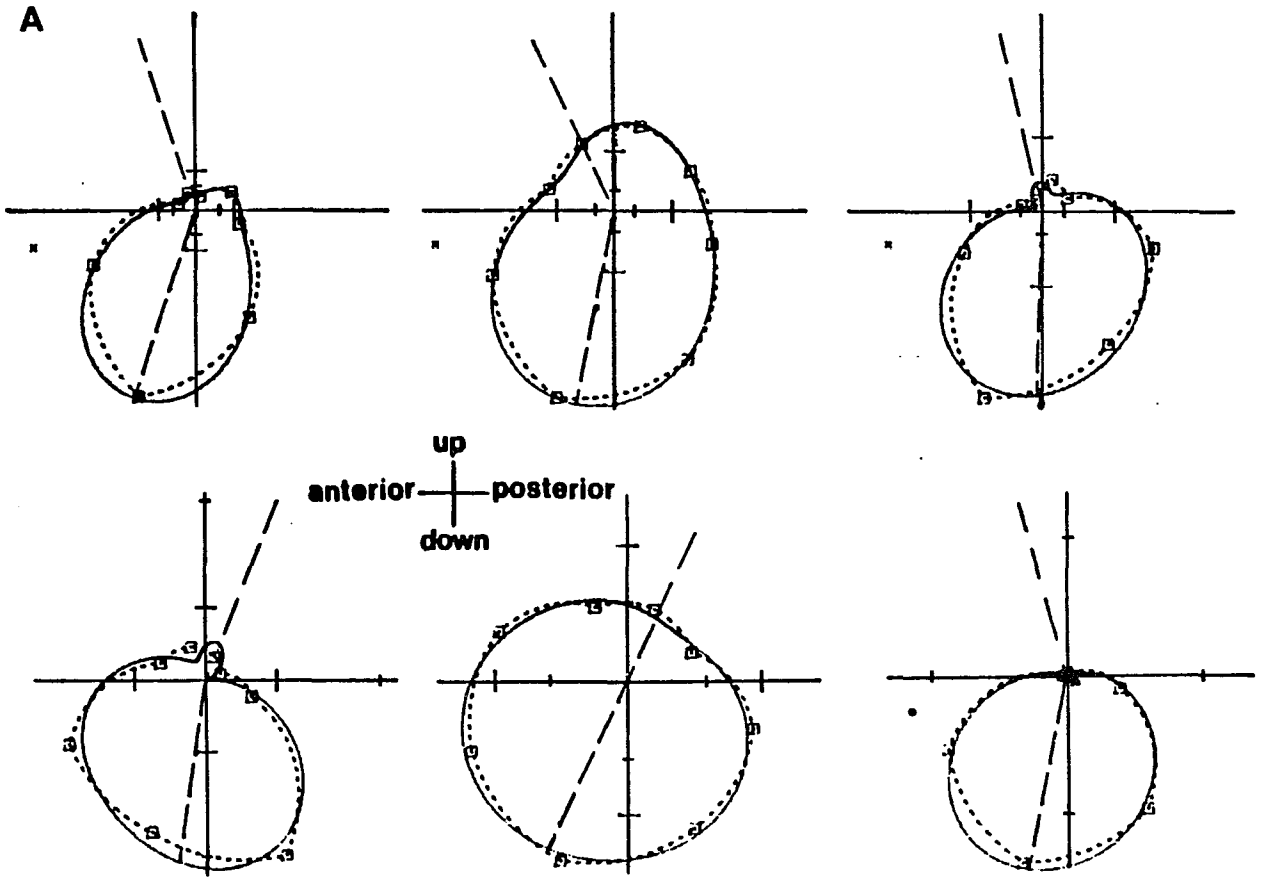
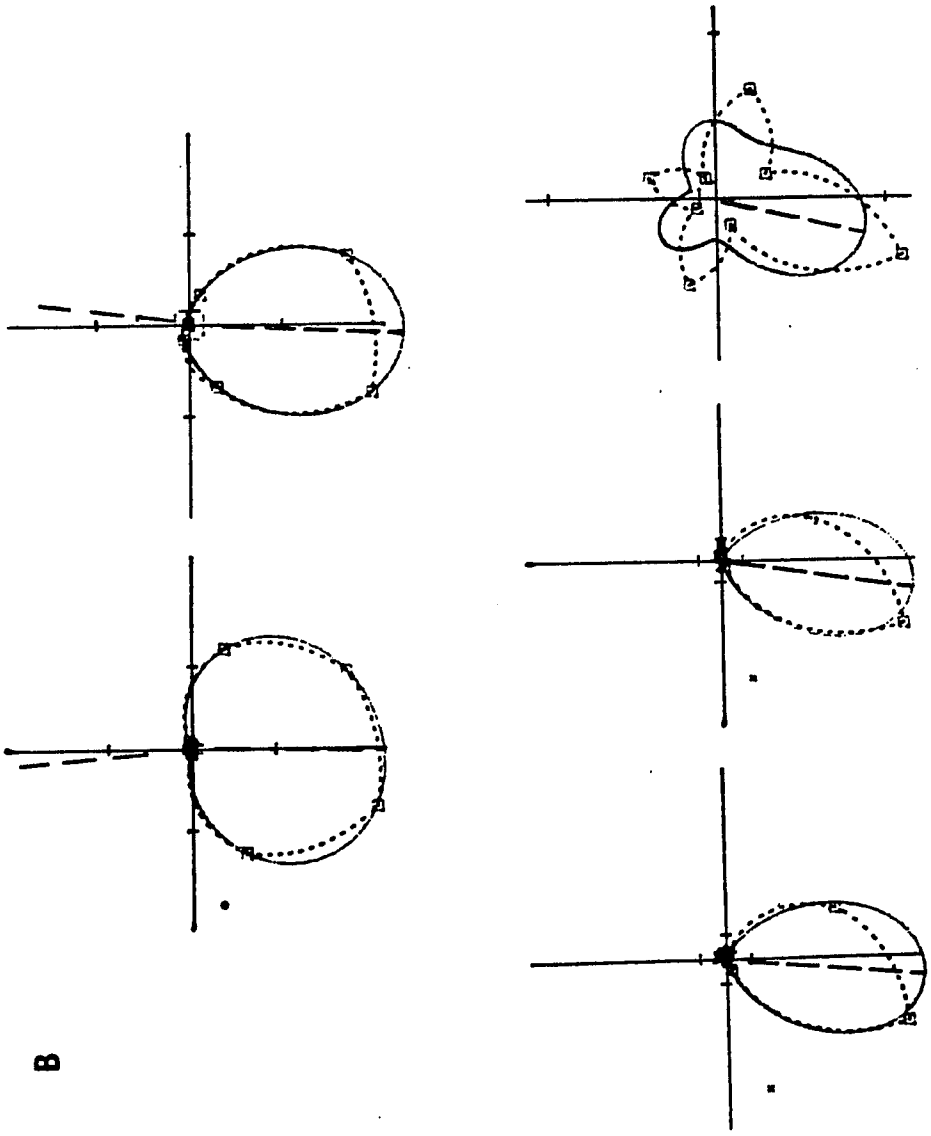
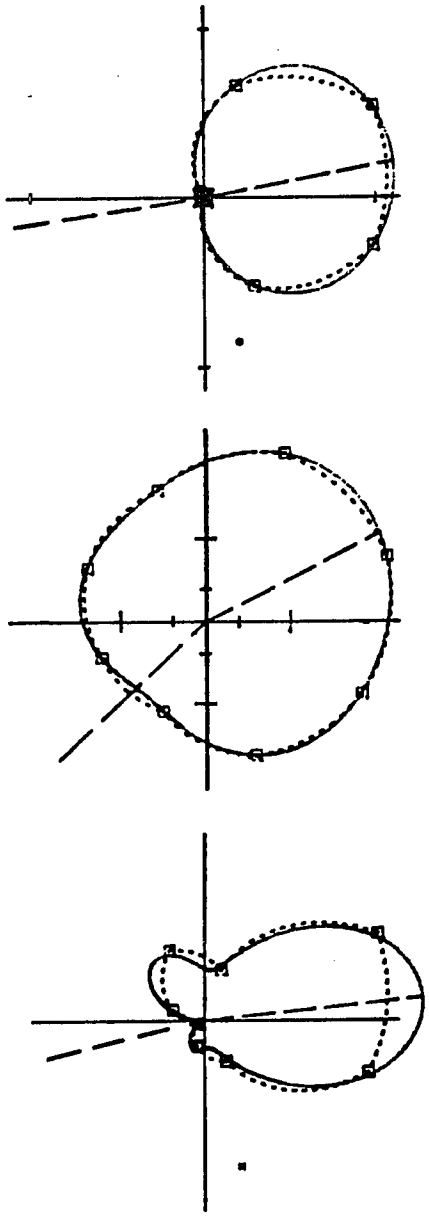

B

Fig. 10A,B and C. Directional tuning plots of units excited by downward movement and inhibited by upward movement. Conventions as in Fig.9.


A
up
anterior
posterior
down

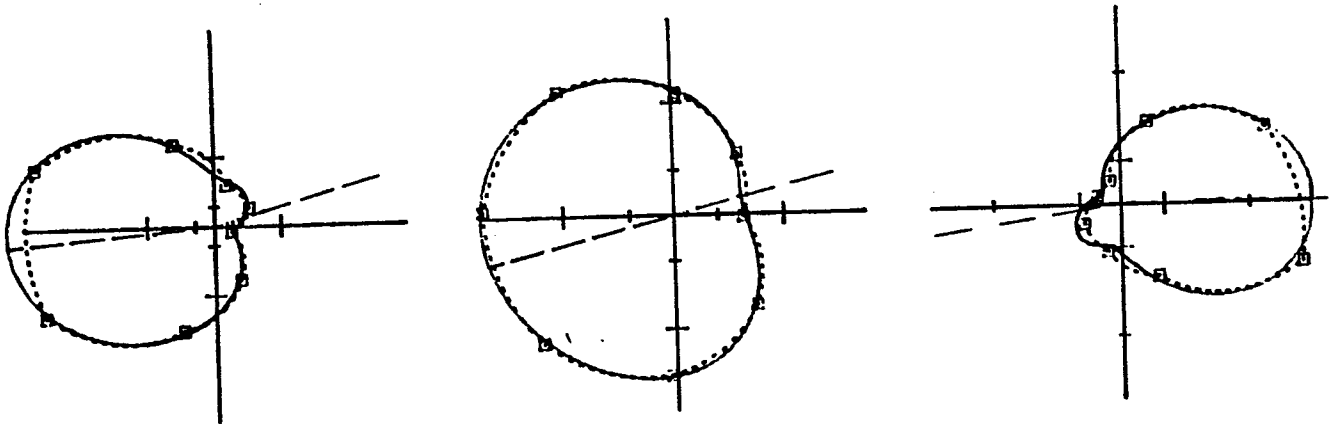


B



C

Fig. 11. Directional tuning plots of units excited by horizontal movement. Conventions as in Fig.9.



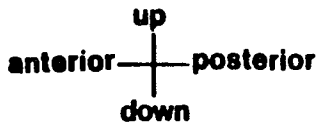

up
anterior
posterior
down

Fig. 12. Directional plot of two unusual bidirectional units. No attempt was made to assign excitatory or inhibitory directions. Conventions as in Fig.9.

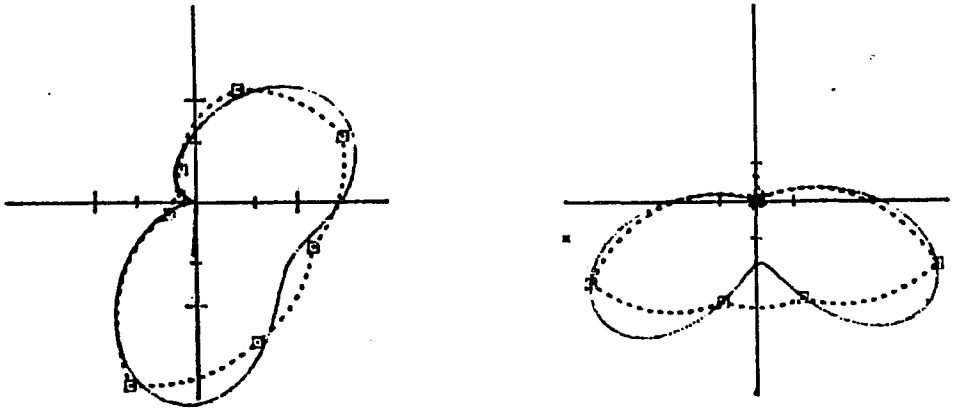
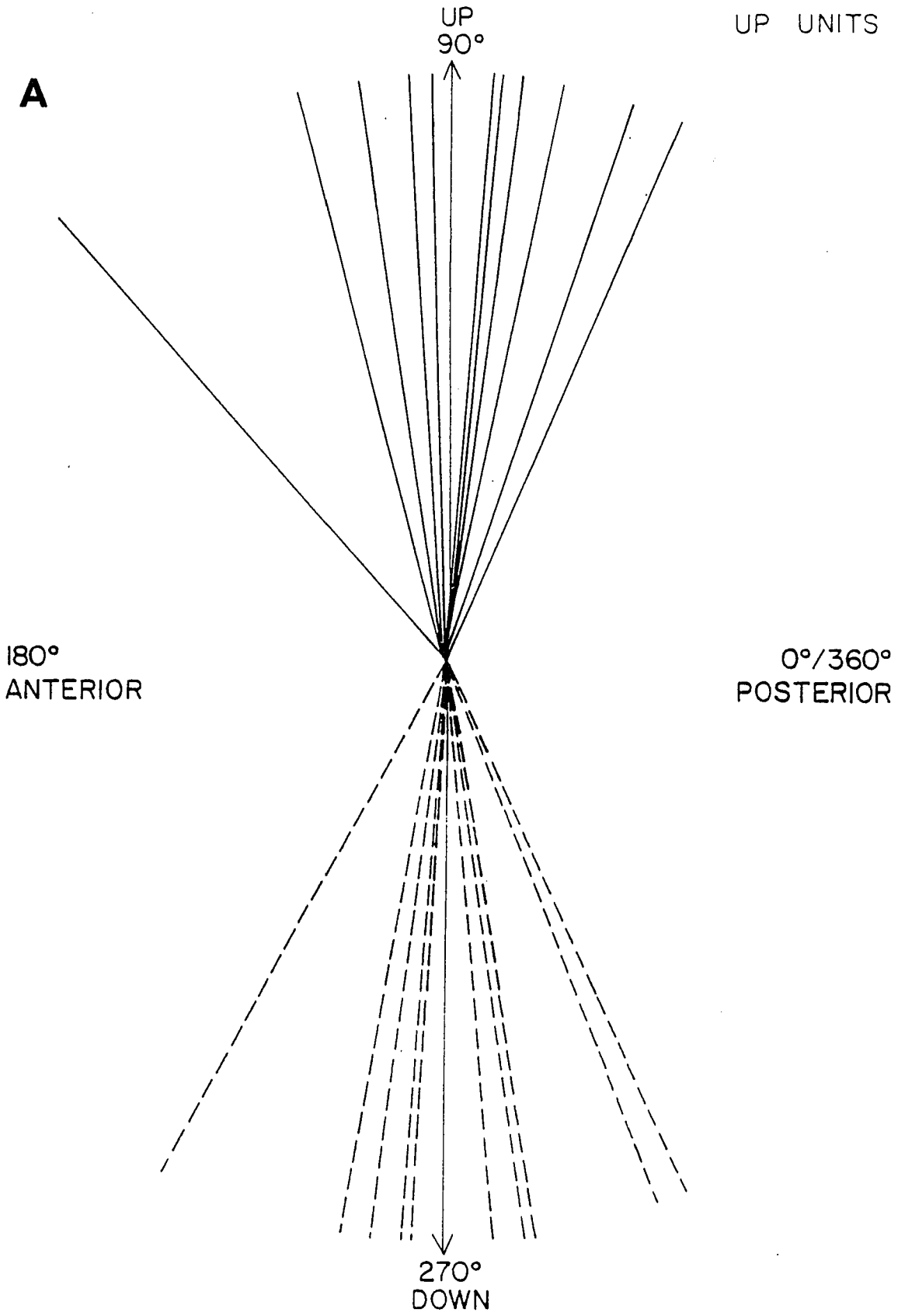

up
anterior
posterior
down

Fig. 13. Summary of excitatory and inhibitory directions of up (13A) and down (13B) units. Excitatory direction indicated by solid line, inhibitory direction by dashed line. The plots include only the excitatory direction for those 4 units with indeterminate inhibitory directions shown in Figs.9 and 10. Line with arrows is exactly vertical.


A
UP
90°
UP UNITS
180°
ANTERIOR
0°/360°
POSTERIOR
270°
DOWN

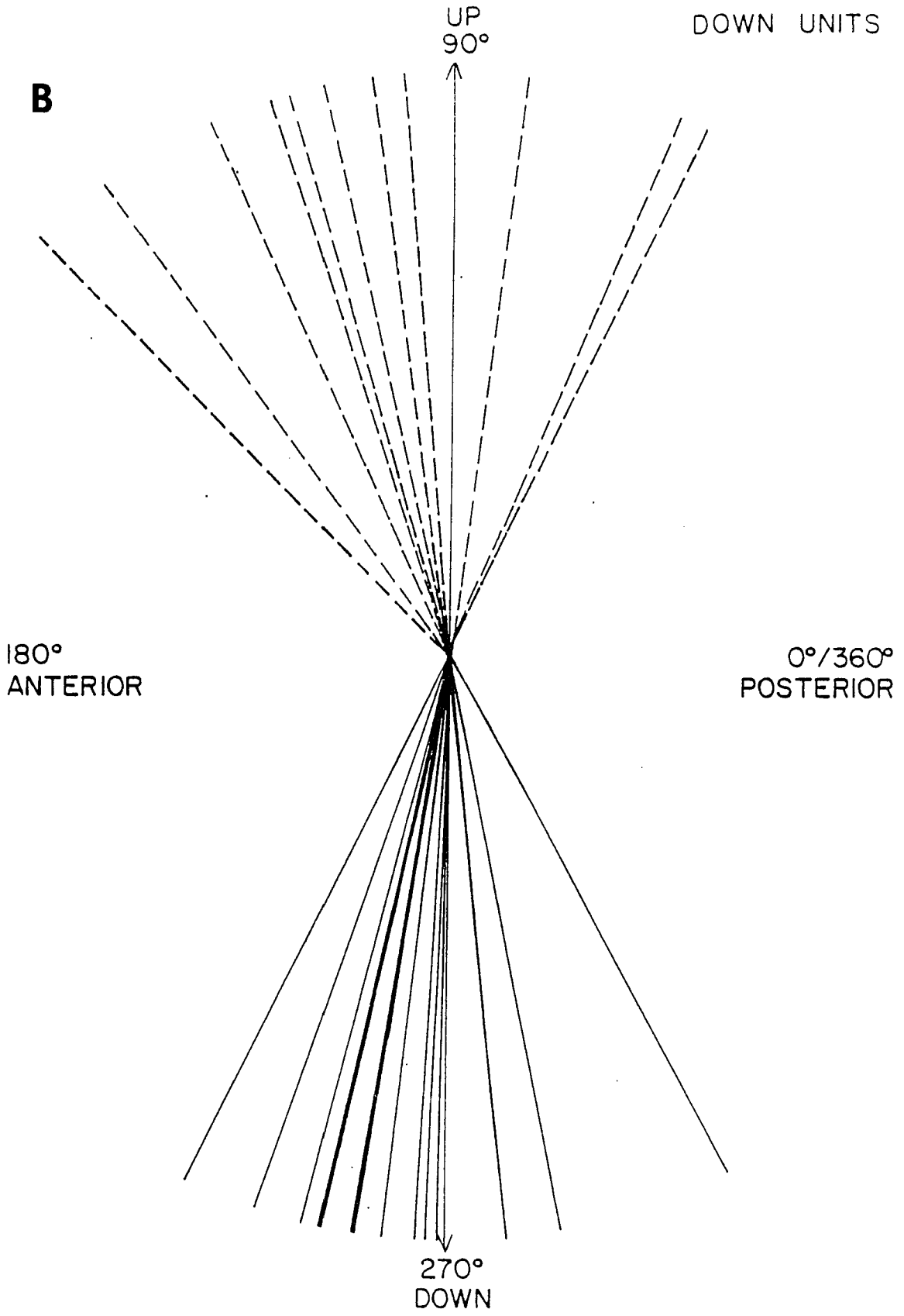

B
UP
90°
DOWN UNITS
180°
ANTERIOR
0°/360°
POSTERIOR
270°
DOWN

Fig. 14. Distribution of difference in angle between excitatory and inhibitory directions of single units. Angles less that 180 deg. indicate that the inhibitory direction is anterior to 180 deg. from the excitatory direction; angles greater than 180 deg. indicate that the inhibitory direction is posterior to 180 deg. from the excitatory direction. Arrows point to median values.

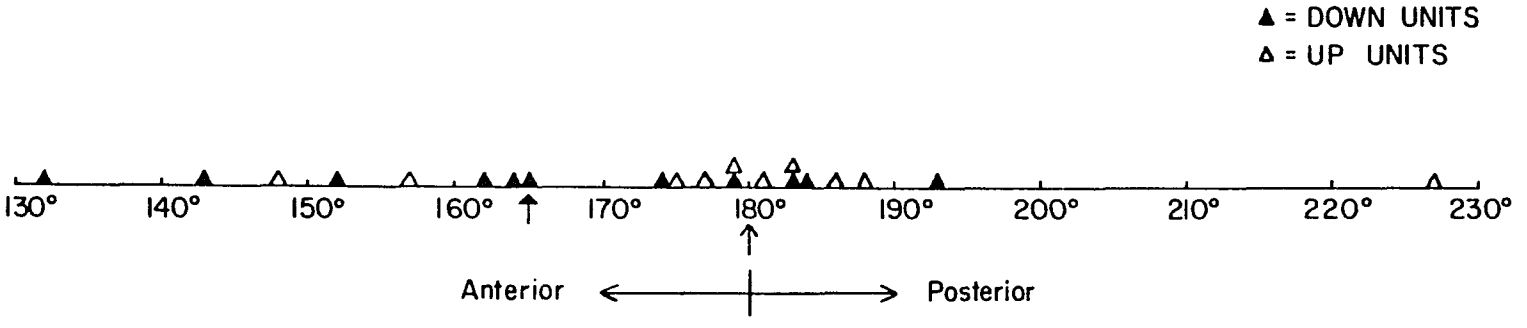
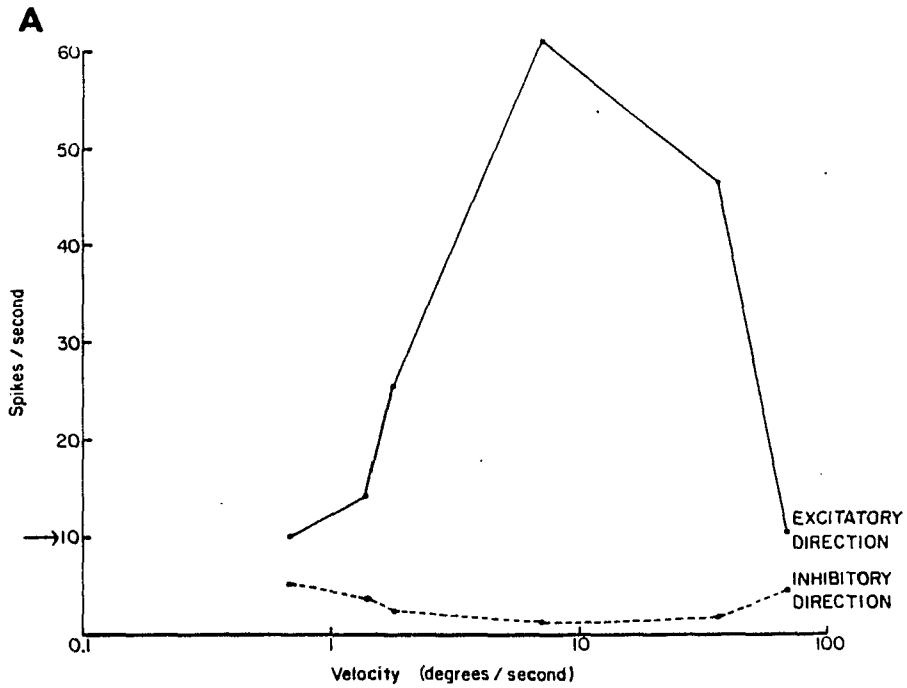
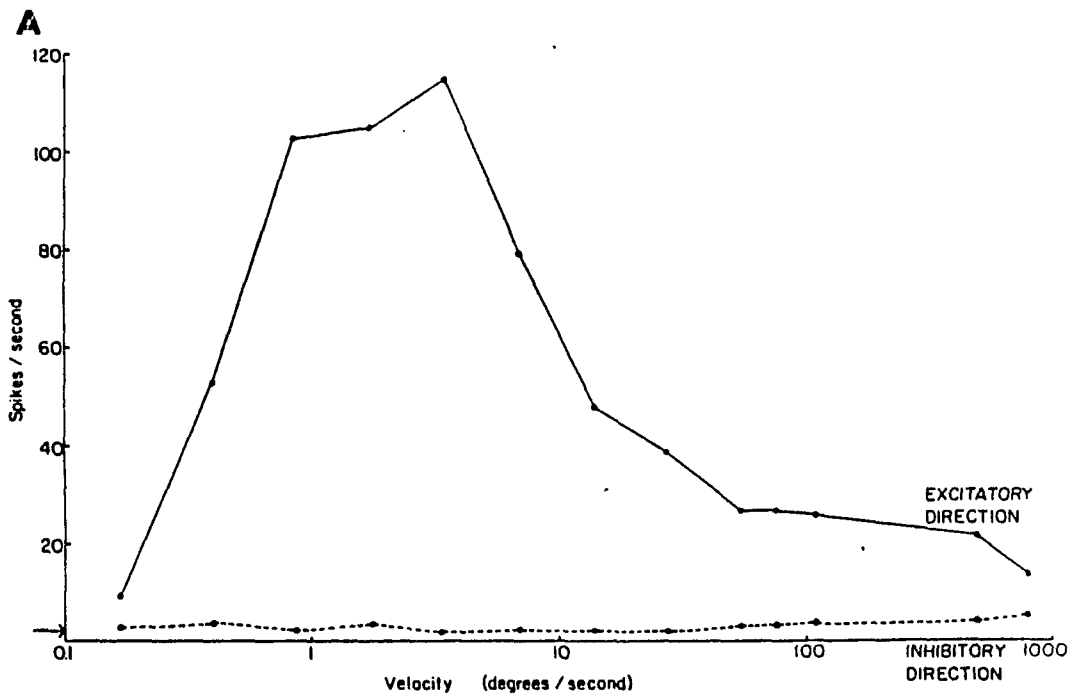
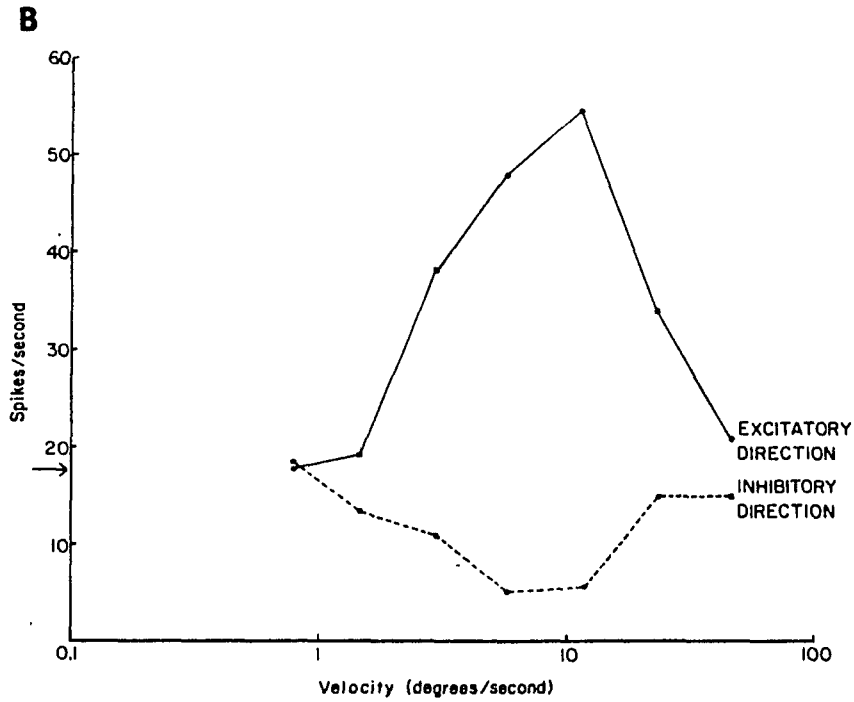

▲ = DOWN UNITS
△ = UP UNITS
130°
140°
150°
160°
170°
180°
190°
200°
210°
220°
230°
Anterior
Posterior

Fig. 15A and B. Velocity tuning curves for 4 single units in nBOR, showing preference for slow movement. A. Units with a velocity-dependent change in spike rate in the excitatory direction. B. Units with a velocity-dependent change in spike rate in both the excitatory and inhibitory directions. Arrows indicate rate of spontaneous activity.


A
60
50
40
30
20
10
Spikes / second
EXCITATORY DIRECTION
INHIBITORY DIRECTION
0.1
1
10
100
Velocity (degrees / second)


A
120
100
80
60
40
20
Spikes / second
EXCITATORY DIRECTION
INHIBITORY DIRECTION
0.1
1
10
100
1000
Velocity (degrees / second)


B
60
50
40
30
20
10
Spikes/second
EXCITATORY
DIRECTION
INHIBITORY
DIRECTION
0.1
1
10
100
Velocity (degrees/second)

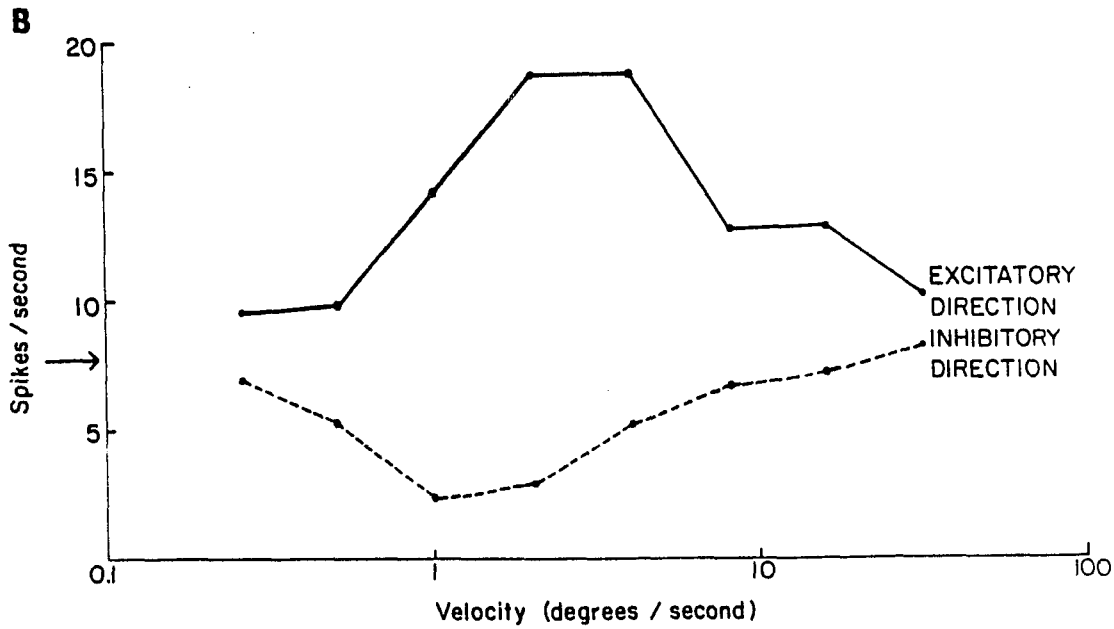

B
20
15
10
5
Spikes / second
EXCITATORY
DIRECTION
INHIBITORY
DIRECTION
0.1
1
10
100
Velocity (degrees / second)

Fig. 16. Illustration of retinotopic organization in nBOR from unit data recorded in single electrode tracks. .=1 unit, *=2 units. Lines connect units recorded in single tracks. Frontal visual fields are represented in the more dorsal part of the nucleus and lateral visual fields in the more ventral part. Heavy diagonal is regression line. Regression equation: y= 113-0.947x

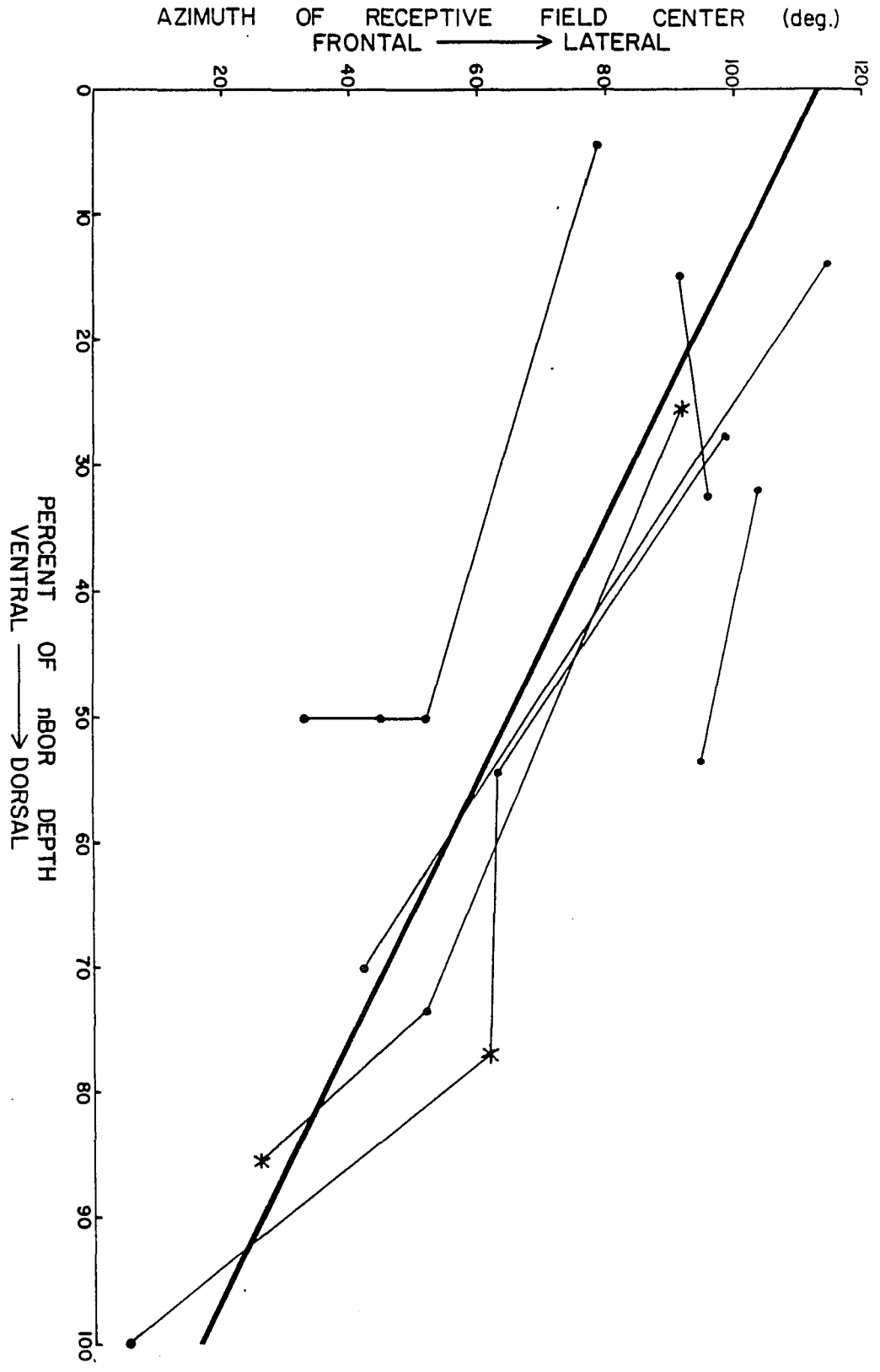

AZIMUTH OF RECEPTIVE FIELD CENTER (deg.)
FRONTAL → LATERAL
0
20
40
60
80
100
120
PERCENT OF nBOR DEPTH
VENTRAL → DORSAL
0
10
20
30
40
50
60
70
80
90
100

Fig. 17. Illustration of retinotopic organization in nBOR from multi-unit data recorded at 44 loci in 5 tracks in 1 animal. Ordinate shows depth of loci in nBOR. Abscissa shows position of loci in rostrocaudal plane (total length of this nucleus was 1175 microns). Symbols indicate azimuth of the center of the visual stimulus: .=41deg.+/-11, o=68deg.+/-15, triangle=90deg.+/-16. Receptive fields progress from frontal to lateral in dorsal to ventral nBOR. Brain loci labeled 1,2 and 3 are referred to in the next figure. The positions labeled D are referred to later in the text.

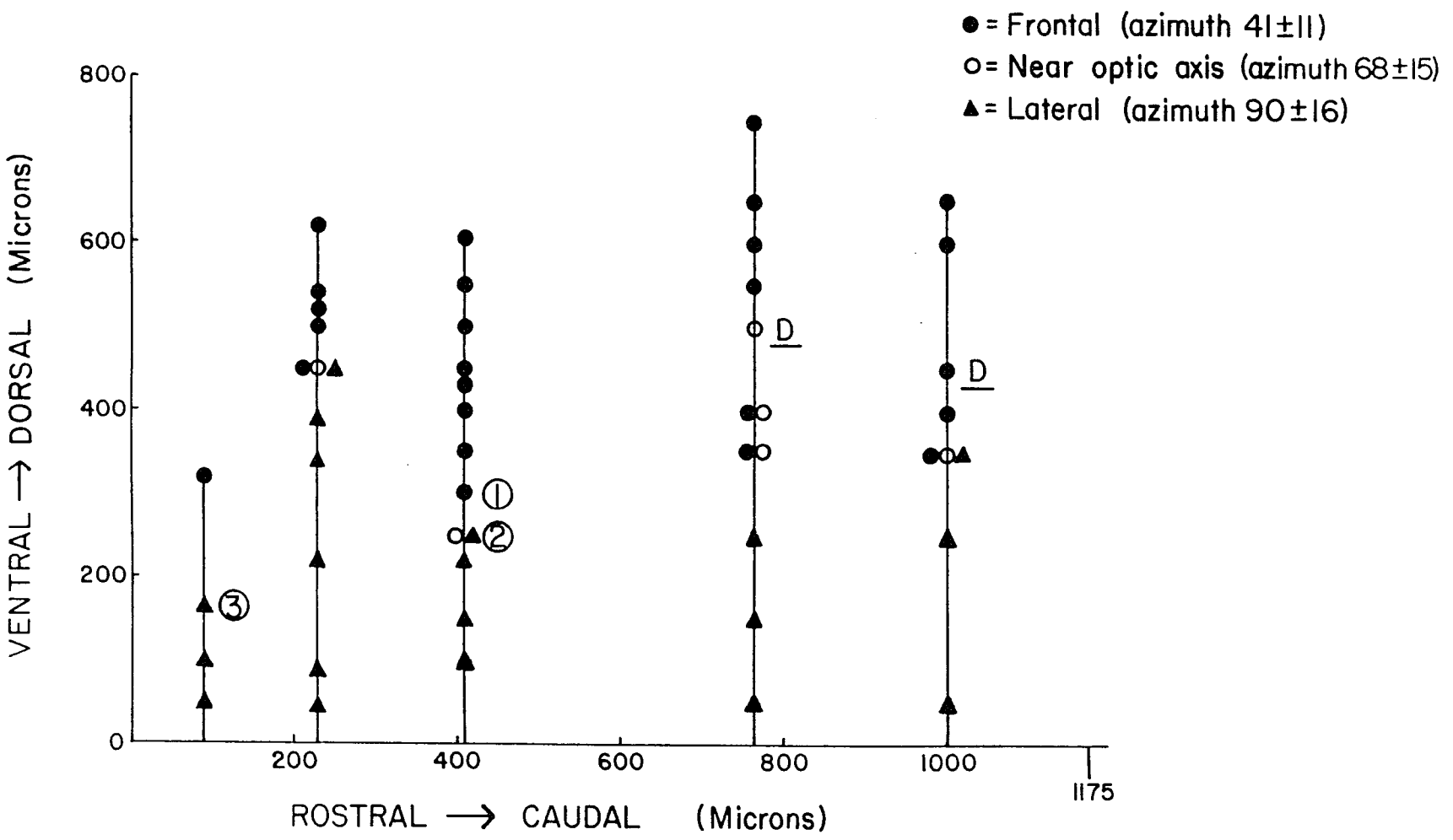

● = Frontal (azimuth 41±11)
○ = Near optic axis (azimuth 68±15)
▲ = Lateral (azimuth 90±16)
VENTRAL → DORSAL (Microns)
800
600
400
200
0
200
400
600
800
1000
1175
ROSTRAL → CAUDAL (Microns)
D
D
①
②
③

Fig. 18. Iso-frequency plots of multi-unit data from brain loci labeled 1,2 and 3 in Fig.17., showing spike counts/sweep at 9 locations of the tangent screen. Azimuth and elevation of the center of tangent screen are shown on ordinates and abscissas. As indicated in Fig.17, units at the dorsalmost site (locus 1) were most responsive to stimuli in the frontal visual field, those at the intermediate site (locus 2) to stimuli in both intermediate and lateral visual fields and those at the ventralmost site (locus 3) to stimuli in the lateral visual field. Contour lines shown every 100 spikes.

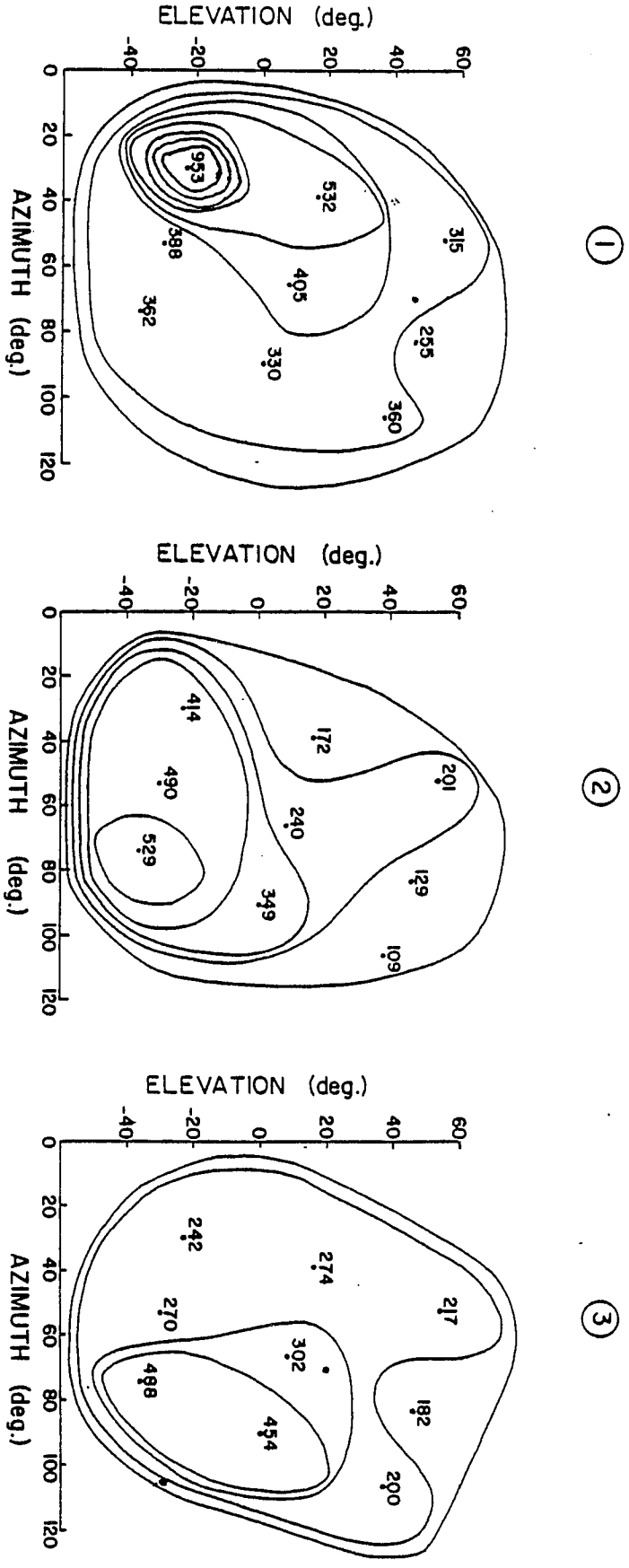

ELEVATION (deg.)
-40
-20
0
20
40
60
AZIMUTH (deg.)
0
20
40
60
80
100
120
953
532
315
588
405
362
255
330
360
①
ELEVATION (deg.)
AZIMUTH (deg.)
414
172
201
490
240
529
129
349
109
②
ELEVATION (deg.)
AZIMUTH (deg.)
242
274
217
270
302
498
182
454
290
③

Fig. 19. Recording sites of units in nBOR. Filled symbols are units excited by downward visual motion. Unfilled symbols are units excited by upward visual motion. Triangles indicate single unit recordings; circles indicate multiple unit recordings: half white/ half black circles indicate presence of both up and down units at these locations. x indicates single units preferring horizontal motion. Calibration bar = 1mm.

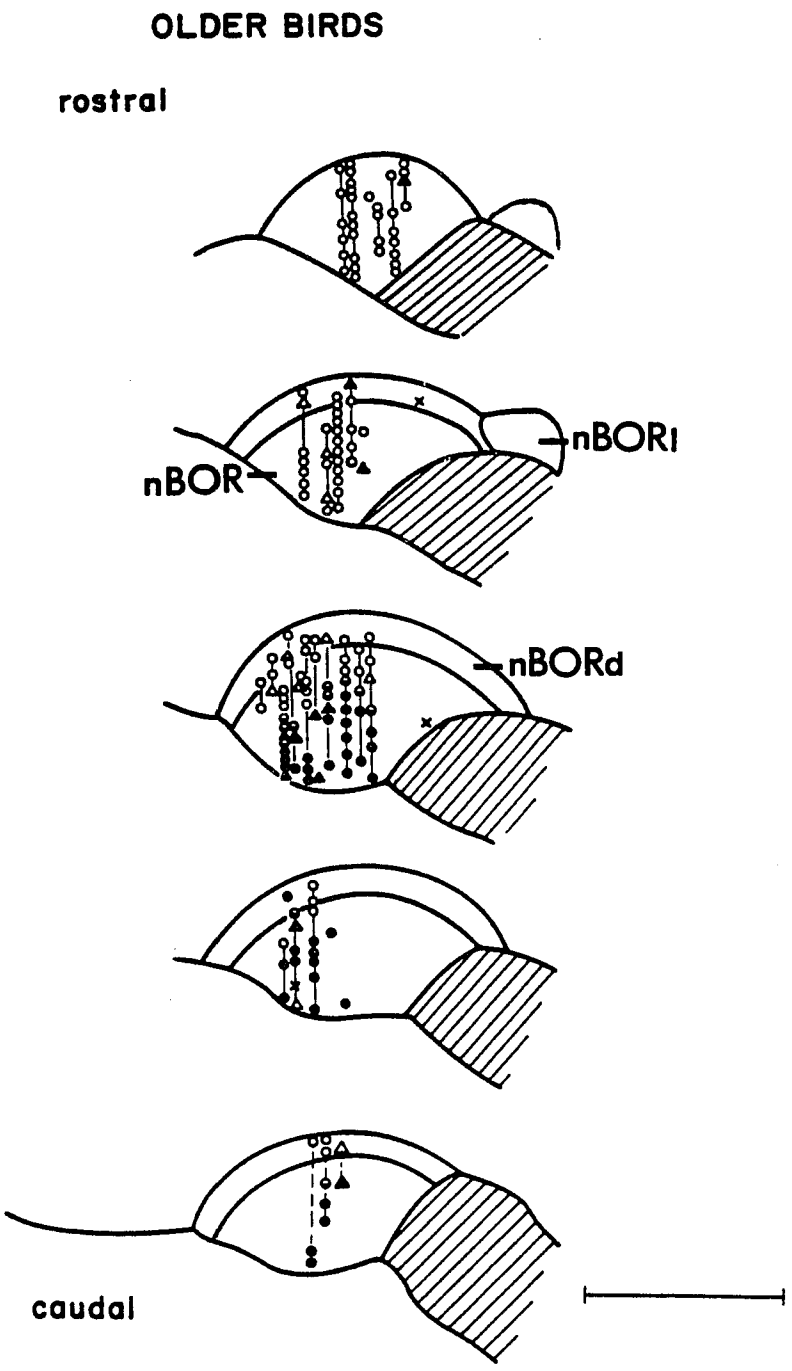
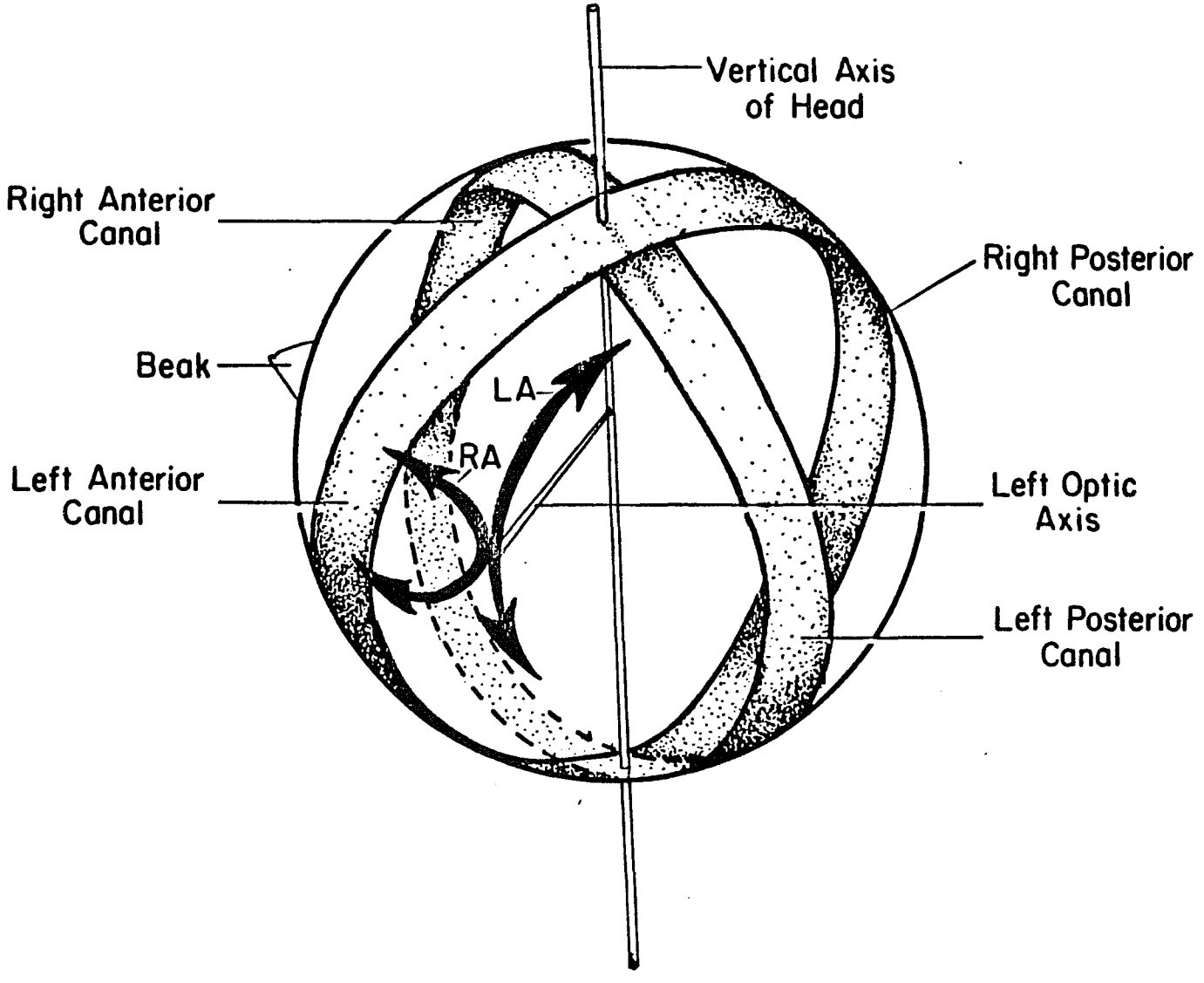

OLDER BIRDS
rostral
nBOR
nBORl
nBORd
caudal

Fig. 20. Photomicrograph of nBOR seen medial to the optic tract (TrO) at the level of the oculomotor nerve (NIII) showing the nBORd (d) and the nBOR proper (p). A marking lesion (l) can be seen in nBOR proper.

Fig. 21. Schematic diagram showing relationship between rotation of vertical semicircular canals and rotation of left eye. Head rotation maximally stimulating the left anterior canal produces movement of the optic axis in the direction of the lower arrow of arc LA; rotation maximally stimulating the right anterior canal produces movement of the optic axis in the direction of the upper arrow of arc RA. In each case, such head movements would cause retinal slip in the opposite direction along each arc.


Vertical Axis
of Head
Right Anterior
Canal
Right Posterior
Canal
Beak
LA
RA
Left Anterior
Canal
Left Optic
Axis
Left Posterior
Canal

CHAPTER 4

POSTNATAL CHANGES IN nBOR

INTRODUCTION

Although postnatal changes in visual structures in mammals have been well documented, there have been fewer studies of such changes in birds. Particularly in chicks it was thought that "[m]aturation of the optic system prior to hatching is evidently one of the preconditions for independent existence from the first day of life." (Sedláček, 1972) and certainly gross behavioral observations would support this. There are, however, several reports of postnatal changes in the visual system in chicks. The electroretinogram attains its final form 5 to 6 days after hatching (Witkovsky, 1963; Blozovski and Blozovski, 1968), cell division in the retina continues in the extreme periphery for up to 2 weeks (Morris et al., 1975), and full differentiation of the retina is not completed until 3 weeks (Rager, 1976). Myelination of retinal ganglion cell axons is completed at the end of the third month and conduction velocities to the tectum increase over the same time period (Rager, 1976). Commissural

connections between the optic tecta are not functional before hatching (Sedláček, 1972). Postnatal visual experience influences the responsiveness of neurons in the Wulst (Brown and Horn, 1979) and spatial acuity improves postnatally, although reportedly within 48 hours of hatching (Over and Moore,1981).

The first report of postnatal changes in the AOS employed metabolic mapping methods which showed that segregation of up and down units was not present in chicks less than one week of age (McKenna and Wallman, 1981). Subsequently, it was shown that the AOS of mammals also undergoes postnatal changes. Units in the AOS of visually deprived cats do not exhibit normal response properties (Grasse and Cynader, 1984). Most units in the LTN and DTN of dark-reared cats respond to visual stimuli only via the contralateral eye, whereas, units in normal cats are binocular. Furthermore, units in deprived animals respond only to low stimulus velocities (approximately 1 deg./sec.) in contrast to units in normal cats which respond to much higher velocities. Most strikingly, in LTN there is a substantial decrease in the incidence of upward direction selective units. Since ablation of the visual cortex in adult cats produces similar changes in the response properties of cells in LTN and DTN (Grasse et al., 1984), it can be concluded that early deprivation influences the development of visual cortical cells which, in turn, influence the response properties of cells in the AOS. Cells in the NOT of decortiate and visually deprived cats also show a decrease in binocular responsitivity and prefer much slower stimulus velocities than those in normal animals (Hoffmann, 1979, 1981). Furthermore,

horizontal OKN in cats (van Hof-van Duin, 1978) and humans (Naegel and Held, 1982) has been shown to change postnatally.

The present study of the electrophysiological properties of neurons in the AOS of hatchling chicks was undertaken to characterize the extent of postnatal development occurring in this system.

RESULTS

In older birds, the main characteristic of units in nBOR is their directional selectivity for slow vertical movement of large parts of the visual field. In neonates 2 to 6 days of age, however, there are two classes of units in nBOR: a directionally selective class like that of older birds and a second class, found only in neonates, which is weakly directional or non-directional. Forty-six single units were recorded from 13 birds, of which 22 were directional and 24 were either weakly directional or non-directional. Units studied quantitively were defined as weakly directional or non-directional if their modulation (discussed more fully below) was less than 0.4; units studied qualitatively showed comparable responses.

Directional Units

These units are highly directionally selective and like those in older birds are best modulated by movement in vertical directions. There is a group of cells excited by generally upward movement and inhibited by downward movement and a second group excited by generally downward movement and inhibited by upward movement. Directional

tuning plots of single units excited by generally upward movement and inhibited by downward movement are shown in Figs. 22A and B. Those excited by generally downward movement and inhibited by upward movement are shown in Fig. 23. The directional tuning of vertical units differs from that in older birds. All up units in neonates prefer movement which is up and anterior (n=9, mean 103 deg.,stan. dev. 7 deg), while the distribution in older birds is centered on up (n=11, mean 90 deg., stan. dev. 18 deg.). On the other hand the distribution of down units in neonates is centered on down (n=6, mean 270 deg., stan. dev. 15 deg.), while most units (11 of 14) in older birds prefer movement down and anterior (n=14, mean 265, stan. dev. 13). Of 5 additional directional units in neonates which were studied only qualitatively, 4 were up units and 1 was a down unit. As in older birds, very few units were best modulated by horizontal movement; these 2 units are shown in Fig. 24.

A summary of the excitatory and inhibitory directions of single units modulated by vertical movement is shown in Fig. 25A and B. The excitatory angles of up units are all up and anterior, while the excitatory angles of down units are both anterior and posterior to vertical. A comparison of the excitatory angles of up units in neonates and older birds shows that they are significantly different (Fisher Exact Probability $p<0.05$). The excitatory angles of down units, however, are not significantly different in the two age groups. The difference in the excitatory angle of up units cannot be attributed to experimental methods since care was taken to position the head of birds of both age groups at the same angle in the stereotaxic

apparatus. It is possible that the difference is due to age-related changes in the position of the eye or head. If this is the case, the angle of the pecten in older birds and neonates should differ. Measurement of this angle using the procedure described in the Methods section did not reveal such a difference. However, as was discussed in that section, the measurement is estimated to be accurate only to within ten degrees. Therefore, an age-related change in the position of the eye or head cannot be ruled out.

Weakly Directional and Non-Directional Units

In neonates, there is an unusual class of cells which are visually responsive, but weakly directional or non-directional. It is unlikely that these units represent an artifact of physiological deterioration of the animal during the experiment, since directional units were sometimes recorded later in the same electrode track. Furthermore, weakly directional and non-directional units were often recorded earlier in an experiment than directional units, even in the same electrode track. Twenty-four weakly directional or non-directional single units were recorded from and 13 were studied quantitatively. The latter are shown in Fig. 26A,B,C and D. Fig. 26A shows units with a weak tendency toward excitation by upward movement; Fig. 26B shows those with a weak tendency toward excitation by downward movement; Fig. 26C those tending to be excited by horizontal movement; Fig. 26D shows those which are non-directional. It is noteworthy that even weakly directional units are most likely to have

vertical excitatory and inhibitory angles, indicating a tendency in the direction of the mature pattern.

Units were tested for visual responsiveness in a variety of ways: turning room lights on and off, turning the slide projector on and off, moving the tangent screen or a large hand-held patterned stimulus, projecting and moving large shadows on the tangent screen. Not all units were tested in all ways, but of 22 units tested 16 gave very strong responses to at least one of the tests and 6 gave weaker responses. Most units responded to turning room lights on or off. Fig. 27 shows an off-unit whose firing rate increased substantially and transiently when the room lights were turned off.

Directional Modulation, Peak Width and Spontaneous Rates

Extensive quantitative recordings from a total of 60 single units, 30 in older birds and 30 in neonates, were made in this study. As shown in Fig. 28, units in neonates compared to those in older birds are less deeply modulated by stimuli in the strongest excitatory and inhibitory directions. Modulation is defined here as $(N_{max}-N_{min})/(N_{max}+N_{min})$ where N_{max} is the number of spikes in the stimulus direction which produced the greatest excitation and N_{min} is the number of spikes in the direction which produced the greatest inhibition. These values are taken from the raw data rather than from the derived values obtained using the Fourier analysis. Modulation of units in older birds is significantly greater than in neonates (Mann-Whitney U test, $p<0.02$). Furthermore, it can be seen that units

in neonates form two distinct groups: one whose modulation is equivalent to that of older birds and a second which is poorly modulated.

Units in neonates tend to be more broadly directionally tuned than those in older birds, as shown in Fig. 29. The 50% peak width used to assess the tuning is the angular distance between the points at which the curve falls to 50% of the maximum of the fitted Fourier function. This 50% peak width is generally narrower for units in older birds than in neonates. There is a tendency for units in neonates to form two groups, although the more narrowly tuned group is larger than the more broadly tuned one.

There is also a trend toward differences in spontaneous firing rates as shown in Fig. 30. Units in neonates tend to have higher spontaneous rates than those in older birds. A logarithmic plot of spontaneous firing rate against depth of modulation is shown in Fig. 31A and B for older birds and neonates, respectively. The proportion of excitatory input exceeds that of inhibitory input across the entire range of spontaneous firing rates for both age groups. However, there is a large group of units in neonates which are poorly modulated compared to those in older birds. These same units also have relatively high spontaneous firing rates, as can be seen in Fig. 31B. A comparison of the number of such units with spontaneous rates over 3.75/sec. and modulation less than 0.4 in older birds and neonates is shown in Table 1. This particular combination relative to all other combinations is significantly higher in neonates than in older birds ($X^2=4.13$, df=1, $p<0.05$), suggesting that high spontaneous

rates are correlated with poor modulation.

Velocity Tuning

Directional units in neonates, like those in older birds, have moderately sharp preferred velocities of movement. Examples of velocity tuning curves for units in neonates are shown in Fig. 32. As in older birds, units respond best to low velocities.

Receptive Fields

Units in neonates have large receptive fields similar to those of older birds. The approximate centers of these receptive fields together with those of older birds are shown in Fig. 33. Most receptive field centers are peripheral to the optic axis; this is in agreement with the predominately peripheral retinal distribution of the DRGCs which provide the afferent input to nBOR (Reiner et al., 1979). Relative to the tip of the pecten, the position of the optic axis is close to the retinal area of high ganglion cell density described by Ehrlich (1981). This comparison was made by measuring the distance from the tip of the pecten to the area of highest ganglion cell density shown on Ehrlich's whole-mount retinal map and, using his magnification factor of 0.15mm/visual degree, measuring the corresponding distance in visual degrees on Fig. 33. The area of highest ganglion cell density was about 10 degrees nasal to the optic axis and approximately 2 degrees below it. This provides further evidence that the centers of the receptive fields of most cells in

nBOR are in the peripheral rather than central retina.

The receptive field centers shown in Fig. 33 are all within +/- 30 degrees of zero elevation. The significance of this boundary is not clear. This result is not due to experimental methods, since I explored more peripheral areas of the visual field. Perhaps most DRGCs have receptive field centers in this part of the visual field. On the other hand, as can be seen in Figs.19 and 35, most units were sampled in the medial half of nBOR. The superior retina is reported to be represented in the more lateral part of nBOR (Ehrlich and Mark, 1984) and this may account for the absence of units with receptive field centers below -30 deg. Other than the presence of the pecten, there is no obvious explanation for the absence of receptive field centers above +30 deg., since the inferior retina is represented in medial nBOR (Ehrlich and Mark, 1984).

Retinotopic Organization of nBOR

As in older birds, a partial retinotopic organization is present in the nBOR of neonates as shown in Fig. 34. The retinotopy is similar to that found in older birds (see Fig. 16) in that units with more frontal visual fields are located in the dorsal part of nBOR and units with more lateral visual fields are located in the more ventral part (t test of whether slope of regression line differs from zero, $t=-2.81$, $df=19$, $p<0.01$). The slopes of the two regression lines for neonates and older birds were not significantly different.

Functional Organization of nBOR

In contrast to the retinotopic organization of nBOR, the functional organization present in older birds differs markedly from that in neonates. In older birds the more rostral part of nBOR contains up units, while the more caudal part contains both up and down units with the up units almost exclusively in the dorsal part of the nucleus and the down units in the ventral part. In contrast, in the neonates both up and down units are present in the ventrocaudal part; in the remainder of nBOR nearly all units recorded were up units, as was the case in the older birds. Fig. 35 shows the directional preferences and recording sites of units in nBOR in neonates. Recordings were made at 68 loci in 16 electrode tracks. Out of approximately 222 directionally selective units, recorded either singly or in small groups, about two-thirds preferred upward movement and one-third preferred downward movement. Table 2 compares the number of up units found in the dorsocaudal and ventrocaudal portions of nBOR in neonates and older birds. There are significantly more up units in the caudoventral portion of nBOR in neonates than in older birds ($x^2=7.19$, $df=1$, $p<0.01$). Furthermore, except in one instance, within each electrode track up units in ventrocaudal nBOR in older birds were always dorsal to down units, but this was not the case in neonates where up units were often ventral to down units.

Location of Weakly Directional and Non-Directional Units in Neonate nBOR

Recording sites of the weakly directional and non-directional single units found in neonates are shown in Fig. 36. Of 22 units recorded, 17 are in the caudal half of nBOR. However, there is no difference in the proportion of weakly directional units recorded in the rostral and caudal halves of the nucleus (8% rostral, 10% caudal). Furthermore, as can be seen from a comparison with Fig. 35, there is overlap in the location of directional, weakly directional and non-directional units. Therefore, there is no apparent, discrete area of the neonate nBOR in which weakly directional and non-directional units are clustered.

DISCUSSION

Neurons in nBOR in neonates differ from those in older animals in three major ways that indicate there is an important postnatal component to the development of the accessory optic system. First, there are some neurons in neonates that are weakly directional or non-directional; such neurons have not been found in older animals. Second, the neurons in neonates that are as strongly directional as those in older animals have somewhat different excitatory directions. Third, the functional organization of neurons by directional preference which is found in older animals is only partially present in neonates. That the accessory optic system continues to develop postnatally is rather surprising since nBOR is one of the earliest

developing visual nuclei in the chick embryo; mitosis is complete by embryonic day 6 and retinal afferentation commences on day 7 and is completed by day 9 (Crossland, 1979).

Weakly Directional and Non-Directional Neurons

In the neonate nBOR there are both directional neurons and neurons which are weakly directional or non-directional. I have not found the latter class of neurons in the nBOR of older chickens and they have not been described in other studies of the adult avian nBOR. Morgan and Frost (1981) found only directionally selective neurons in pigeon nBOR. In another study in the same species, 96% of the neurons were directionally selective or maximally responsive to movement along specific axes (Britto et al.,1981). In the present study many weakly directional and non-directional neurons were recorded from the same animal or same electrode track with directionally selective neurons, so that it is unlikely that their lack of directional selectivity is due to an effect of anesthetic on the neonate.

A comparison of units studied quantitatively (30 in older birds and 30 in neonates) shows that those of neonates have significantly lower depth of modulation than those of older birds. Neurons in neonates also tend to have higher spontaneous activity than those in older birds. A limit with the method used here to assess modulation is that it is inherently influenced by the level of spontaneous firing rate. In order to avoid this problem, another method of assessing modulation which is not biased by level of spontaneous firing rate was

used. The raw number of spikes in both the excitatory and inhibitory directions of units were plotted against spontaneous firing rate for each unit (see Fig. 31A and B). Using this method, it can be seen that several units in neonates do, in fact, have both high spontaneous firing rates and poor depth of modulation. The number of such units is significantly greater in neonates than in older birds.

Most of the weakly directional units in neonates were slightly modulated by vertical motion, but seldom by horizontal motion, indicating that some synaptic input comparable to that found in older birds is already present. The poor depth of modulation of these units could be improved by changes which result in increased excitatory and increased inhibitory inputs. A decrease in spontaneous firing rates, however, would require changes that result in decreased excitatory and/or increased inhibitory inputs. Since an increase in inhibitory inputs would account for maturation of both modulation and spontaneous activity, this may be an important component in the development of nBOR. There is substantial evidence that directional selectivity in visual neurons in the retina is dependent upon an inhibitory mechanism (Wyatt and Daw, 1975). This is also the case in the optic tectum, although it is unknown whether inhibitory input comes directly from retinal afferents or from interneurons in the tectum (Jassik-Gerschenfeld et al., 1970). The directional selectivity of some classes of cells in the visual cortex is dependent upon an inhibitory input from interneurons (Sillito, 1977).

The development of direction selectivity of neurons has been studied to some extent in other species. It occurs postnatally in cat

and rabbit visual cortex. Directionally selective neurons are present around the time of eye opening in kittens but their numbers increase and their tuning narrows over a three week period (Pettigrew,1974). In immature rabbits there are significantly fewer directionally selective neurons, but those present are reported to be as well tuned as those of adults (Murphy et al., 1983). Visual experience is required for both the preservation and development of directional selectivity in cat and rabbit visual cortex. Kittens deprived of vision do have directionally selective neurons, but they are more broadly tuned and the number of such neurons is significantly less than in non-deprived kittens (Pettigrew, 1974). In rabbits, there appear to be three populations of directionally selective cells in the cortex whose dependence upon visual experience varies, since the number of directionally selective neurons in neonates is less than in normal adults, equal to lid-sutured adults, but greater than strobe reared adults. This can be interpreted as some neurons requiring visual experience to develop, others developing independently of vision and still others not being maintained unless directional motion is present (Murphy et al., 1983). Neurons in the NOT of cats with visual experience have lower rates of spontaneous activity and slightly more specific directional tuning curves than those which have been deprived of vision (Hoffmann, 1979). The effect of visual deprivation on the directional selectivity of single units in nBOR has not been investigated. However, the metabolic mapping pattern in chicks visually deprived for three weeks is similar to that of neonates rather than 3-to-5 week-old normals and vertical and

torsional OKN is impaired to a much greater extent than horizontal OKN (McKenna et al., 1983). It is clear that visual experience is necessary for the development of nBOR, but the exact effects of such experience remain to be investigated.

Directionally Selective Neurons

While there are weakly directional or non-directional neurons in the nBOR of neonates, many directionally selective neurons are also present. These latter neurons are as well modulated and narrowly tuned as those of older birds; however, they differ somewhat in their directional preferences. In neonates, one population responds to downward motion and a second population responds to upward and anterior motion. In older birds one population responds predominantly to downward and anterior motion and the second population responds to upward motion. These differences raise a question concerning the significance of these preferred directions of motion. The directional preferences of neurons in older birds may be correlated with directions of motion seen when the anterior canals are maximally stimulated: upward motion corresponding to stimulation of the ipsilateral anterior canal and downward and anterior motion corresponding to stimulation of the contralateral anterior canal. Furthermore, these directional preferences of neurons in older birds correspond approximately to the two directions of visual motion which produce the greatest gain in non-horizontal OKN (Wallman and Velez, 1985). These are down and counterclockwise (contralateral

semicircular canal plane) and up (ipsilateral canal plane). The directions of motion preferred by neurons in neonates (downward and up and anterior), on the other hand, do not correlate with the stimulation of particular semicircular canals relative to movement of the optic axis of the left eye, nor is there a correspondence with the direction of visual motion which produces the greatest gain in non-horizontal OKN. In neonates, the peak gain of non-horizontal OKN is to one direction of motion--up and counterclockwise--and this is the direction of motion seen when both anterior canals are simultaneously and equally stimulated (Wallman and Velez, 1985). It is noteworthy, however, that both the directional preferences of units in nBOR and OKN differ in neonates and older birds, although they do not differ in the same way. There are two populations of directionally selective neurons in the neonate, one preferring up and anterior motion, and the other preferring downward motion, yet the peak gain of non-horizontal OKN is to one direction of stimulus motion only, i.e. up and counterclockwise.

Two important conclusions can be drawn with respect to the neonate. First, sensory input at the level of nBOR differs from that in older birds. Second, the correspondence between sensory input at the level of nBOR and motor output as manifested in optokinetic eye movements is not organized as it is in older birds. How might the sensory input be modified during the course of postnatal development? The developmental modeling of sensory input to nBOR has some parallels in other parts of the visual system. As mentioned earlier, it is common for directional tuning, as well as orientation and binocularity

tuning to become sharper during postnatal development of the visual cortex. Furthermore, it has been shown that orientation selective cells in the visual cortex can be biased by exposure to restricted visual environments during the critical period (Hirsch and Spinelli, 1970; Leventhal and Hirsch, 1975; Stryker et al., 1978). Similarly, the directional properties of cortical neurons in cats can be biased by visually restricted rearing environments (Cynader et al., 1975; Daw and Wyatt, 1976). The strongly directionally selective neurons in nBOR appear as fully developed and as narrowly tuned as those of older birds, yet their mean excitatory directions are perhaps somewhat different. The transformation of the excitatory directions to those characteristic of older birds could be due to the postnatal development of the weakly directional or non-directional units and/or to a shift in the tuning of the directional units. Such changes may involve the formation or activation of new synapses and/or the retraction or silencing of others.

The major question, however, is what determines the direction in which sensory input is modified. Visual experience or feedback may be important, however, it is possible that a correspondence with vestibular input is equally important. At present, there are no known inputs from the vestibular system to nBOR. It appears then that such a correspondence takes place further downstream, possibly at the level of the vestibular nuclei, or cerebellum or even at the oculomotor nuclei. Singer (1979) has suggested that fully functional synapses can be preserved or suppressed according to the behavioral relevance of the sensory signals which they transmit. Such relevance may be

determined by a comparison with other sensory maps or motor commands and may be important in preventing inadequate sensory signals from having a behavioral effect. There is evidence that the development of orientation selectivity in at least some cortical cells is dependent upon ocular motility, although the nature of this dependence is unknown (Imbert, 1979). Indeed, it seems appropriate that the accessory optic system, which is so closely involved in producing adequate compensatory eye movements to particular directions of retinal slip, should have a period of development during which visual, vestibular or visuomotor feedback or integration can shape incoming sensory signals so that only relevant directions of motion have a behavioral effect.

An explanation of the second conclusion, i.e., that the correspondence between sensory input at the level of nBOR and motor output as manifested in optokinetic eye movements is not organized in neonates as it is in older birds, poses a greater problem. Non-horizontal OKN in neonates shows a high gain to only one direction of visual stimulus motion. That OKN is up and excyclorotational and is elicited by up and posterior stimulus motion in the superior visual field. Units in nBOR in neonates do not respond to this stimulus motion. Instead, they respond to up and anterior motion and to downward motion to a somewhat lesser extent. One possible explanation for this lack of correspondence between sensory input and motor output is that the signal in nBOR is transformed further downstream and that this transformation results in the observed eye movements. Why such a transformation should be present in neonates and not in adults where there is reasonable correspondence between directions represented in

nBOR and directions of OKN is obscure. Another possibile explanation is that there is no transformation downstream, but that the signals from nBOR, i.e., up and anterior and down somehow combine to produce the observed eye movements. This could result from the particular functional organization of nBOR in neonates, which differs from that in adults and which will be considered next.

Functional Organization

Organization by directional preference differs markedly in neonates and older birds. While in both groups rostral nBOR and the dorsal half of caudal nBOR contain only up units, the ventral half of caudal nBOR contains only down units in older brids and both up and down units in neonates. This difference between neonates and older birds is highly significant.

How nBOR acquires its final functional organization is unknown. Neurons could migrate along with their afferents, but such a late migration of differentiated cells seems unlikely. Neurons in improper positions could die, but although neuronal cell death is a common occurrence, it is unlikely to occur at such a late, postnatal stage. The most likely mechanisms involve the same kind of developmental events proposed for the changes in directional selectivity discussed above. Several anatomical studies of the development of the nervous system indicate that initially widespread ramifications of dendrites or axon terminals and apparent connections between them often become more restrictive or selective as development progresses (Jacobson,

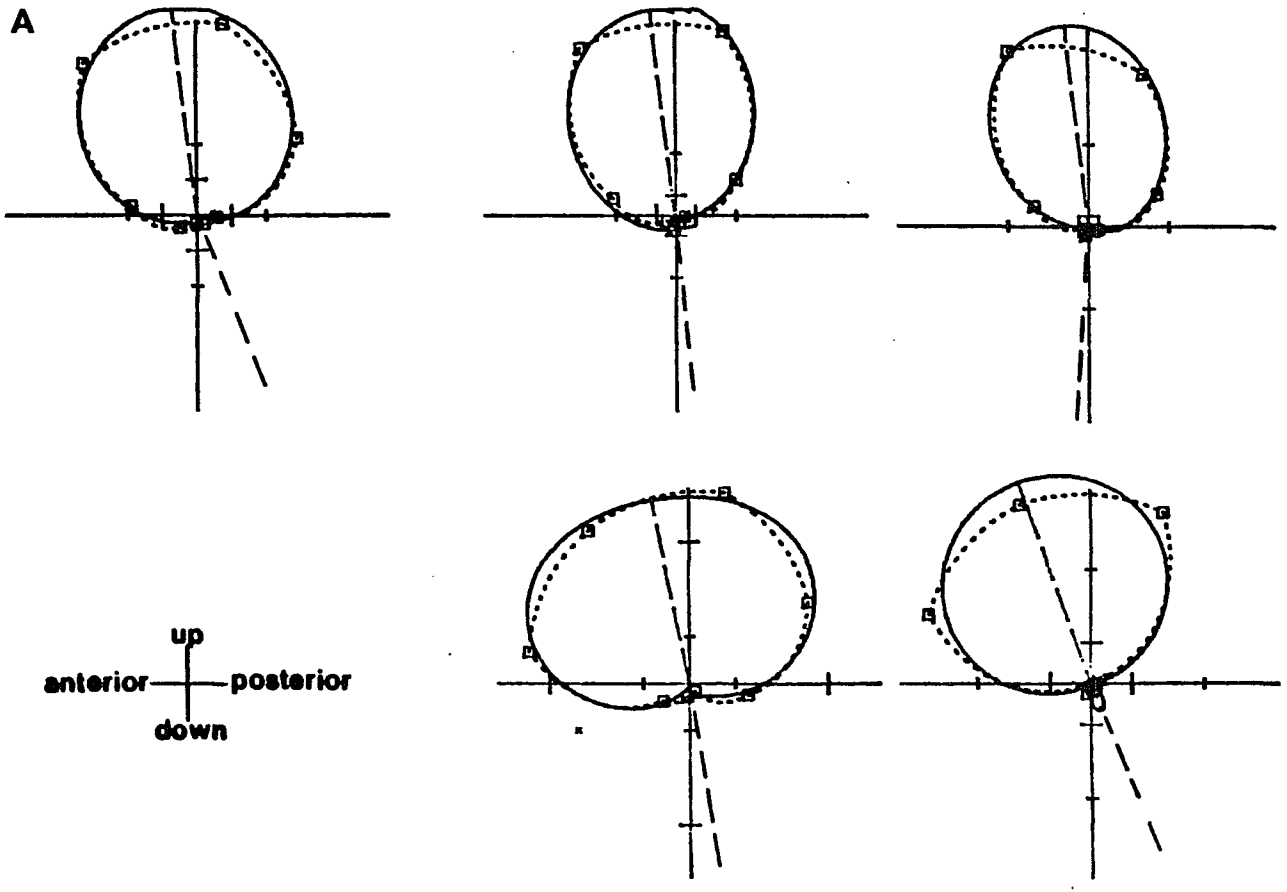
1978; Purves and Lichtman, 1980). Such a pattern of development has many important theoretical implications relevant to the formation of proper connectivity. However, only a few studies have provided direct evidence for the elimination of functioning synapses. In the embryo this has been demonstrated between cochlear nerve and cochlear nucleus (Jackson and Parks, 1982). Postnatally, this has been demonstrated at the neuromuscular junction (Bennett and Pettigrew, 1974; Changeux and Danchin, 1976) and between climbing fibers and Purkinje cells (Crepel et al., 1976). It is possible that synapses between afferents carrying upward signals and neurons in ventrocaudal nBOR are eliminated. Also, there is evidence that afferents in the retinotectal projection in frogs and fish change their projection sites during development (Fraser, 1983; Easter and Stuermer, 1984; Reh and Constantine-Paton, 1984, Steurmer and Easter, 1984). This presumably involves not only synapse elimination, but also the formation of new synaptic connections. It is possible that afferents transmitting upward signals to ventrocaudal nBOR likewise change their projection sites to neurons in dorsocaudal nBOR. Breakage and reformation of synaptic connections is thought to be important in the formation of ocular dominance columns in cats (LeVay et al., 1978). Another possibility is that the synapses transmitting upward signals are not eliminated, but are inhibited or silenced.

Changes in the functional organization of nBOR may be a reflection of postnatal changes in the periphery. Cell division occurs in the extreme periphery of the retina for 2 weeks after hatching (Morris et al., 1975) and full differentiation of the retina is not complete

until 3 weeks (Rager, 1976). The electroretinogram attains its final form 5 to 6 days after hatching (Witkovsky, 1963; Blozovski and Blozovski, 1968). Furthermore, myelination of retinal ganglion cell axons is not completed until the end of the third month (Rager, 1976). Some of these changes may account for changes in the properties of central neurons. A postembryonic change in the tonotopic organization of the peripheral acoustical system in chicks apparently accounts for a change in the tonotopic organization of central nuclei (Rubel and Ryals, 1983; Lippe and Rubel, 1983). In addition, there is some evidence that centrifugal fibers may synapse on displaced retinal ganglion cells (Maturana and Frenk, 1965) and development of this system could result in changes in the periphery, although centrifugal fibers apparently do not affect the directional selectivity of retinal ganglion cells in general (Miles, 1972a,b,c; Pearlman and Hughes, 1976a,b). In addition to retinal afferents to nBOR there are other afferents which could presumably develop later and could account for developmental changes in the nucleus. The visual Wulst projects to nBOR. Although, to date, no directionally selective cells have been found there (Wilson, 1980), the possibility remains that they exist. In cats, the visual cortex projects to the AOS (Berson and Graybiel, 1980; Marcotte and Updyke, 1982) and this input influences the upward directional selectivity of units in LTN (Grasse et al., 1984). Afferents from the contralateral nBOR project only to nBORd (Brecha et al., 1980). However, they could influence neurons in the ventral part of the nucleus through interneurons.

In summary, this is the first study of the postnatal development of the accessory optic system employing unit recording. It has provided the first evidence that directional selectivity, which is a property of nBOR units in older birds, is incompletely developed at hatching. It has confirmed the incomplete development of the functional organization of nBOR first described in chicks by McKenna and Wallman (1981) and has extended these findings to show that postnatal functional reorganization is confined to up units, and down units are organized as they are in older birds. In addition, it has shown that the precise tuning of directionally selective units in neonates differs from that found in older birds. This, together with the absence of directional selectivity in some units and the different pattern of functional organization found in the neonate may account for the differences in OKN in neonates and older birds described by Wallman and Velez (1985).

Fig. 22A and B. Directional tuning plots of units excited by upward movement and inhibited by downward movement. Conventions as in Fig.9.


A
up
anterior
posterior
down

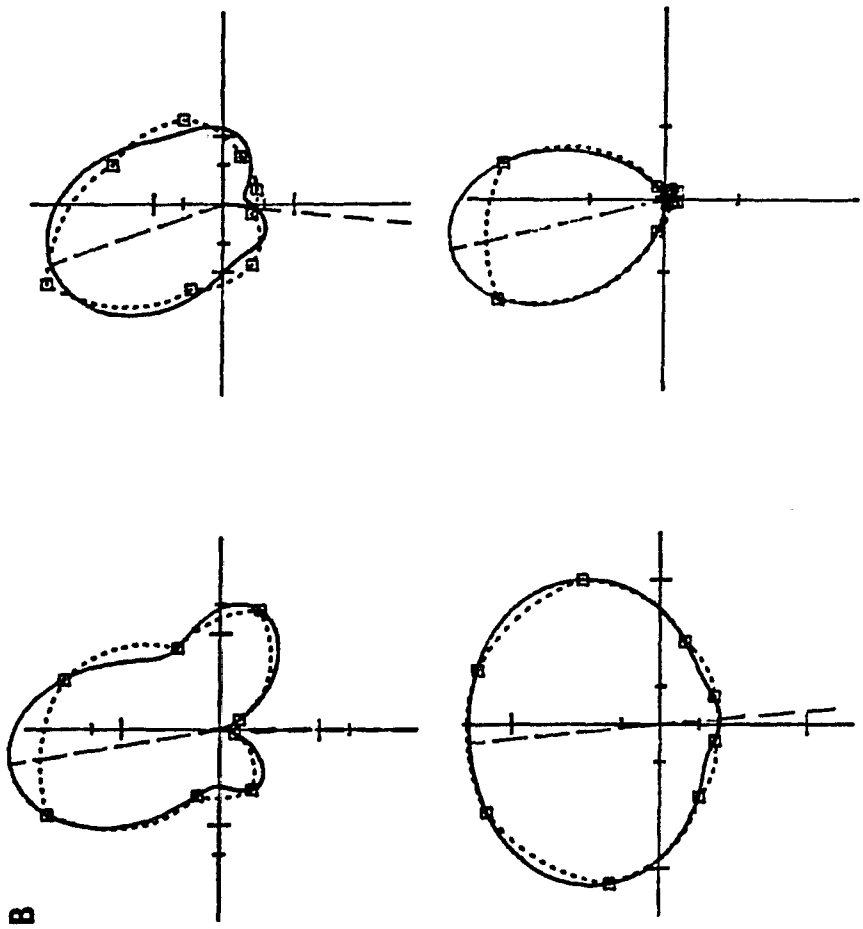

B

Fig. 23. Directional tuning plots of units excited by downward movement and inhibited by upward movement. Conventions as in Fig.9.

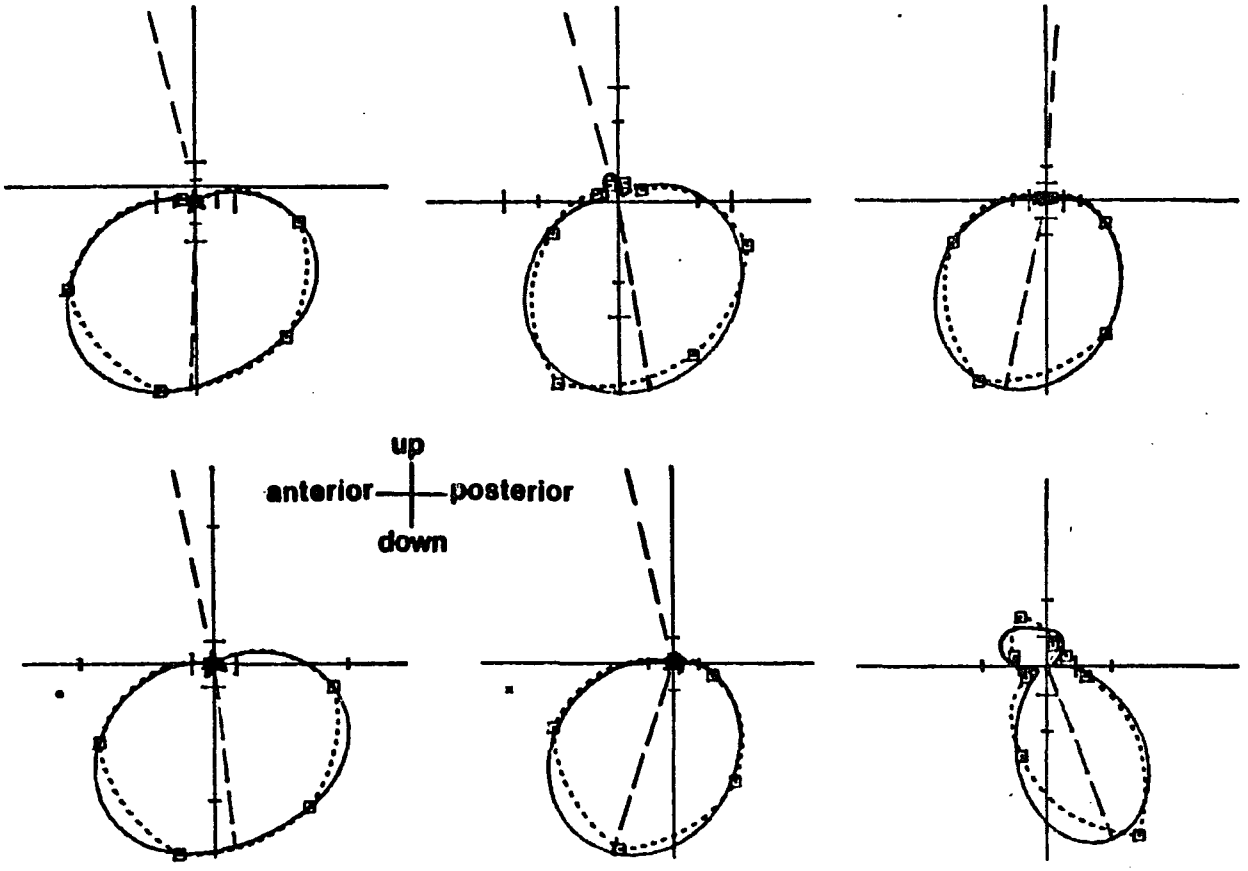

up
anterior
posterior
down

Fig. 24. Directional tuning plots of units excited by horizontal movement. Conventions as in Fig.9.

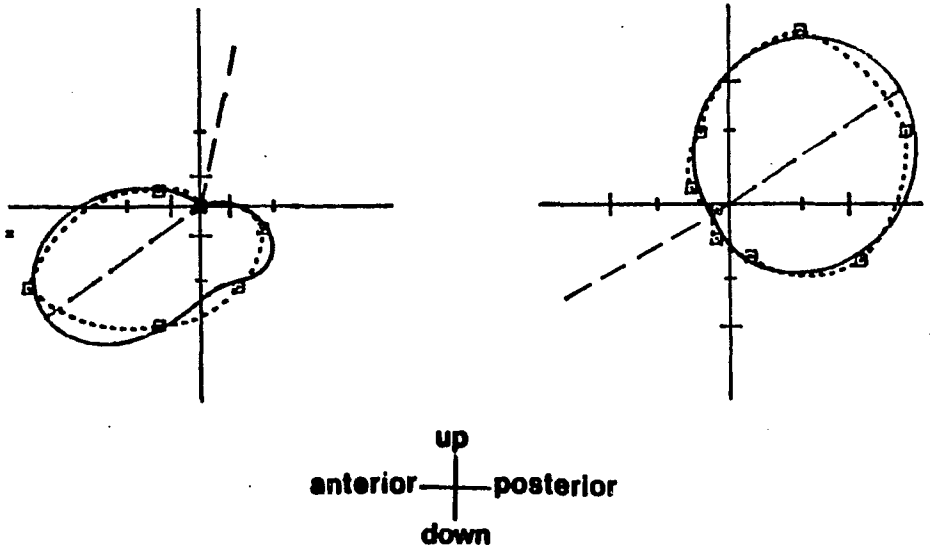
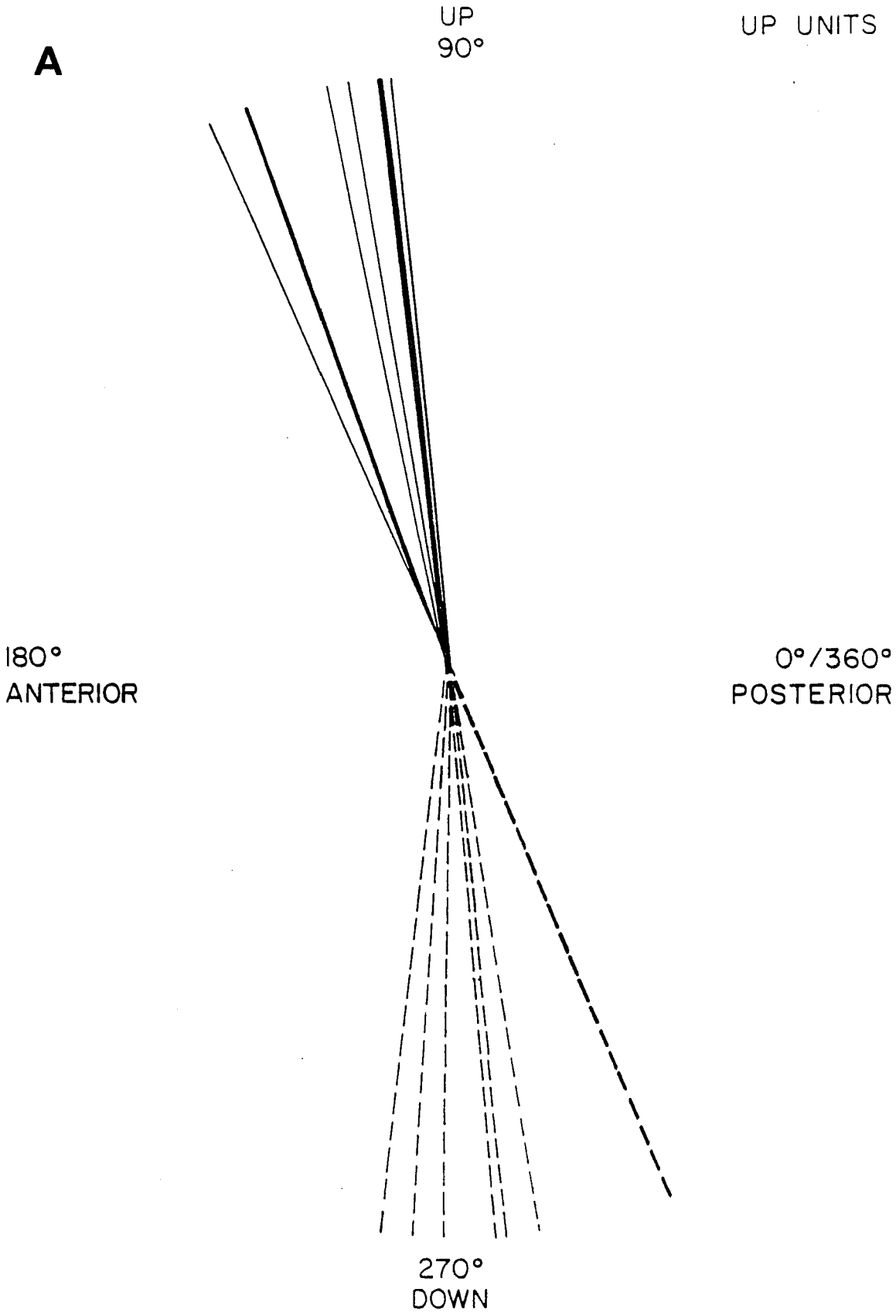

up
anterior
posterior
down

Fig. 25. Summary of excitatory and inhibitory directions of up (25A) and down (25B) units. Excitatory direction indicated by solid line, inhibitory direction by dashed line. The plots include only the excitatory direction for those 2 units with indeterminate inhibitory directions shown in Figs. 22 and 23.


A
UP
90°
UP UNITS
180°
ANTERIOR
0°/360°
POSTERIOR
270°
DOWN

B

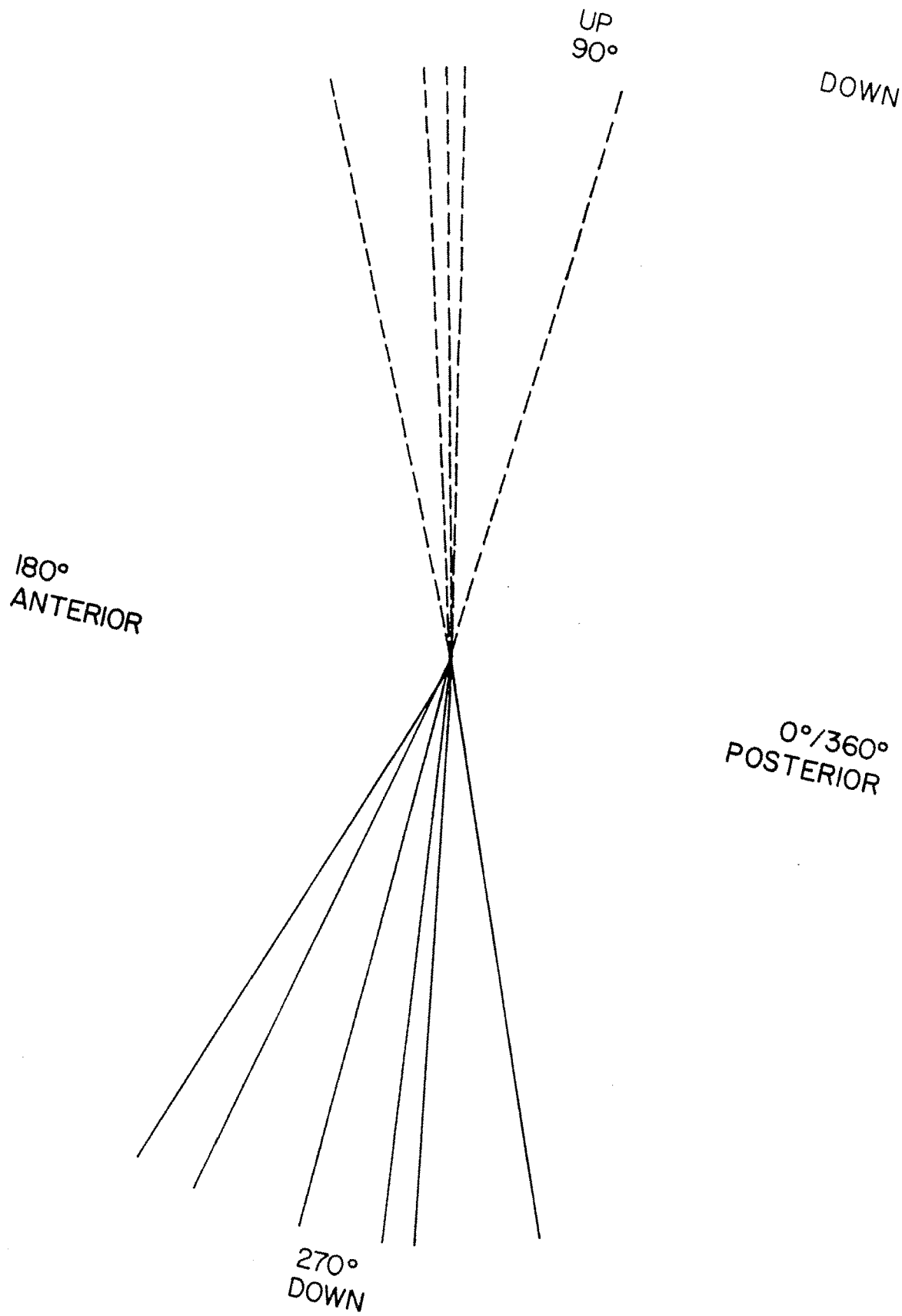
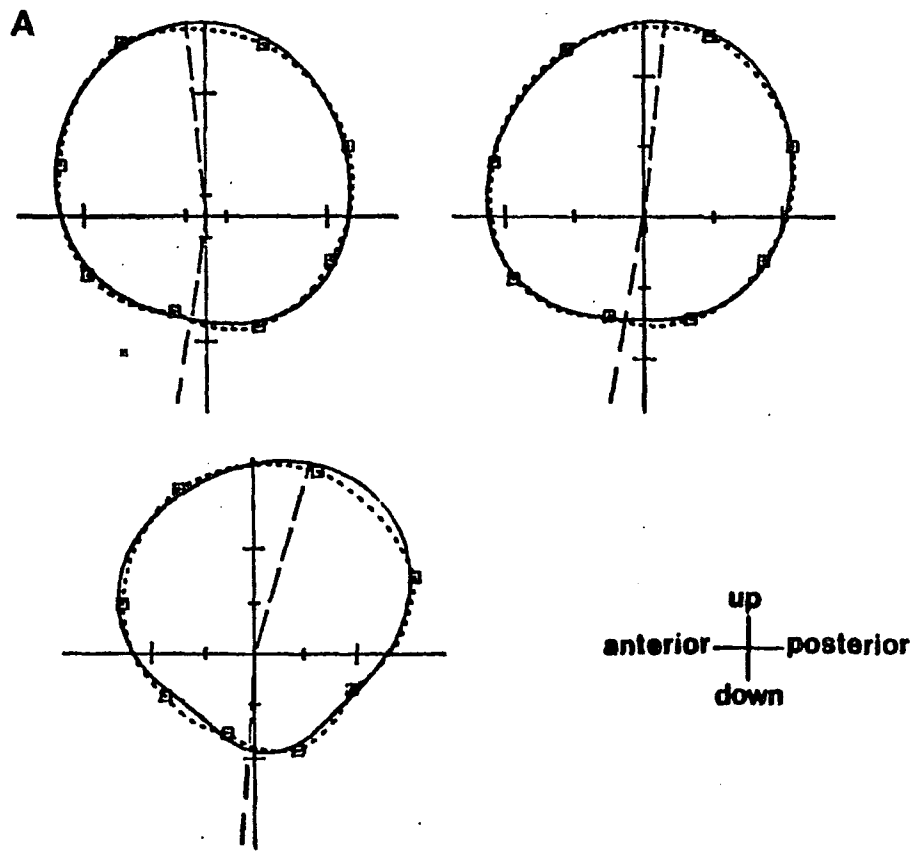
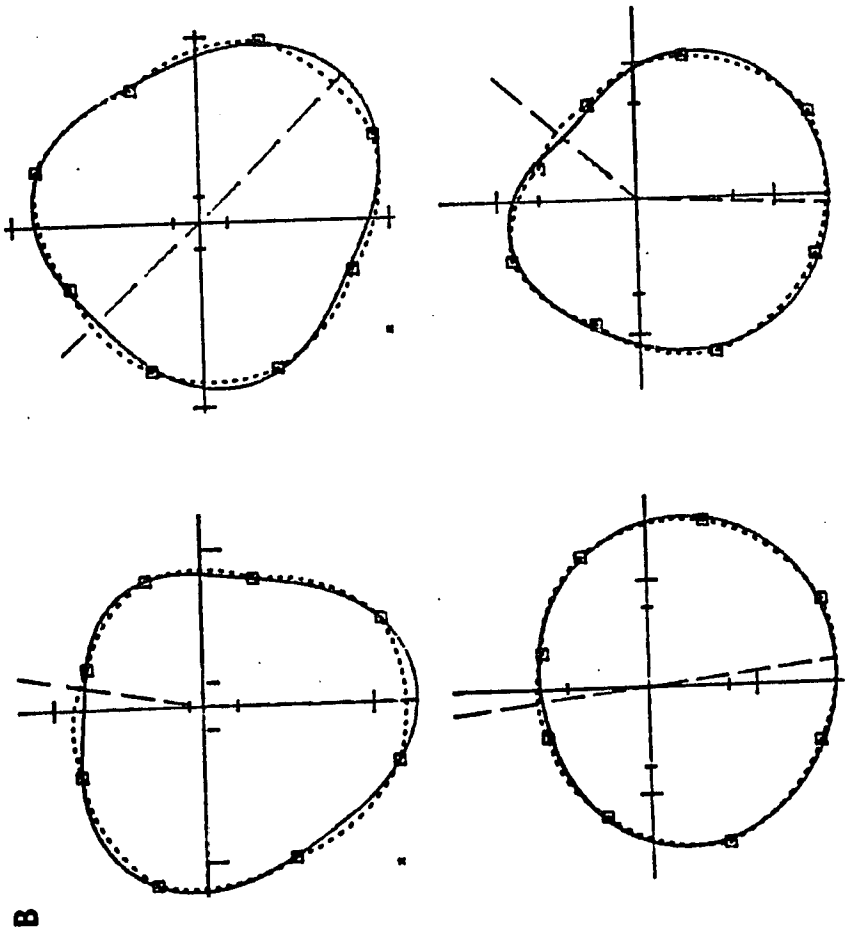
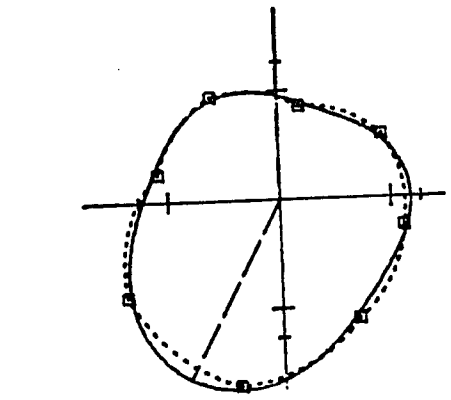


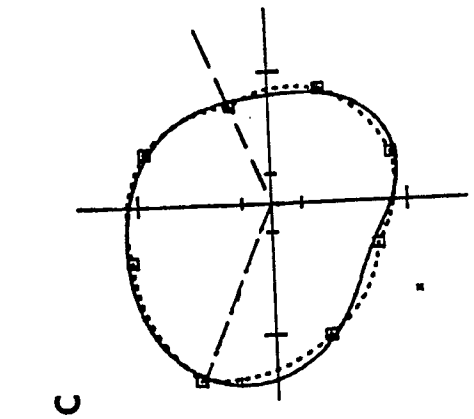
Fig. 26. Tuning plots of weakly and non-directional units. A. Units with a weak tendency toward excitation by upward movement. B. Units with a weak tendency toward excitation by downward movement. C. Units with a weak tendency toward excitation by horizontal movement. D. Non-directional units. In A, B and C dashed lines indicate weak excitatory and weak inhibitory directions. Other conventions as in Fig.9.


A
up
anterior
posterior
down



B





C

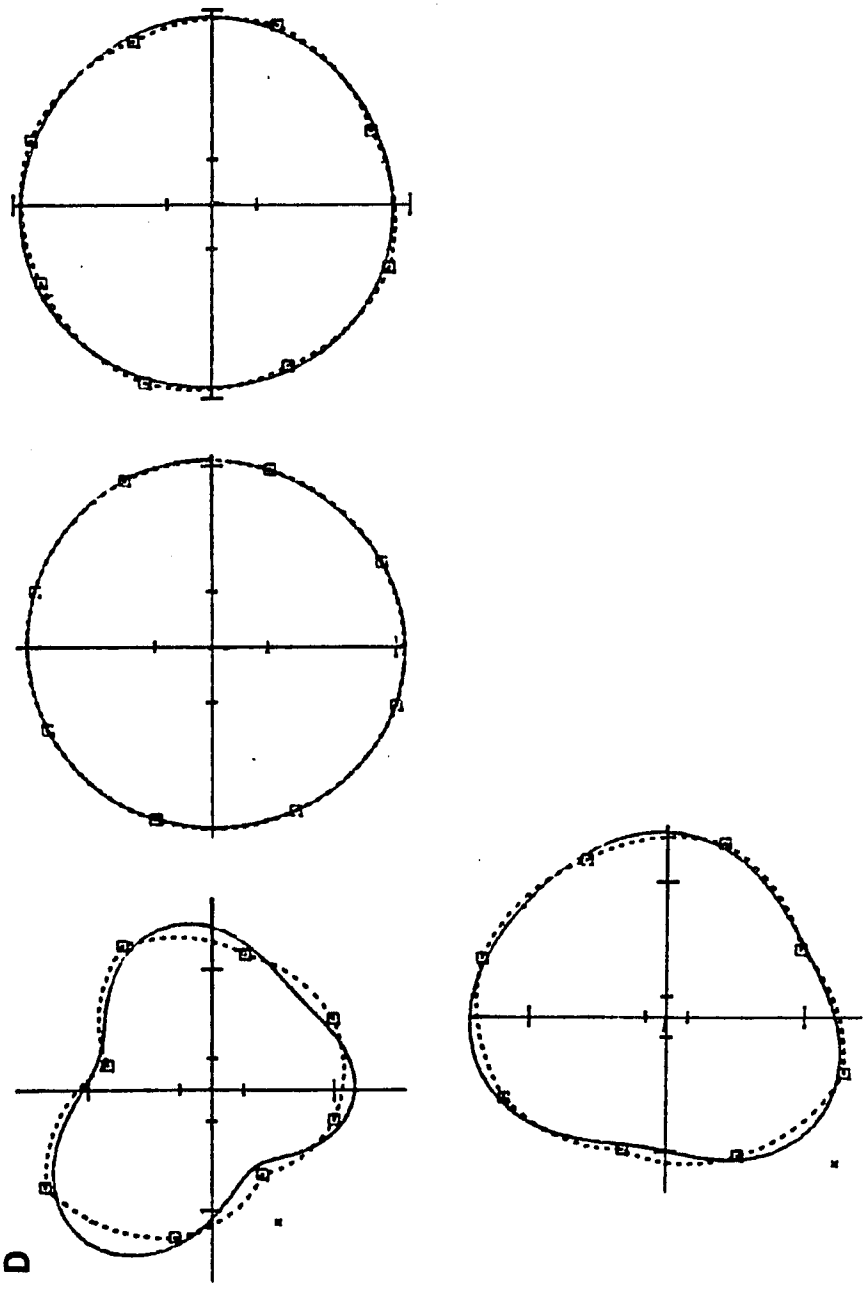

D

Fig. 27. Example of response of a unit to turning room lights off. Lights were off at the beginning of the trace. Downward deflection of the upper trace indicates lights on and upward deflection indicates lights off. As shown in the lower trace unit responds to lights off with a substantial and transient increase in firing rate. Calibration bar =1 sec.

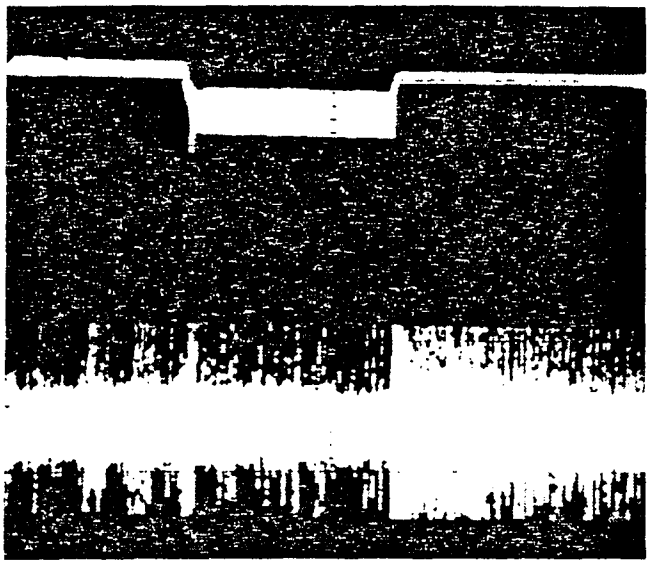


Fig. 28. Histograms comparing directional modulation of units in older birds (n=30) and neonates (n=30). Modulation is defined as $(N_{max}-N_{min})/(N_{max}+N_{min})$, where N_{max} is the number of spikes in the stimulus direction which produced the greatest excitation and Nmin is the number of spikes in the direction which produced the greatest inhibition. Arrows point to median values of 0.876 for older birds and 0.764 for neonates.

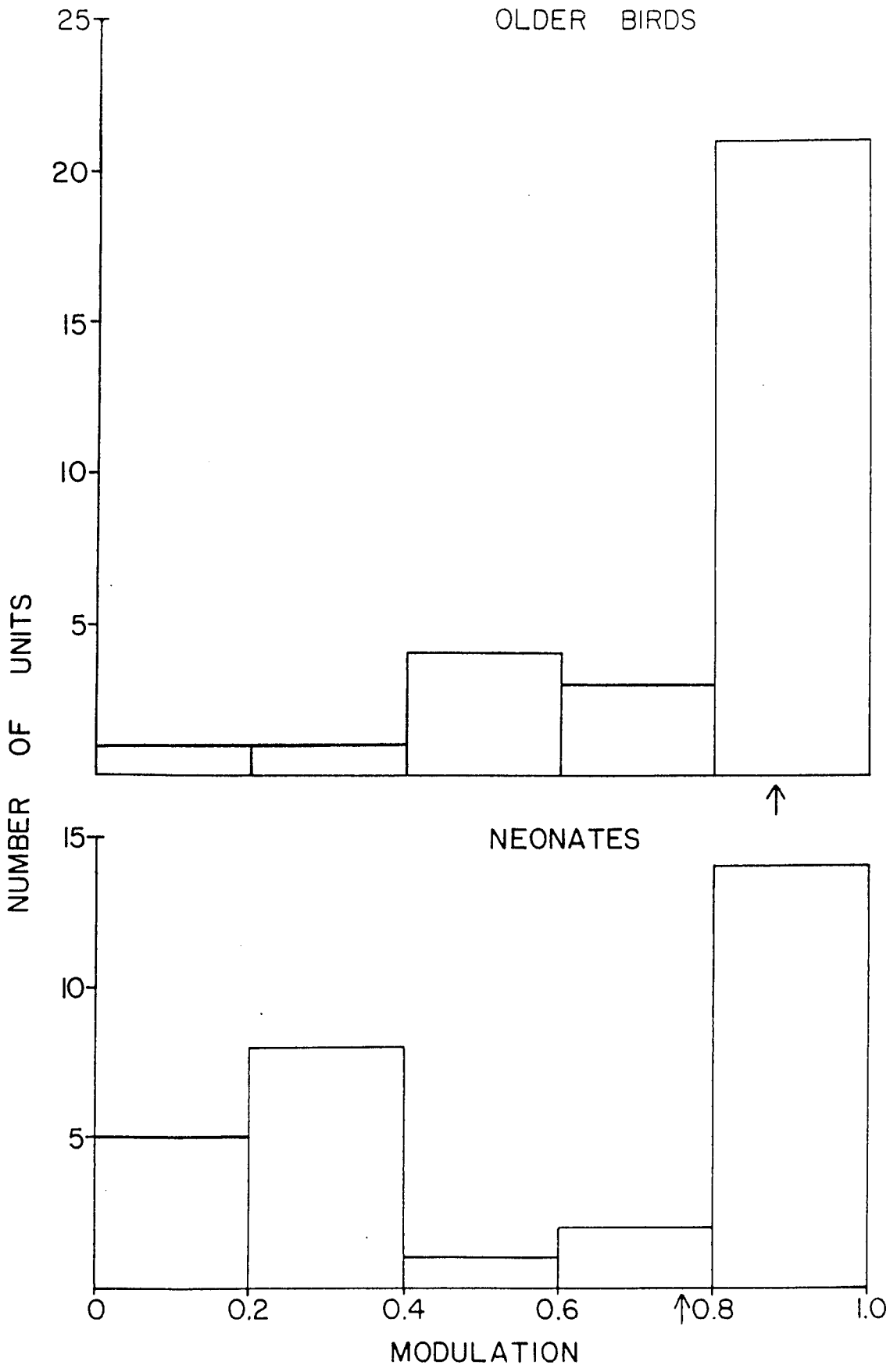

OLDER BIRDS
25
20
15
10
5
NUMBER OF UNITS
NEONATES
15
10
5
0
0.2
0.4
0.6
0.8
1.0
MODULATION

Fig. 29. Histograms comparing narrowness of directional tuning of units in older brids (n=28) and neonates (n=28). The 50% peak width used to assess the tuning is the angular distance between the points at which the curve fell to 50% of the maximum of the fitted Fourier function. *Except for one neonate unit, the curves of all other units shown at 360 degrees did not fall to 50% of the maximum.

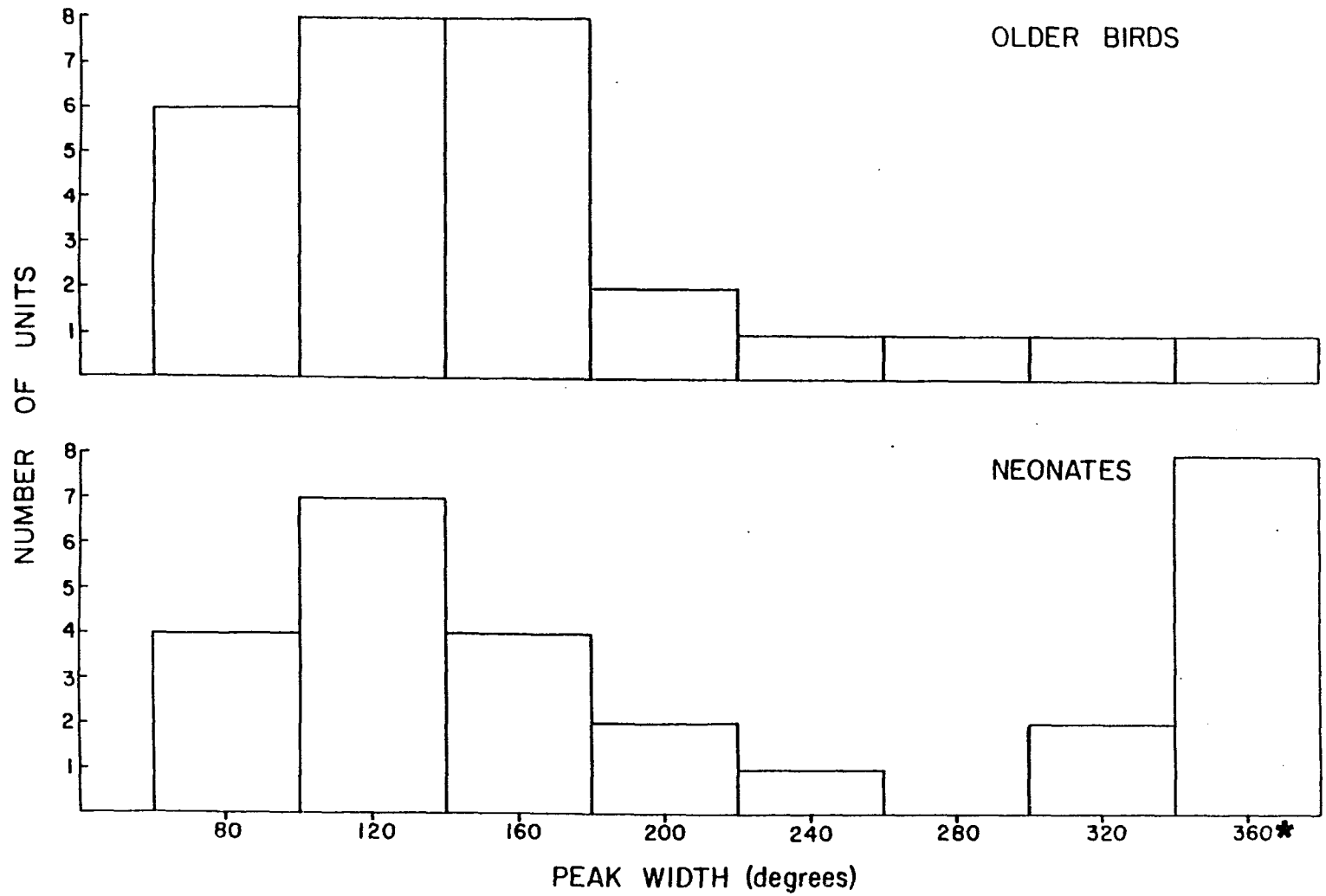

OLDER BIRDS
NEONATES
NUMBER OF UNITS
1
2
3
4
5
6
7
8
80
120
160
200
240
280
320
360*
PEAK WIDTH (degrees)

Fig. 30. Histograms comparing spontaneous activity of units in older birds (n=25) and neonates (n=30).

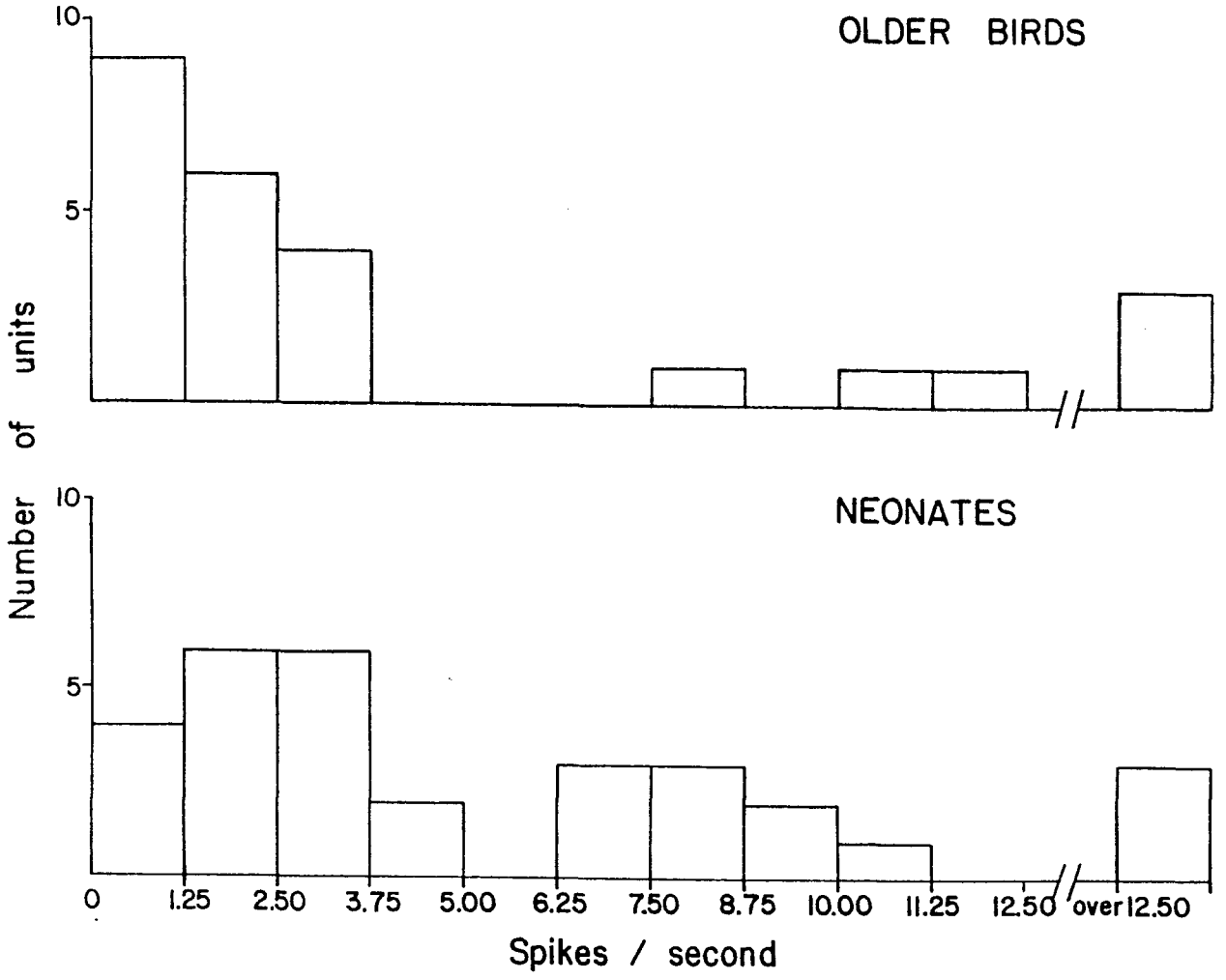
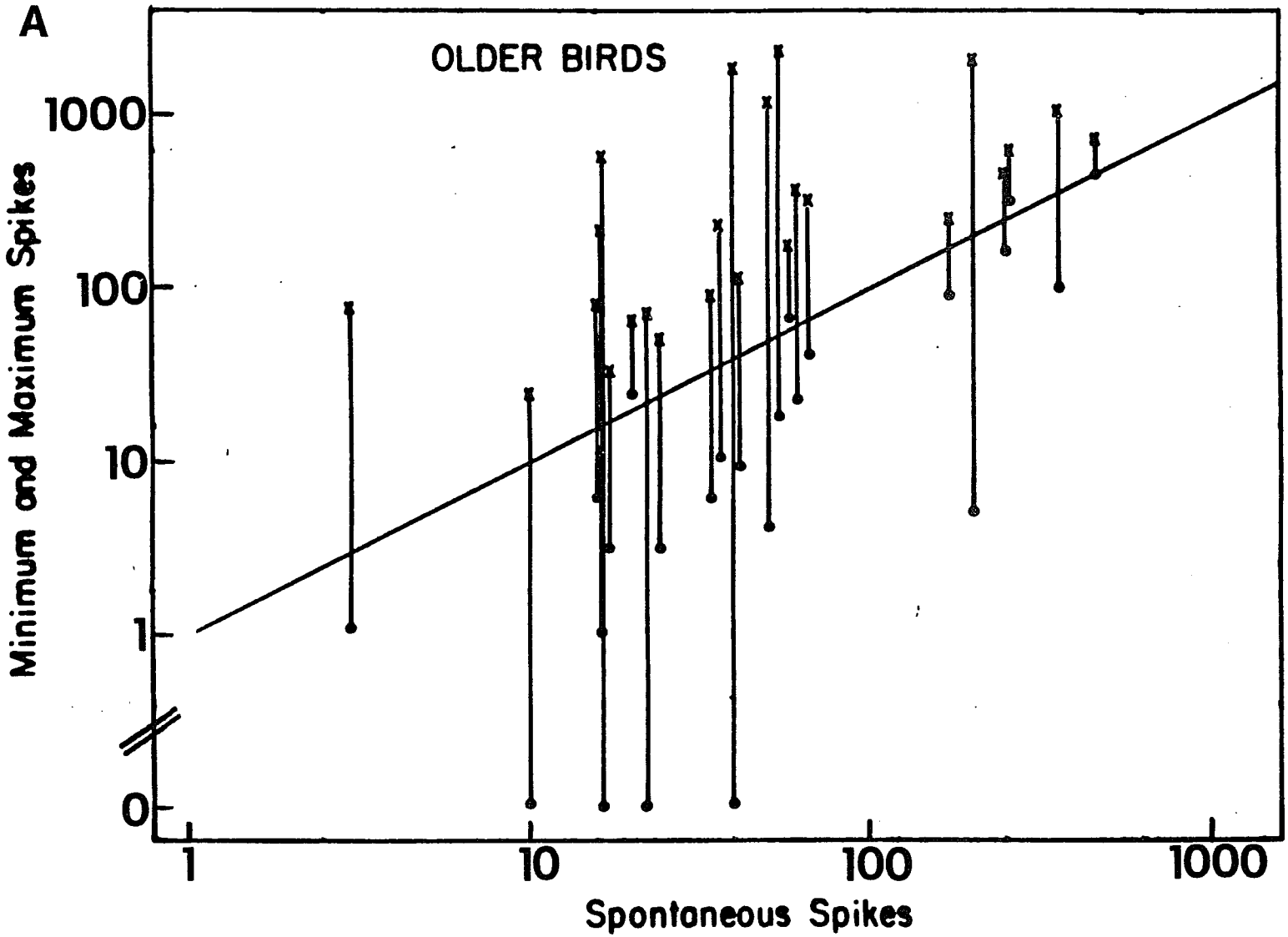

OLDER BIRDS
NEONATES
Number of units
10
5
10
5
0
1.25
2.50
3.75
5.00
6.25
7.50
8.75
10.00
11.25
12.50
over 12.50
Spikes / second

Fig. 31. Logarithmic plot of modulation of units against level of spontaneous firing for total stimulus presentation. x= number of spikes in the direction of greatest excitation; o = number of spikes in the direction of greatest inhibition. Vertical lines connect these values for individual units. Diagonal marks the number of spontaneous spikes for each unit. A. Older birds. B. Neonates.


A
OLDER BIRDS
Minimum and Maximum Spikes
1000
100
10
1
0
1
10
100
1000
Spontaneous Spikes

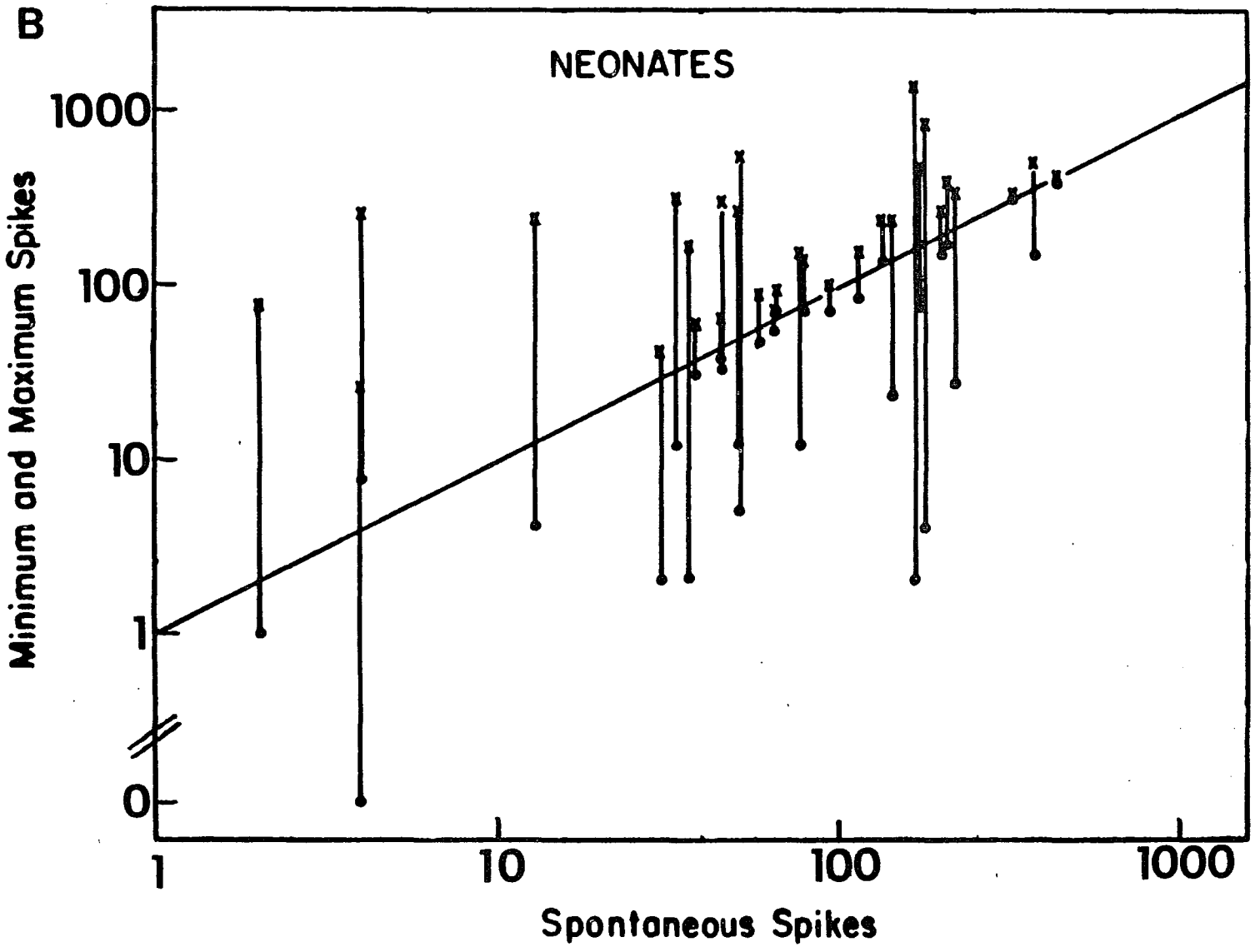
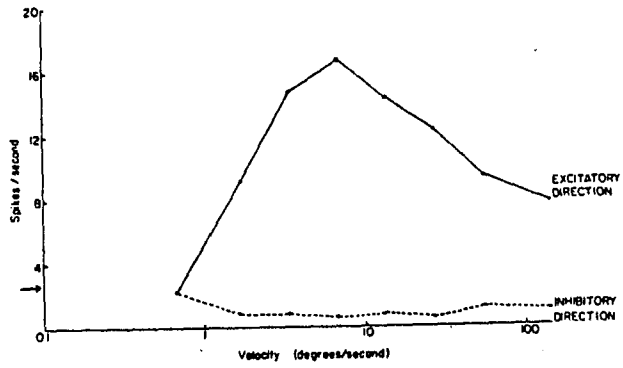
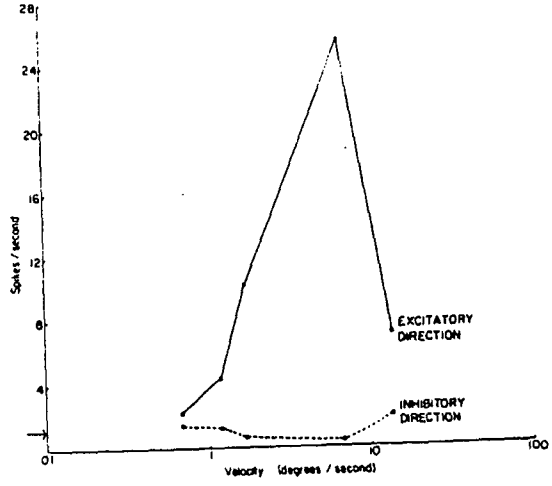

B
NEONATES
1000
100
10
1
0
Minimum and Maximum Spikes
1
10
100
1000
Spontaneous Spikes

TABLE 1. Number of units in neonates and older birds with both high spontaneous firing rates greater than 3.75 spikes/sec. and low modulation less than 0.4 compared to other combinations of spontaneous rates and modulation.
See text for further explanation.

	Older Birds	Neonates
High spontaneous rate and low modulation	2	11
Other combinations	23	21

Fig. 32. Velocity tuning curves for 3 units in nBOR showing preference for slow movement. Arrows indicate rate of spontaneous activity.


20
16
12
8
4
Spikes / second
EXCITATORY DIRECTION
INHIBITORY DIRECTION
01
1
10
100
Velocity (degrees/second)


28
24
20
16
12
8
4
Spikes / second
EXCITATORY DIRECTION
INHIBITORY DIRECTION
01
1
10
100
Velocity (degrees / second)

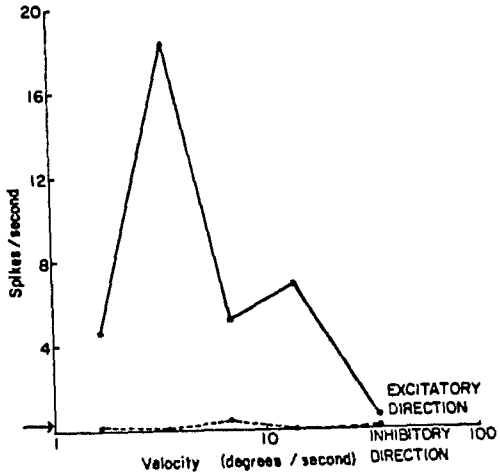

20
16
12
8
4
Spikes / second
EXCITATORY DIRECTION
INHIBITORY DIRECTION
1
10
100
Velocity (degrees / second)

Fig. 33. Receptive field centers of units in nBOR. Most are peripheral to the estimated position of the optic axis (indicated by circled asterisk). Black circles=units in older birds, white circles=units in neonates. Shaded area represents approximate position of the pecten. Visual stimuli could not be presented beyond the boundary indicated by solid line.

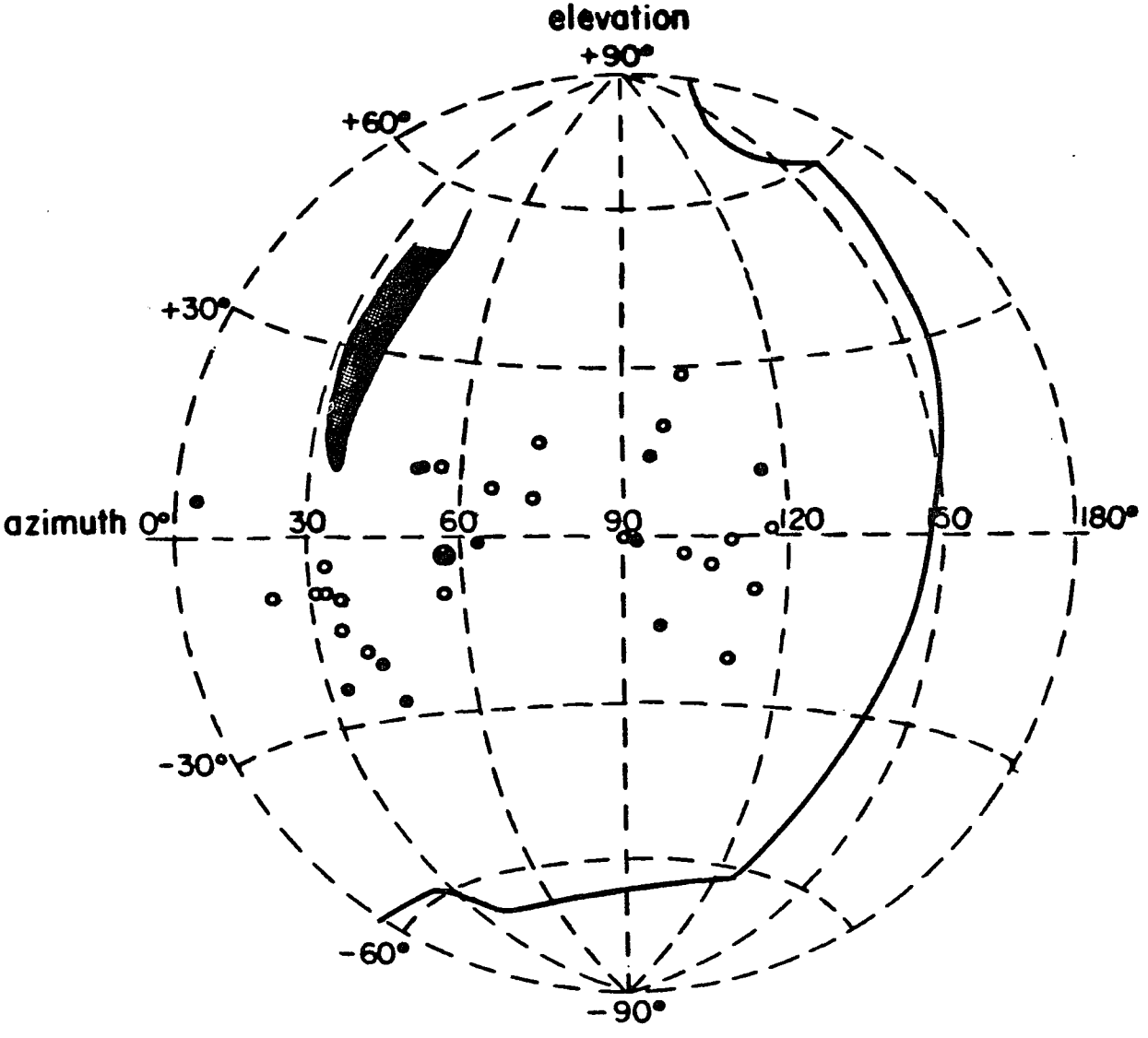

elevation
+90°
+60°
+30°
azimuth 0°
30
60
90
120
150
180°
-30°
-60°
-90°

Fig. 34. Illustration of retinotopic organization in nBOR. Lines connect single units recorded in the same electrode track. There is a tendency for frontal visual fields to be represented in the more dorsal part of the nucleus and lateral visual fields in the more ventral part. Heavy diagonal is regression line. Regression equation: $y=107-0.64x$

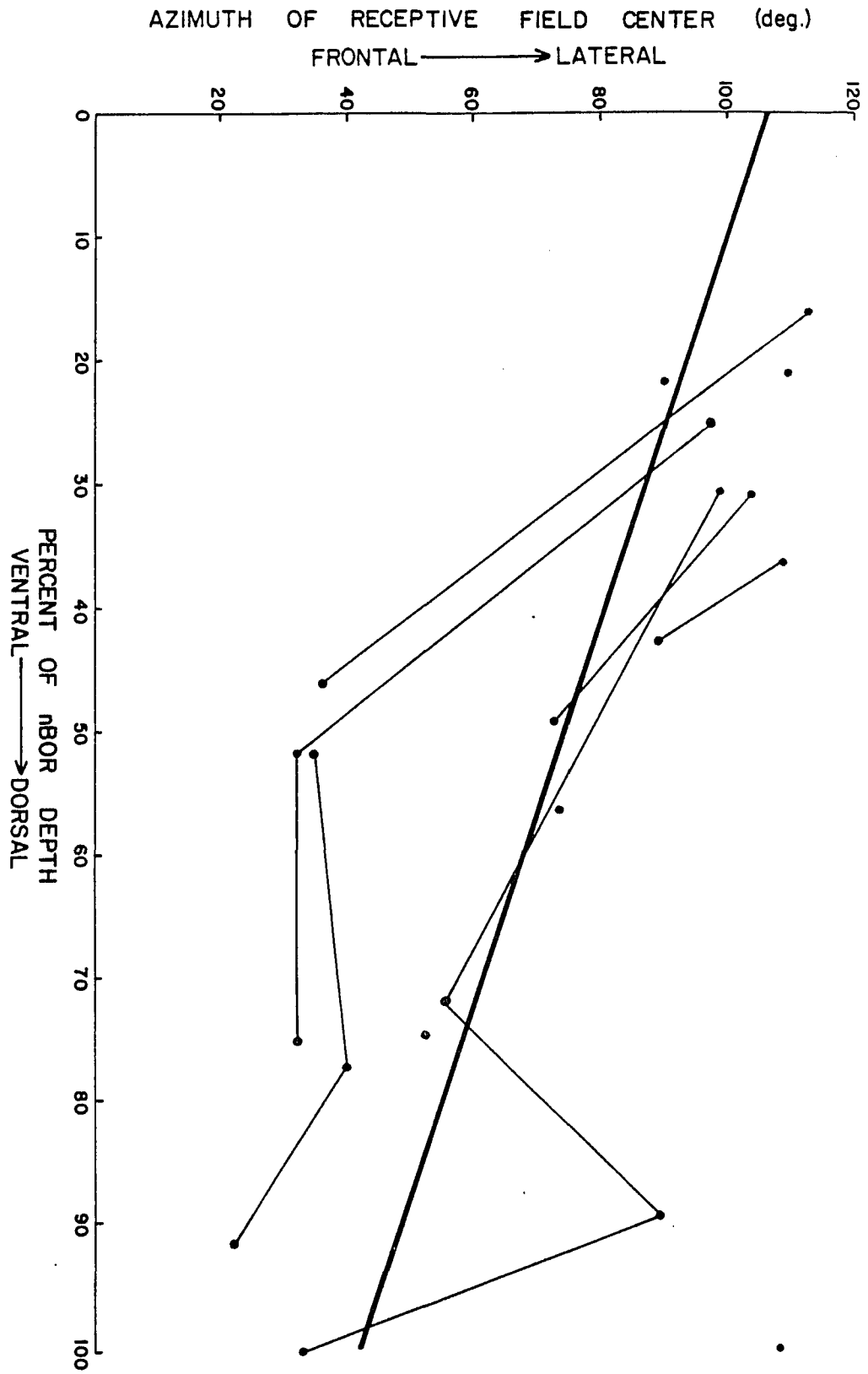

AZIMUTH OF RECEPTIVE FIELD CENTER (deg.)
FRONTAL ⟶ LATERAL
20
40
60
80
100
120
0
10
20
30
40
50
60
70
80
90
100
PERCENT OF nBOR DEPTH
VENTRAL ⟶ DORSAL

Fig. 35. Recording sites of units in nBOR. Filled symbols are units excited by downward visual motion. Unfilled symbols are units excited by upward visual motion. Triangles indicate single unit recordings; circles indicate multiple unit recordings: black and white circles divided horizontally indicate up and down units dorsal to down units only; black and white circles divided vertically indicate up and down units dorsal to up units. x indicate single units preferring horizontal motion. Calibration bar=1mm.

NEONATES

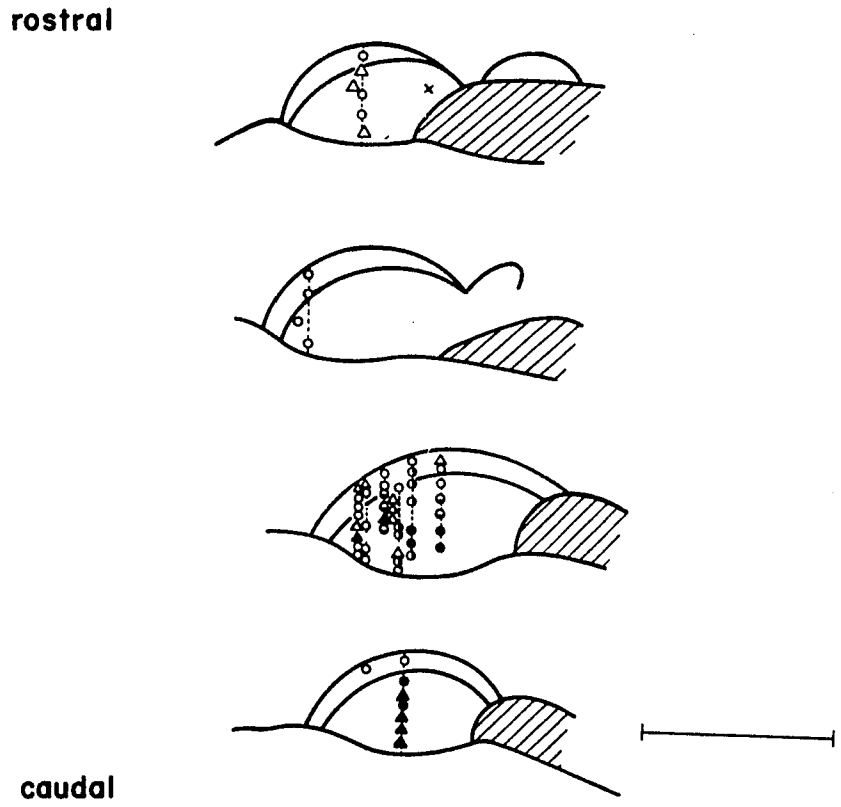
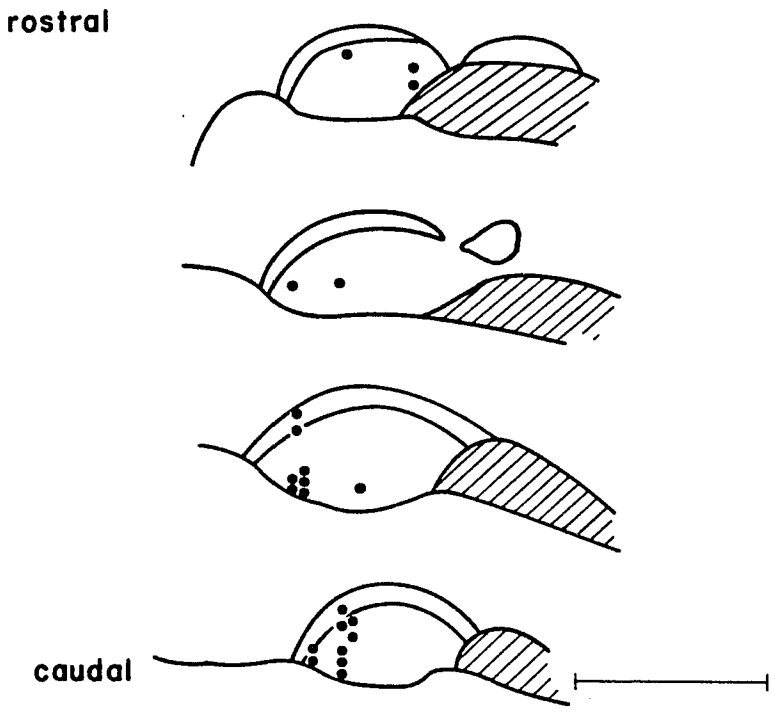


TABLE 2. Number of up units in neonates and older birds in dorsocaudal and ventrocaudal nBOR.

	Dorsocaudal	Ventrocaudal
Neonates	23	15
Older Birds	42	7

Fig. 36. Recording sites of weakly and non-directional units in nBOR in neonates. Calibration bar=1mm.

NEONATES



CHAPTER 5

EYE MOVEMENTS EVOKED BY ELECTRICAL STIMULATION OF nBOR

RESULTS

Electrical stimulation of nBOR in all animals resulted in horizontal nystagmus. In some experiments it resulted in horizontal nystagmus with the slow phase in the nasal-to-temporal direction, while in others the slow phase was in the temporal-to-nasal direction. Vertical and torsional nystagmus were absent. Raw records of the results of electrical stimulation in 2 animals are shown in Fig.37 A and B; nystagmus in the temporal-to-nasal direction is shown in the upper trace in A and in the nasal-to-temporal direction in the upper trace in B. The apparent vertical eye movements which appear in the lower trace in B are comparable to those recorded from the same bird in response to a visual horizontal stimulus (see initial segment of lower trace in Fig.41.), which does not produce a vertical eye movement. Such apparent vertical eye movements appeared on the raw records of all birds viewing a horizontal visual stimulus. This is very strong evidence that these apparent vertical eye movements are an

artifact of the recording method resulting from the difficulty of being certain that the coil used for recording vertical eye movements is excatly horizontal.

That electrical stimulation did not produce vertical or torsional eye movements was not due to the inability of the eye to move in these directions since vertical and torsional responses to visual stimuli were normal in all 8 animals for which this was tested.

After a few initial experiments which showed that electrical stimulation of nBOR produced eye movement in either the nasal-to-temporal or temporal-to-nasal direction, lesions were made in the nBOR contralateral to the experimental one. The rationale for the lesions was based on the fact that OKN in birds monocularly viewing a visual stimulus has a higher gain in the temporal-to-nasal direction when the measured eye is the seeing eye, but a higher gain in the nasal-to-temporal direction when the measured eye is the covered eye (Gioanni et al., 1981). Therefore, it was postulated that the nasal-to-temporal nystagmus found in some of the electrical stimulation experiments resulted from stimulation of pathways involving the contralateral side of the brain. Since nBOR sends efferents to the contralateral nBOR, this commissural pathway was eliminated by lesioning the nBOR contralateral to the electrically stimulated one. In three birds the lesion was successfully placed in nBOR and in one bird it was dorsal and somewhat rostral to nBOR. In these experiments with lesioned birds, electrical stimulation of the intact nBOR still resulted in either nasal-to-temporal or temporal-to-nasal nystagmus. Therefore, the hypothesis that the nasal-to-temporal nystagmus might

involve the contralateral nBOR was disproved. Consequently the data from lesioned birds have been pooled with those from intact birds since there were no differences between them.

A summary of the eye movements resulting from electrical stimulation of nBOR in 10 animals is shown in Table 3. Nystagmus in the nasal-to-temporal direction occurred most frequently, although nystagmus in the temporal-to-nasal direction occurred in some animals. Velocities of nystagmus in the temporal-to-nasal direction were somewhat higher than those in the nasal-to-temporal direction. A similar asymmetry is present in the OKN of birds monocularly viewing a visual stimulus. The stimulus variables which resulted in the eye movements are also shown in Table 3. Current ranged from 50 to 200 μA and frequency from 80 to 200 Hz. The effect of current strength and frequency on the velocity of horizontal nystagmus is shown in Fig.38A and B, respectively. Both higher currents and frequencies resulted in eye movements of higher velocities, a common occurrence when stimulating oculomotor pathways. The increase in response to higher currents probably involves the recruitment of a larger population of neurons, while the increase in response to higher frequencies is probably due to an increase in the firing rates of neurons.

Based on the directional tuning characteristics of neurons in nBOR, it was hypothesized that electrical stimulation of the nucleus would result in vertical and/or torsional eye movements. In each experiment, horizontal, vertical and torsional eye movements were recorded. That only horizontal nystagmus resulted is shown in Fig.39. The upper trace in A shows horizontal and the lower trace vertical eye

movements recorded simultaneously in response to electrical stimulation; it is evident that the stimulation results in horizontal nystagmus. Fig.39B shows torsional eye movements in response to electrical stimulation recorded in the same animal. A comparison of this trace with the upper one in A likewise shows that the response is that of horizontal nystagmus.

In some experiments I explored the relationship between horizontal nystagmus resulting from a visual optokinetic stimulus with that resulting from an electrical stimulus. These stimuli were presented separately and then under 2 conditions: 1) the visual stimulus was presented in the same direction as the nystagmus that resulted from electrical stimulation 2) the visual stimulus was presented in the direction opposite to that of the nystagmus which resulted from electrical stimulation. The results are summarized in Fig.40; condition 1 is shown in A, condition 2 in B. Although the magnitude varies, there is always an increase in the velocity of nystagmus when both electrical and visual stimuli produce eye movements in the same direction (Fig.40A). This functional summation of the two stimuli argues that the electrical stimulation is activating a normal OKN-producing locus (or loci) in the brain. That the electrically stimulated locus is a powerful one in the pathway producting OKN can be seen from the results of the experiments in which the visual and electrical stimuli produce nystagmus in opposite directions (Fig.40B). In all cases the electrical stimulation is more effective than the visual stimulation. In three animals electrical stimulation resulted in nystagmus in the direction opposite to that produced by

the visual stimulus. In the fourth animal, although the direction of nystagmus was not reversed, the response to the visual stimulus (7.9 deg/sec) was substantially reduced (0.9 deg/sec). Fig.41 shows an example of the reversal of the direction of visually-produced OKN (temporal-to-nasal OKN) by the electrical stimulus (nasal-to-temporal nystagmus).

It was of interest to determine whether the direction of nystagmus produced by electrical stimulation was correlated with the stimulation site in nBOR. The result of this analysis is shown in Fig.42, which summarizes the sites of stimulating electrodes and the directions of horizontal nystagmus resulting from the stimulation. It can be seen that anatomical location bears no evident relationship to direction of nystagmus, since both nasal-to-temporal and temporal-to-nasal nystagmus occur throughout various locations in nBOR.

DISCUSSION

The most surprising result of these experiments is the finding that electrical stimulation of nBOR results in horizontal rather than vertical or torsional nystagmus, since several lines of evidence point to an important role for nBOR in non-horizontal OKN. Single unit recording shows that most neurons in nBOR respond best to motion in vertical directions, although a small minority of units respond best to horizontal motion. In addition, 2-deoxy-D-glucose studies of nBOR show that it is heavily labeled in chickens viewing a vertical

optokinetic stimulus, but that labeling is minimal when the optokinetic stimulus is horizontal (McKenna and Wallman,1981). Furthermore, lesions of nBOR proper and nBORd in chickens abolish vertical and torsional OKN, while horizontal OKN is not affected (Wallman et al.,1981).

However, the horizontal nystagmus generated by electrical stimulation in the present experiments is indistinguishable from that normally resulting from a horizontal optokinetic stimulus. Furthermore, electrical stimulation increases the slow-phase velocity of ongoing horizontal OKN, which retains its normal characteristics. In addition, when visual and electrical stimulation produce nystagmus in opposite directions, electrical stimulation not only blocks ongoing OKN, but it generates nystagmus in the opposite horizontal direction. These findings suggest that the neural pathway being electrically stimulated has an important role in the regulation of horizontal nystagmus.

There are several possible explanations for these contradictory findings. 1) The fact that electrical stimulation of nBOR did not generate non-horizontal nystagmus is not necessarily in conflict with the evidence that nBOR has an important role in vertical and torsional OKN. It is possible that electrical stimulation of nBOR activates both up and down vertically responsive neurons and that this inherently contradictory stimulus results in cancellation of vertical nystagmus altogether. However, the fact that stimulation at all sites in nBOR resulted in horizontal nystagmus argues against this since the more rostral sites contain up units almost exclusively. 2) Horizontal

nystagmus could have resulted from current spread (which was not measured in these experiments) to the nBOR1 or to some other as yet unidentified nearby pathway for horizontal OKN. Metabolic mapping studies have shown that nBOR1 responds to both temporal-to-nasal and nasal-to-temporal optokinetic stimuli (McKenna and Wallman, 1981, 1984). A lesion study in pigeons provides evidence for an important role of nBOR in nasal-to-temporal OKN and a secondary role in temporal-to-nasal OKN (Gioanni et al.,1983b). However, these lesions appear to be more extensive than those described by Wallman et al., (1981), although the latter also found deficits in horizontal OKN when lesions extended beyond nBOR. In cats, lesions of LTN and MTN produced deficits in horizontal OKN and VOR (Clément and Magnin, 1984), even though cells in these nuclei respond to vertical rather than horizontal visual stimuli. However, in some cases lesions of adjacent brain areas produced similar results. Arguing against current spread in the present experiments is the finding that stimulation at all sites produced horizontal nystagmus and the direction of nystagmus did not vary with current strength. 3) Horizontal nystagmus could have resulted from antidromic stimulation of axon collaterals. The nBOR receives afferents from the DRGCs of the retina, the contralateral nBOR and the visual Wulst (analog of the mammalian visual cortex) (Rio et al., 1983). However, it is unknown whether any of these inputs are collaterals. Furthermore, this hypothesis would require that they be collaterals of neurons projecting to brain regions involved in horizontal OKN. The LM is a pretectal nucleus known to be important in horizontal OKN (McKenna and Wallman, 1981; Winterson and Brauth,

1981; Gioanni et al., 1983a; Morgan et al., 1983). Although LM receives a retinal input, it is unknown whether this input is from the DRGCs or other retinal ganglion cells. The Wulst projects to LM (Miceli et al., 1979; Bodnarenko and McKenna, 1984) but it is unknown whether the same neurons also project to nBOR. 4) Horizontal nystagmus could have resulted from stimulation of efferent pathways from nBOR to brain regions important in horizontal OKN. The nBOR projects to 3 such regions: the LM, the inferior olive and the vestibulocerebellum (Brecha et al.,1980). Although the functional role of these projections is unknown and although it is clear that horizontal OKN in chickens is unaffected by lesions of nBOR (Wallman et al., 1981), the possibility remains that the effect of electrical stimulation is via these pathways. LM, which receives a major projection from nBOR (Brecha et al., 1980) contains a large population of neurons, which respond to horizontal stimulus motion and a substantially smaller population responsive to vertical stimulation motion (Winterson and Brauth, 1981; Morgan et al., 1983; Winterson pers. comm.). Although details of synaptic connections in LM are unknown, it is possible that electrical stimulation of varied sites in nBOR differentially excites or inhibits nasal-to-temporal or temporal-to-nasal neurons in LM. Compared to LM, little is known about the inferior olive in birds. However, it is clearly important in horizontal OKN in rabbits (Barmack and Hess, 1980 a,b; Barmack and Simpson, 1980), and possibly in vertical OKN as well (Simpson et al, 1981). Similarly, although the functional role of the vestibulocerebellar folia to which nBOR projects is unknown, the

vestibulocerebellum in mammals does have a role in horizontal and vertical OKN (Simpson and Hess, 1977; Simpson et al., 1981; Waespe et al., 1983).

It is not possible to compare the results presented here with those of other species, since electrical stimulation of the accessory optic system in other species has not been reported. However, such a comparison would obviously be fruitful.

Fig. 37. A. Example of temporal-to-nasal nystagmus in response to electrical stimulation. Top trace shows horizontal nystagmus; downward deflection is in the temporal-to-nasal direction and upward deflection is nasal to temporal. Middle trace shows vertical eye movement; downward deflection is upward eye movement and upward deflection is downward eye movement. Lower trace shows onset and offset of electrical stimulus which was 80Hz, 0.2msec pulse duration, 200 μA of current. Calibration bars as in B. B. Example of nasal-to-temporal nystagmus in response to electrical stimulation. Top trace shows horizontal nystagmus, upward deflection is in the nasal-to-temporal direction and downward deflection is temporal to nasal. Middle trace shows vertical eye movement; downward deflection is downward eye movement and upward deflection is upward eye movement. Lower trace shows onset and offset of electrical stimulus which was 200Hz, 0.2msec. pulse duration, 50 μA of current. Horizontal calibration bar=1 sec; vertical calibration bar=3 deg.

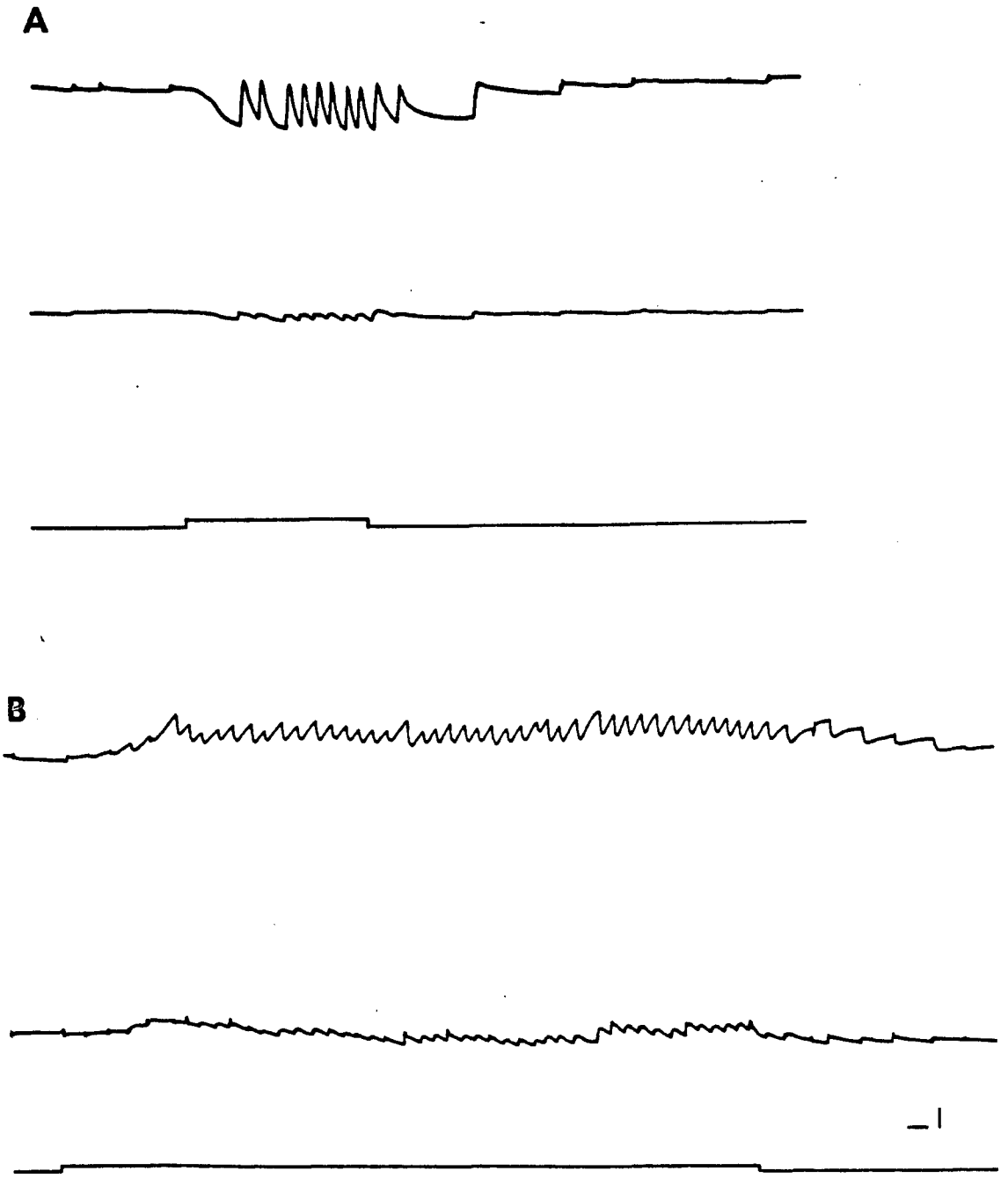

A
B
1

TABLE 3. Direction and velocity characteristics of horizontal nystagmus evoked by electrical stimulation of nBOR.

Bird #	Direction of Nystagmus	Slow-Phase Velocity of Nystagmus (deg./sec.)	Lesion	Electrical Stimulus Variables		
				Current (μA)	Frequency (Hz)	Pulse Duration (msec.)
1	temporal to nasal	7.9	dorsal to contra-lateral nBOR	100	80	0.2
2	temporal to nasal	7	none	200	80	0.2
3	temporal to nasal	5.5	none	100	80	0.2
4	nasal to temporal	5	none	50	80	0.2
5	nasal to temporal	5	none	50	200	0.2
6	nasal to temporal	5	contralateral nBOR	50	130	0.2
7	nasal to temporal	4.2	none	125	80	0.2
8	nasal to temporal	2.7	contralateral nBOR	50	80	0.2
9	nasal to temporal	1.9	none	175	120	0.2
10	nasal to temporal	1	contralateral nBOR	200	80	0.2

Fig. 38. A. Effect of stimulus current strength on slow-phase velocity. B. Effect of stimulus frequency on slow-phase velocity. In both A and B lines connect responses in individual animals; x=temporal-to-nasal nystagmus, =nasal-to-temporal nystagmus.

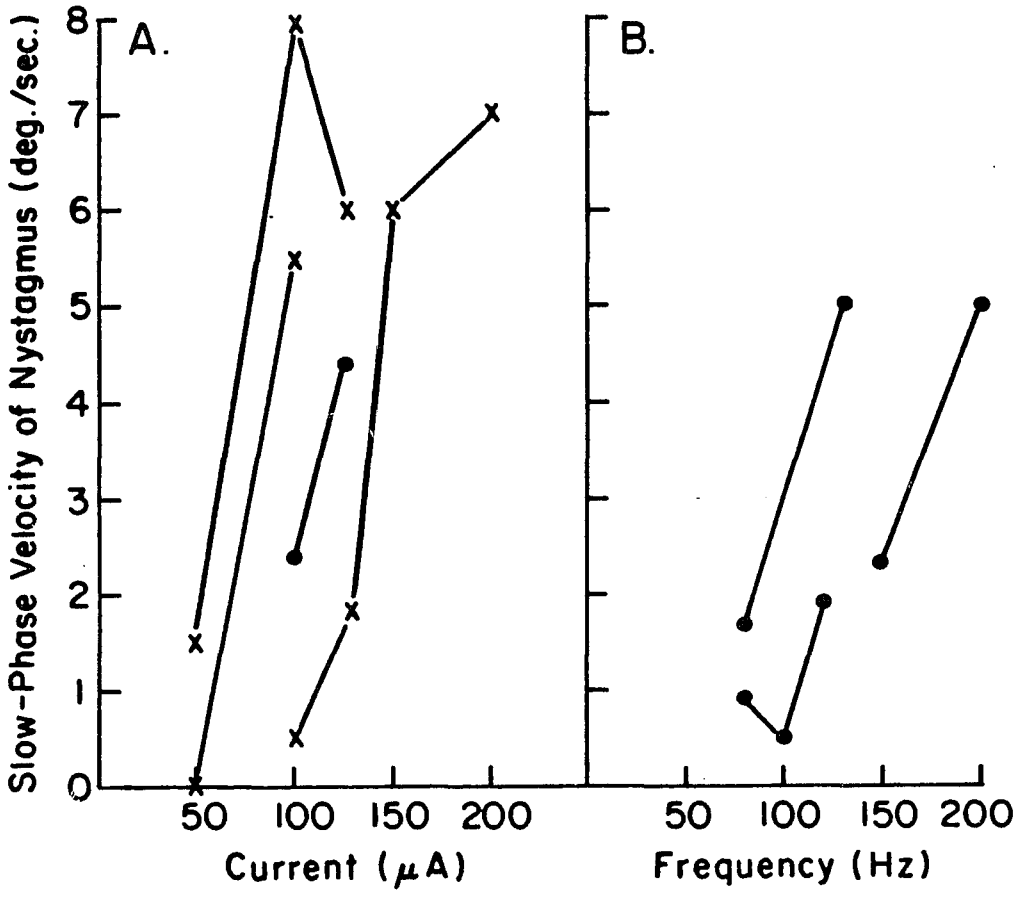

A.
B.
Slow-Phase Velocity of Nystagmus (deg./sec.)
0
1
2
3
4
5
6
7
8
50
100
150
200
Current (μA)
50
100
150
200
Frequency (Hz)

Fig. 39. A. Example of simultaneous recording of horizontal and vertical eye movements in response to electrical stimulation. Upper trace shows horizontal nystagmus. Upward deflection is nasal to temporal; downward deflection is temporal to nasal. Middle trace shows vertical eye position. Upward deflection is up; downward deflection is down. Lower trace shows onset and offset of electrical stimulus, which was 150Hz, 0.2msec. pulse duration, 50 μA. Calibration bars as in Fig. 37. B. Example of recording of torsional eye movement in the same animal and with the same electrical stimulation as in A. Upper trace shows torsional eye position. Upward deflection is clockwise; downward deflection is counterclockwise. Lower trace shows onset and offset of electrical stimulation. Calibration bars as in Fig.37.

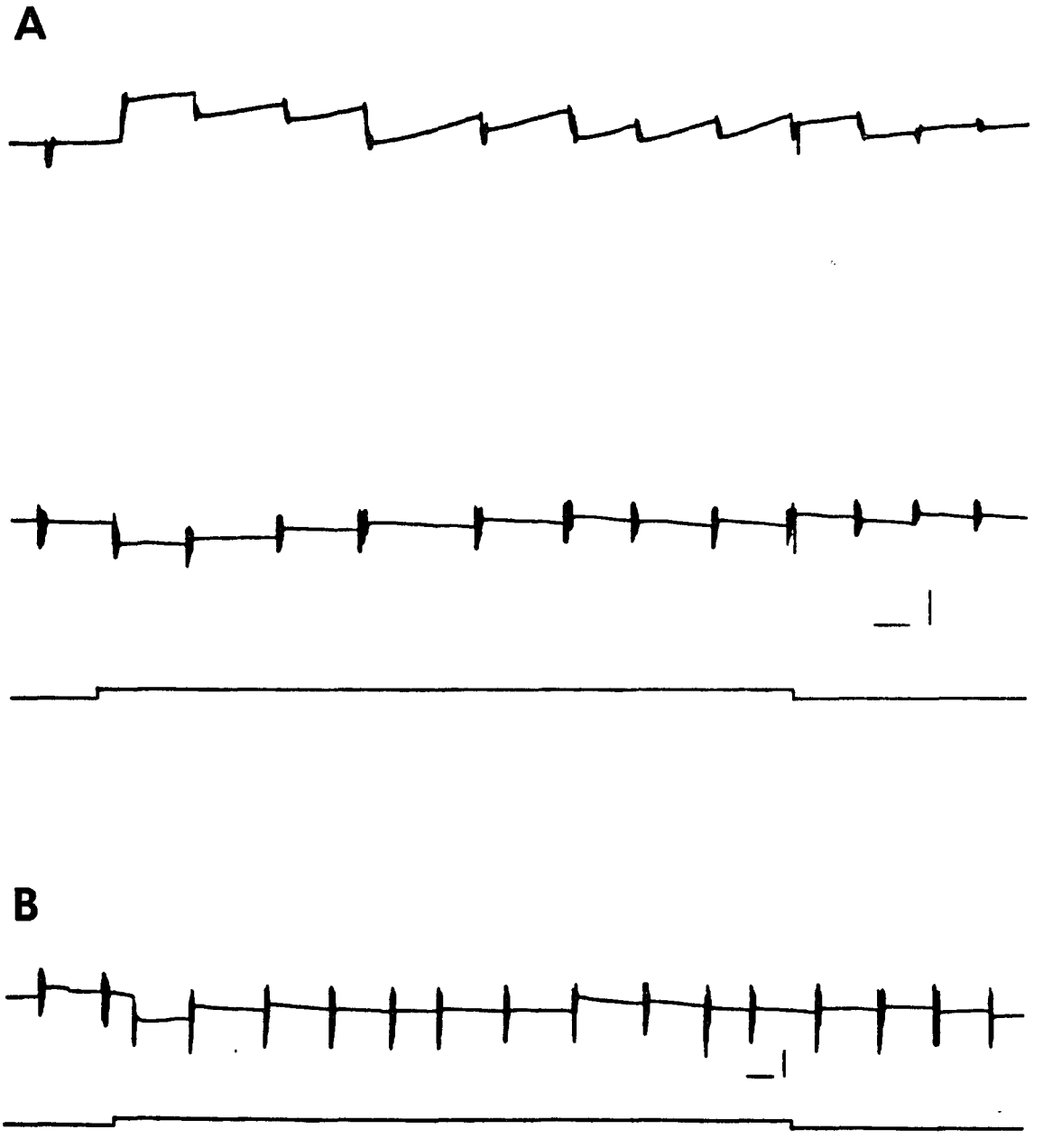

A
B

Fig. 40. A. Comparison of nystagmus in response to visual and electrical stimulation when both produce nystagmus in the same direction. For each of 4 animals histograms show direction and velocity of nystagmus response to 1) visual stimulation only=v, 2) electrical stimulation only=e, 3) concurrent visual and electrical stimulation=v+e. Compared to visual or electrical stimulation alone, there is an increase of varying magnitude in the velocity of the nystagmus when both stimuli are presented concurrently. B. Comparison of nystagmus response in same animals as in A when visual and electrical stimulation produce nystagmus in opposite directions. (Response to electrical stimulation for individual animals is the same as in A.) When both stimuli are presented concurrently, the nystagmus is in the direction produced by electrical rather than visual stimulation in three animals. In the fourth animal, the nystagmus is in the direction of the visual stimulus, but its velocity is greatly reduced.

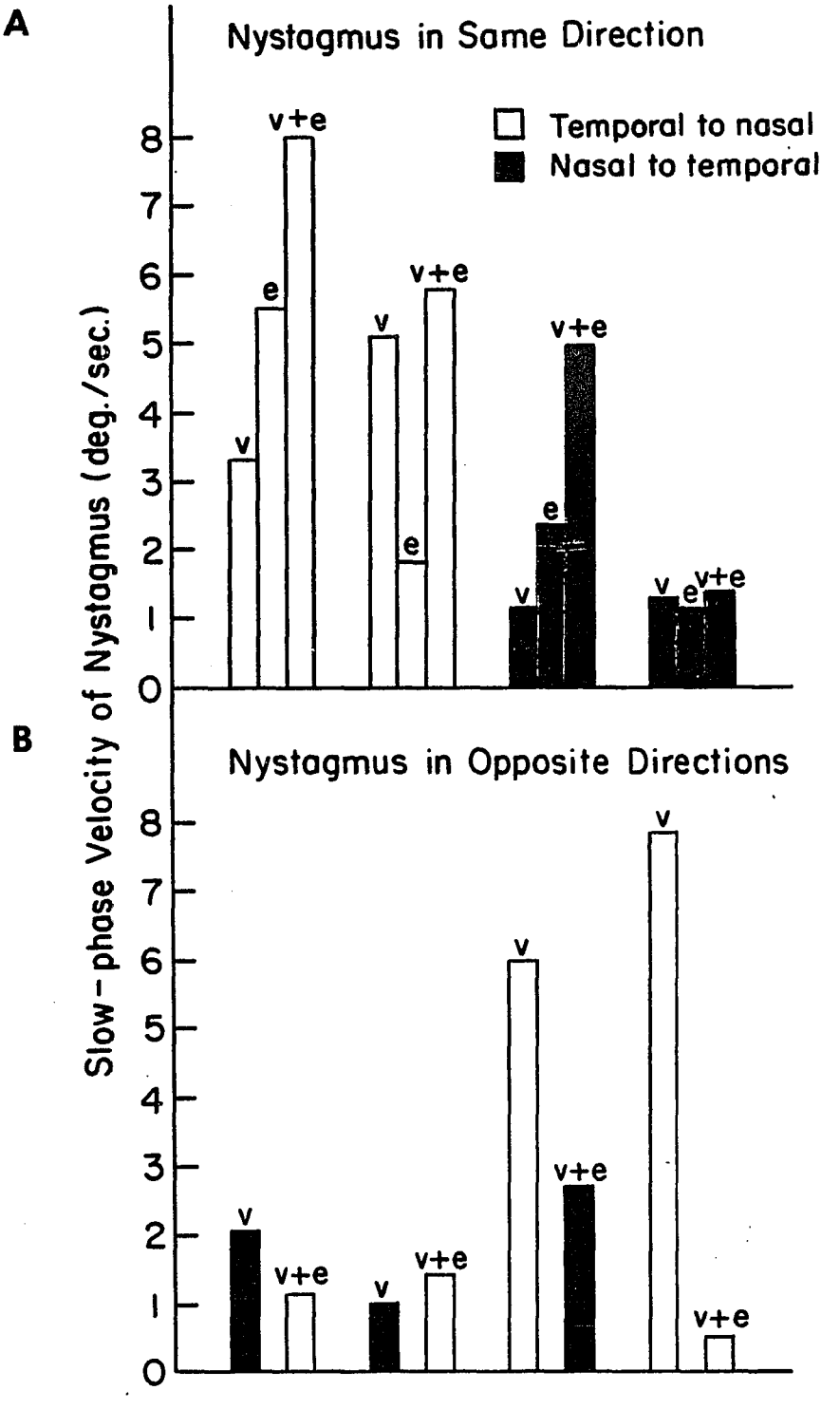

A
Nystagmus in Same Direction
Temporal to nasal
Nasal to temporal
B
Nystagmus in Opposite Directions
Slow-phase Velocity of Nystagmus (deg./sec.)
0
1
2
3
4
5
6
7
8
v
e
v+e

Fig. 41. Example of reversal of the direction of OKN by electrical stimulation. At the beginning of the record the animal was viewing a temporal to nasal OKN stimulus (50 deg/sec velocity). Several seconds after the onset of electrical stimulation (150Hz, 0.2 msec., 50 microamperes) the direction of the nystagmus became reversed. Upper trace shows horizontal nystagmus; downward deflection is temporal-to-nasal and upward deflection is nasal-to-temporal. Middle trace shows vertical eye position; downward deflection is down and upward deflection is up. Lower trace shows onset and offset of electrical stimulation. Calibration bars as in Fig.37.

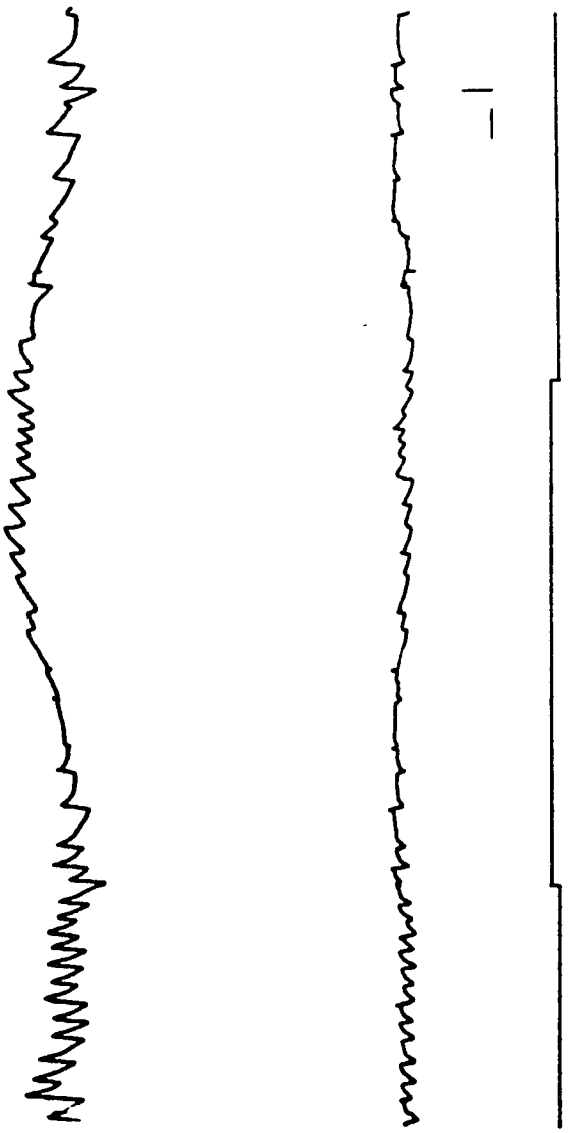
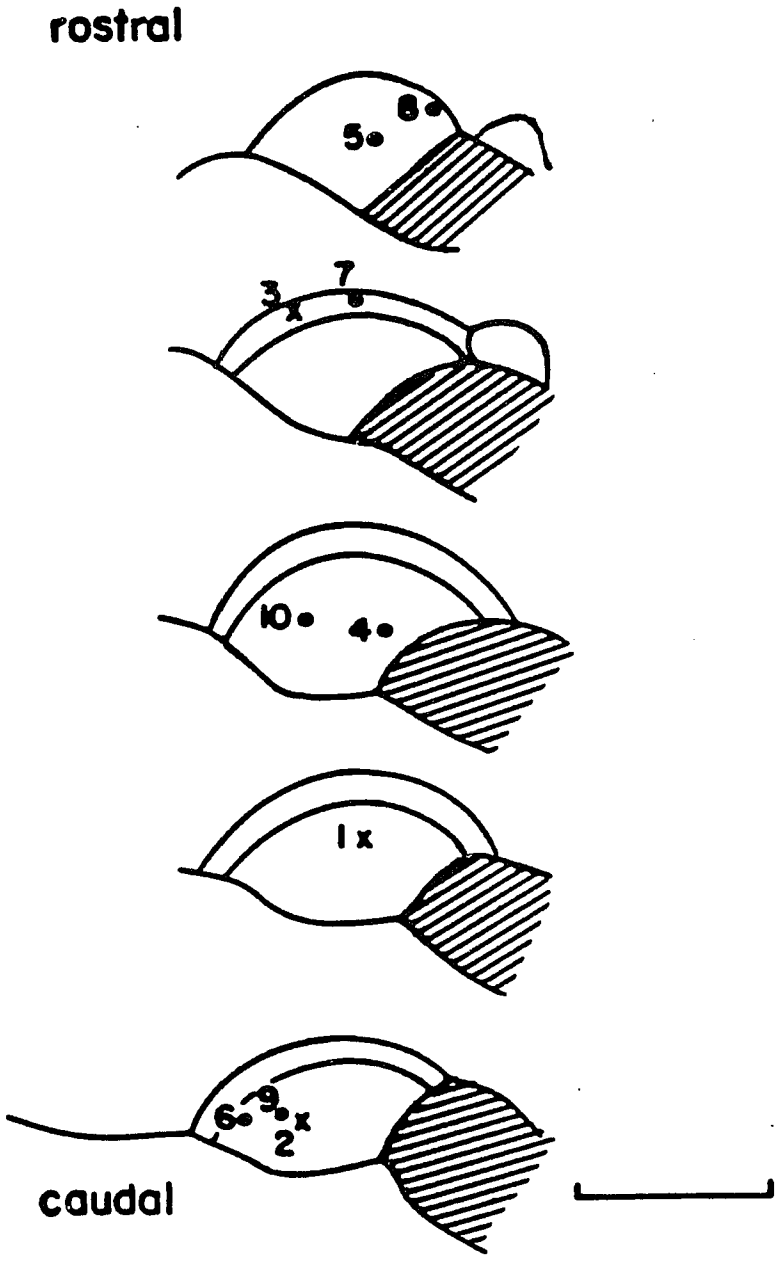


Fig. 42. Summary of locations in nBOR from which horizontal nystagmus was evoked by electrical stimulation. x=temporal-to-nasal nystagmus, .=nasal-to-temporal nystagmus. Numbers to the left of symbols refer to birds in Table 3. Calibration bar=1mm.


rostral
8
5
7
3
10
4
1
9
6
2
caudal

CHAPTER 6

SUMMARY

The purpose of this study was to investigate the functional role of nBOR in birds using single unit recording and electrical stimulation, and to investigate the postnatal development of nBOR using single unit recording. The following points summarize the findings.

1)Single unit recordings in nBOR suggest that it has a role in vertical stabilizing eye movements. Cells in nBOR have unusually large receptive fields peripheral to the optic axis. They respond best to large, richly patterned stimuli moving slowly (2 to 4 deg./sec.) in vertical directions and they never respond to small stationary stimuli.

The functional organization of nBOR, in which neurons responsive to upward movement are segregated from those responsive to downward movement, differs from the classical anatomical divisions of the nucleus. A partial retinotopic organization unrelated to the anatomical divisions, but closely related to the functional divisions was also found. The functional organization of nBOR is partially related to known efferent projections to the oculomotor nuclear complex. Only neurons detecting upward motion in the frontal visual field appear to

project to oculomotor neurons which move the eye upward, while both neurons detecting upward and downward motion throughout the visual field may project to oculomotor neurons which move the eye downward.

2)Electrical stimulation of nBOR resulted in horizontal nystagmus. In spite of the fact that few units respond to horizontal motion, this suggests that nBOR may have a role in regulating horizontal stabilizing eye movements. This may occur via efferent pathways from nBOR to those areas of the brain that have a role in horizontal stabilizing eye movements.

3)Single unit recordings showed that the properties of cells in nBOR in neonates differ substantially from those in older animals, indicating that there is an important postnatal component to the development of the accessory optic system. Directional selectivity, which is a property of cells in older birds, is present in some neurons in neonates, but absent in others. This indicates that some neurons develop directional selectivity postnatally and raises the possibility that visual experience may have a role in this development. The segregation of neurons responsive to upward and downward movement, which is present in older birds, is only partially present in neonates. Specifically, units responsive to upward movement are found in that portion of nBOR which contains only downward-responsive cells in older birds. This suggests that the functional organization of nBOR changes substantially during the postnatal period. These differences in the nBOR of neonates and older birds may account for the differences in stabilizing eye movements that have been shown to exist in the two age groups.

APPENDIX

Abbreviations Used in the Text

AOS	accessory optic system
BOR	basal optic root
DRGC	displaced retinal ganglion cells
DTN	dorsal terminal nucleus
INC	interstitial nucleus of Cajal
LM	lentiform nucleus of the mesencephalon
LTN	lateral terminal nucleus
MTN	medial terminal nucleus
nBOR	nucleus of the basal optic root
nBORd	dorsal nucleus of the basal optic root
nBORl	lateral nucleus of the basal optic root
NOT	nucleus of the optic tract
OKN	optokinetic nystagmus
VOR	vestibulo-ocular reflex

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