1-1-1987

An electrophysiological investigation of the pretectal nucleus (lentiformis mesencephali) in the frog (Rana pipiens).

Carol Kwei-Levy
University of Massachusetts Amherst

AN ELECTROPHYSIOLOGICAL INVESTIGATION OF THE PRETECTAL NUCLEUS (*LENTIFORMIS MESENCEPHALI*) IN THE FROG (*RANA PIPIENS*)

A Dissertation Presented

by

Carol Kwei-Levy

Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May, 1987

Department of Psychology

AN ELECTROPHYSIOLOGICAL INVESTIGATION OF THE PRETECTAL NUCLEUS (*LENTIFORMIS MESENCEPHALI*) IN THE FROG (*RANA PIPIENS*)

A Dissertation Presented

by

Carol Kwei-Levy

Approved as to style and content by:

Prof. Katherine V. Fite, Chairman of Committee

Prof. Paul Herron, Member

Prof. Neil Montgomery, Member

Prof. Gordon Wyse, Outside Member

Prof. Seymour Berger, Department Head
Department of Psychology

to Sandy and Marc

ACKNOWLEDGEMENT

I would like to thank my committee members for all of their help and encouragement- Professors P. Herron, N. Montgomery and G. Wyse. I would especially like to thank Prof. K. Fite for her support and for believing that people can succeed if they try.

I would also like to acknowledge all of the help and friendship from Lynn Bengston, Jay Alexander and their menagerie. To Diane Hayden, my thanks from one new Mom to an experienced Mom and good friend.

ABSTRACT

An Electrophysiological Investigation of the

Pretectal Nucleus (Lentiformis Mesencephali)

in the Frog (Rana pipiens)

May, 1987

Carol Kwei-Levy

B.S., Columbia University

Ph.D., University of Massachusetts

Directed by: Professor K. V. Fite

An electrophysiological investigation was made of the nucleus lentiformis mesencephali (nLM) in the frog Rana pipiens, to determine the involvement of nLM in the mediation of horizontal optokinetic nystagmus (OKN). Control experiments demonstrated the following results: Units recorded under monocular conditions demonstrated a significant number responsive to the moving stimuli, but no significant preferences were noted for any particular stimulus angle, direction or velocity. The units also recorded under binocular conditions demonstrated no significant preferences for stimulus angle or direction, and did not show the same significant responsiveness to moving stimuli as did the units under monocular conditions.

After intraocular injection of picrotoxin, a significantly higher percentage of the units demonstrated a two- to threefold magnitude increase in response rate over the baseline level than units in control experiments.

Multi-unit analyses did not correspond to results obtained in single-unit analyses regarding the stimulus angle, direction or velocity resulting in the greatest increase in single-unit response rates.

Although an analysis of unit response by unit location in nLM revealed no significant results for control experiments, there were some slight preferences observed for stimulus angle based upon the rostral versus caudal loci of the units in nLM. In the picrotoxin experiments, rostrally located units in nLM demonstrated a significant preference for temporonasal stimulus directions.

The data suggest that inhibition of unit response rates under binocular stimulating (OKN) conditions does occur in nLM, possibly due to: 1) the presence of monocularly influenced units, 2) ipsilateral inhibition, or 3) inhibition mediated via the contralateral nLM in binocular conditions.

Although there exists much anatomical evidence suggesting that the anuran nLM is homologous to the nucleus of the optic tract in mammals, an additional physiological similarity (i.e. unit increase in response rate under horizontal OKN stimulus conditions) was not found in this experiment.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Rana pipiens, or leopard frogs, represent a unique transition between aquatic and terrestrial vertebrates. Information gained from neurobiological analyses of the leopard frogs' central visual system has been extensively utilized as a model for visual processing and as a model for comparison with other terrestrial or aquatic species. Leopard frogs are also relatively simple organisms behaviorally, highly visual, inexpensive, easy to maintain, and have been the subject of study for over 30 years. Thus, a large literature exists which provides a broad base upon which to explore further the neural correlates of visuomotor behaviors (Fite, 1976, Llinas and Precht, 1976).

The pretectal nuclear complex, located between the caudal thalamus and midbrain, receives a major input from the retina in frog (Scalia and Fite, 1974) and has been studied with regard to various components of visually guided behavior such as the optokinetic nystagmus (OKN) response (Cochran et al., 1980, Ingle, 1980, Montgomery et al., 1981), wavelength discrimination (Kicliter, 1973), and prey catching in toads (Ewert, 1974) and salamanders (Finkenstadt, 1980).

The anuran pretectum is of particular interest to investigators as it has a great deal of involvement in horizontal optokinetic nystagmus (hOKN) (Montgomery et al.,1985). There is a range of variation in the number and configuration of pretectal fields in

amphibians: salamanders appear to have two pretectal areas while anurans seem to have three fields. The nucleus lentiformis mesencephali (nLM), one of the retinorecipient pretectal fields, has direct retinal afferents, three nonvisual afferents and two efferent projections. Most of these pathways are also involved in the mediation of the optokinetic response to some degree. Lesions of the frog pretectum, or of nLM alone, demonstrate the importance of pretectal structures in OKN functioning, as they result in a substantial decrease in OKN (Fite et al.,1980, Montgomery et al.,1982).

Optokinetic nystagmus is the reflexive compensatory motion of the head and eyes following the motion of an image across the retina. Research has been done not only on frogs (Lazar, 1973, Montgomery et al., 1981), but also on turtles (Hertzler and Hays, 1967, Fite et al.,1979), rabbits (Baarsma and Collewijn, 1974, Collewijn and Kleinschmidt, 1975, Dufosse et al., 1978, Simpson et al., 1979, Erikson et al., 1980, Neverov et al., 1980), birds (Hodos and Bonbright, 1975, Fite et al., 1979, McKenna and Wallman, 1980, Gioanni et al., 1983), cats (Carpenter, 1972, Thoden et al., 1979, Harris et al., 1980, Hoffmann and Schoppmann, 1981, Montarolo et al., 1981), and monkeys (Pasik and Pasik, 1964, Miles and Fuller, 1974, Pasik et al. 1977, Grosser et al., 1979, Hepp et al., 1982). Comparative neuroanatomical research on the pretectum has not been limited to amphibians, but also has included fish (Reperant et al., 1979, Ebbesson and Meyer, 1980, Grover and Sharma, 1981), birds (Hodos and Bonbright, 1975, Fite et al., 1979, McKenna and Wallman,

1980, Gionni et al., 1983), rat (Legg, 1977, Scalia and Arango, 1979, Robertson et al., 1980), rabbit (Collewijn, 1975, Maekawa and Kimura, 1981), cat (Bon et al., 1977, Itoh, 1977, Abols and Basbaum, 1979, Schoppmann and Hoffmann, 1979, Grahm and Berman, 1981, Hoffmann and Schoppmann, 1981), monkey (Benevento et al., 1977, Weber and Hutchins, 1982), and tree shrew (Weber and Harting, 1980).

The pretectal optic complex consists of retinal projection fibers and postsynaptic cell bodies associated with the 1) posterior thalamic neuropil, 2) uncinate neuropil, and 3) the large-celled pretectal nucleus (Scalia and Fite, 1974). As reported by Montgomery et al.(1985),historically the posterior thalamic nucleus designated by Bellonci (1888) was divided into two parts: the area pretectalis and an area homologous to the lateral geniculate nucleus (Herrick, 1925). "Area pretectalis" was changed to the "nucleus pretectalis" (Lazar, 1969), to the "large-celled pretectal nucleus" (Scalia and Gregory, 1970), to the "so- called large celled pretectal nucleus" (Scalia and Fite, 1974). The "nucleus pretectalis" as designated by Lazar (1969), is now believed to have contained both the pretectal nucleus and the "uncinate neuropil" (Scalia and Fite, 1974). The area considered by Herrick (1925) to be homologous to LGN is now believed to correspond to the posterior thalamic nucleus originally designated by Bellonci (1888). Recently, Wilczynski and Northcutt (1977) and Montgomery et al. (1985) have suggested that the large-celled pretectal nucleus of anurans is homologous to the nucleus lentiformis mesencephali (nLM) of reptiles and birds.(They will be considered

homologous in this study). In anurans, nLM receives the largest component of pretectal optic afferents in all 3 vertebrate classes.

In mammals, the nucleus of the optic tract (NOT) has been suggested as a homologous structure to nLM, and has been implicated in the mediation of OKN (Collewijn, 1975,1977, Dubois and Collweijn, 1979). The pretectal complex of anurans demonstrates many of the same characteristics of NOT (see Cochran et al., 1980, Katte and Hoffmann, 1980, Wilczynski and Northcutt, 1977, Montgomery et al., 1985), and it has thus been suggested that the frog pretectal nLM is homologous to the mammalian NOT.

In anurans, visually responsive units of the optic pretectal complex have been found to be responsive to sudden dimming of the entire visual field (von Wietersheim and Ewert, 1978), to direction-specific movement of the large-field stimuli (Cochran et al., 1980, Katte and Hoffmann, 1980), and to play a major role in the detection of stationary objects (Ingle, 1980). The large-celled pretectal nucleus of Rana pipiens contains three types of cells: 1)large, elongated cells (25 μm diameter), 2)medium, elongated cells (12-13 μm diameter), and 3)small, stellate cells (7.5-9 μm diameter) (Montgomery et al., 1985). In addition, cells of the posterior lateral nucleus and some cells in the posterior thalamic pretectal gray send dendrites into nLM (Montgomery et al., 1985).

The pretectum of frogs receives input from the retina, optic tectum, and accessory optic system (Rubinson, 1981, Montgomery et al., 1981, Montgomery et al., 1985). The large-celled pretectal nucleus, nLM, receives predominantly contralateral input from the

retina (Scalia and Fite, 1974, Wilczynski and Northcutt, 1977). Contralateral retinal afferents terminate most densely in the central and superficial portions of nLM, while ipsilateral retinal afferents terminate in most parts of nLM except the central portion. There are also afferent connections with the anterior thalamus, nucleus of the basal optic root (nBOR), mesencephalic pretectal gray, nucleus interstitialis of the medial longitudinal fasciculus and optic tectum. Efferent connections include those with the ventral rhombencephalon, nBOR, optic tectum and contralateral nLM.

In Xenopus, as compared to Rana, there is a denser and more extensive ipsilateral retinal projection to the thalamic and pretectal areas (Levine, 1980), possibly due to the greater size of the Xenopus binocular field.

Some studies have examined the response properties of single units from caudal thalamic regions in the anuran brain, which may also have included pretectal retinorecipient and postsynaptic areas (Ewert, 1971, Vesselkin et al., 1971, Brown and Ingle, 1973, Brown and Marks, 1977, Gaillard and Galand, 1979, Cochran et al., 1980, and Katte and Hoffmann, 1980). Cells in these areas seem to have large receptive fields (>60^{o}) (Brown and Marks, 1977, Manteuffel, 1984), spontaneous activity (2-16/sec.) (Katte and Hoffmann, 1980, Manteuffel, 1984, Cochran et al., 1984), and sensitivity to slow visual pattern velocities (5-10^{o}/sec.) (Cochran et al., 1984), although within a broad range of velocities (0.02-75^{o}/sec.), the response strength is supposedly independent of stimulus speed (Katte and Hoffmann, 1980). Pretectal units also demonstrate directional

selectivity, increased firing rates with temporal-to-nasal stimulation and decreased rates with nasotemporal stimulation (Cochran et al., 1984, Manteuffel, 1984).

In other studies using monocular stimulation, frogs (Birukov, 1937), turtles, and guinea pigs (Hayes and Ireland, 1972), and rabbits (Fukuda and Tokita, 1957) demonstrate OKN response only to temporal-nasal stimulation. Pigeons (Conley and Fite, 1980, Gioanni et al., 1981) and chickens (Fukuda, 1959), however, demonstrate an OKN response to nasotemporal stimulation, but one that is weaker than the response to temporal-nasal stimulation.Cats and primates (Van Hof-Van Duin, 1978, Pasik and Pasik, 1964) display symmetrical nystagmus for both directions of stimulation. In frogs, pretectal units seem to increase unit activity levels in response to horizontal movements over other directions (Cochran et al., 1984). Research by Katte and Hoffmann (1980) described two types of direction specific cells in frogs: 1) cells which demonstrated a greater response to preferred directions and a lesser response (less than the spontaneous level) to opposite directions, and 2) cells which preferred vertical stimulus directions. In the study by Katte and Hoffmann, 25 out of 32 units were horizontally oriented and 7 units preferred vertical directions. The "horizontal" units were located mostly in the pretectal areas while the "vertical" units were located more in the mesencephalic tegmentum. Another study by Grigonis (1982) described two units in nLM which responded to horizontal or vertical, striped moving patterns, and did not demonstrate directional selectivity. The units

responded best to a stimulus velocity of 10^{o}/ sec. as opposed to velocities greater than 15^{o}/ sec.

In mammals, research on rabbit retinal ganglion cells (Oyster and Barlow, 1967) has shown that there are two groups of directionally selective cells: 1) on-off type- these cells respond to stationary light spots flashed in the receptive fields, resulting in a discharge at the beginning and end of the flash, and 2) on type- these cells respond only at the beginning of the stimulus presentation at slow velocities (up to 1^{o}/ sec.). Cell responses in the "on-off" groups seem to correspond to the directions of displacement of objects produced by the four rectus muscles. Also, a study by Wyatt and Daw (1974) demonstrated that the direction sensitive retinal ganglion cells in rabbits respond better to moving spots than to moving bars. Wyatt and Daw (1974) have proposed that amacrine cells, which have asymmetric connections, are responsible for directional selectivity. Research on the rabbit nucleus of the optic tract (Collewijn, 1975) has demonstrated the following unit properties: 1) maintained unit discharges of 25-50 spikes/ sec., 2) large receptive fields (up to 40 x 150^{o}), 3) excitation in one direction and inhibition in the opposite direction (most units responsive to anterior movement), 4) responsive within a wide range of velocities (.01-20^{o}/ sec.), 5) responsive to random patterns, stripes and edges, and 6) retinotopic distribution of the units in NOT seemed to be random.

Research on the cat (Kanaseki and Sprague, 1974) has described seven pretectal nuclei: 1) nucleus pretectalis anterior, pars

compacta, 2) n. pretectalis anterior, pars reticularis, 3) n. p. medialis, 4) n. p. posterior, 5) n. tractus opticus (NOT), 6) n. p. subopticus, and 7) n. p. olivaris. Retinal projections terminate contralaterally primarily in n.p. posterior, n. tractus opticus and n.p. olivaris. Ipsilateral projections terminate mostly in the n. tractus opticus and n.p. olivaris. In NOT, direction selective cells receive retinal projections from small retinal ganglion cells located near the area centralis. The contralateral projection is much greater than the ipsilateral projection, by a factor of ten (Ballas et al., 1981). Electrophysiological research on the cat NOT (Hoffmann and Schoppmann, 1975) has described the following unit properties: 1) spontaneous activity (usually 20 spikes/sec. or more), 2) direction selectivity for temporonasal, horizontal units (30 out of 30 units, and in this study, it is important to mention that "horizontal" directions included all directions except vertical up (0°) and vertical down (180°), 3) strong responses were generated to large patterns, 4) optimal velocities were within 1-10°/ sec. A decrease in activity was seen for velocities from 10-50°/ sec. and activity rates fell below spontaneous levels for velocities between 50-100°/ sec., 5) the contralateral eye was more effective in driving the cells than was the ipsilateral eye, and 6) units did not habituate easily. In a related study by Schoppmann and Hoffmann (1979), 220 units were examined in the cat nuclei pretectalis anterior and nucleus pretectalis posterior, with the following results: 1) 21% of the units were responsive to slow movement (less than 100°/ sec.) and were direction selective, 2) 19% were slow movement, non-direction

selective, 3) 24% were nonselective for stimulus velocity and direction, and 4) 36% were "jerk" movement selective, non-direction selective. It has been suggested that the pretectum in the cat is important for modulation of the pupillary light reflex, learning of visual discrimination habits (Harutiunian-Kozak et al., 1970) and in OKN responses (Schoppmann and Hoffmann, 1979).

When the large-celled pretectal nucleus is lesioned, there is a substantial reduction in head and eye saccades to optokinetic stimulation which occurs at all stimulus velocities (Montgomery et al., 1982), as well as a possible disruption of normal prey-catching behavior called "disinhibition" (Ewert, 1970, Finkenstadt, 1980). Lesions of the pretectal nucleus superficialis synencephali in pigeons result in an almost total disappearance of OKN when the contralateral eye is stimulated in a temporo-nasal direction and an increase in OKN when the ipsilateral eye is stimulated in a temporonasal direction (Gioanni et al., 1983).

Recently, OKN directional asymmetry has been found to be altered in frogs following a monocular intravitreal injection of picrotoxin, a GABA antagonist. This manipulation results in the disappearance of OKN mediated through the injected eye but facilitation of OKN mediated through the opposite eye, with the additional appearance of a naso-temporal component. Hence, it was hypothesized that GABA-ergic retinal neurons may be responsible for the inhibition of the naso-temporal component of frog OKN (Bonaventure et al., 1983).

In other studies, researchers have examined the effects of picrotoxin (and GABA) upon neuronal activity in the visual system of

other species as well. These experiments have shown that picrotoxin abolishes the directional selectivity of directionally sensitive cells and changes the velocity specificity of the ON-type ganglion cells in the rabbit retina (Daw and Ariel, 1981), increases amplitude and decay time of ganglion cell responses in the frog (Burkhardt, 1972), induces a spatial reorganization of the receptive field of ON-OFF ganglion cells in the frog (Bonaventure and Wioland, 1981), and reduces or eliminates the directional selectivity of directionally selective cells in turtles (Ariel and Adolph, 1985). Picrotoxin substantially reduces the surround component of Y-cells in the cat (Kirby and Enroth-Cugell, 1976), and, in frog retinal ganglion cells, picrotoxin seems to abolish the inhibition exerted by the surround upon the center of the ganglion cell's receptive field (Bonaventure and Wioland, 1981). GABA, for which picrotoxin is an antagonist, inhibits cells of all response types in the carp, except for the OFF-center tonic cells, which are affected less (Glickman et al., 1982). In the avian retina, GABA is accumulated by horizontal and amacrine cells (Karten and Brecha, 1983), while in the carp, it is hypothesized that GABA is released only by the amacrine cells (Glickman et al., 1982). In the catfish, the red cone horizontal cells have been found to be GABAergic, and these cells are important in light adaptation (Lasater and Lam, 1984).

In this study, properties of units recorded from the frog nLM were examined using an optokinetic stimulus pattern, with particular attention given to the effects of stimulus angle and stimulus velocity upon unit response rate. The effects of picrotoxin

injections on nLM OKN response properties were also examined, especially concerning the appearance of a naso-temporal component. Since picrotoxin is a GABA antagonist, theoretically it was expected that increases in receptive field areas of ganglion cells would occur and that inhibition of the center of the field exerted by the surround would be abolished. Hence, it was predicted that if nasotemporal responses were normally inhibited by GABA, nasotemporal OKN responses to monocular stimulation would appear after injection of picrotoxin. Picrotoxin reportedly also causes an increase in the duration of ON and OFF discharges, which leads to an increase in the number of spikes recorded as a result of visual stimulation (Bonaventure et al., 1983). In this study, therefore, the appearance of a nasotemporal response to horizontal OKN stimuli under monocular conditions and an increase in spontaneous response rates were both predicted.

CHAPTER II

METHODS

Normal Experiments

Twenty-nine adult Rana pipiens, each approximately 9 cm in body length, were maintained on a 12-hour light-dark cycle, at 20-24°. Prior to surgery, the frog was immersed in an aqueous solution of tricaine methanesulfonate (1:500) for 25-30 minutes. The anesthesized frog was then placed on a wooden block designed to hold the head securely between two metal rods. The eyes were kept elevated throughout the experiment with a moistened ball of cotton inserted into the mouth. The frog was maintained under anesthesia by covering the body with a kimwipe soaked in tricaine (1:500). The dorsal surface of the skull was first exposed by making longitudinal and lateral skin incisions and folding the skin to either side. Surrounding muscle and tissue were dissected away to avoid disrupting major blood vessels during subsequent surgery. The cranium was then removed using a dental drill, and the dura stripped away, exposing the tectum for electrode insertion.

The electrodes used for recording and lesioning were glass micropipettes filled with Woods-metal (range= 0.1-5 megohms at 1000 Hz). Electrodes were pulled with a David Kopf vertical pipette puller (model 700D) to a tip diameter of 5-10 microns. The pipettes were filled with the Woods-metal and then plated with gold and platinum (See procedure of Dowben and Rose (1953)). Electrode

impedance was measured using a Frederick Haer Impedance Checker (range for electrodes: 0.1-5 megohms at 1000 Hz).

The stimulus apparatus consisted of a modified film strip projector having a 120-volt, 300-watt bulb, and a reversible DC motor and gear assembly attached to a framework containing 16 mm sprockets. The projector produced a continuously moving stimulus pattern which was rear-projected onto a screen placed in front of the frog (25 cm), filling a large portion of the subject's frontal field of view (Approximately 100°). The stimulus pattern consisted of a repetitive black-and-white, striped pattern consisting of bars of equal width (1.5 cm). In addition, the projector was fitted with a dove prism which, when rotated to various positions, allowed movement of the stimulus at any angle across the screen. Three different stimulus velocities were used ($6, 15, 24^{\circ}$/sec).

The pretectal area was located by a search pattern of electrode penetrations starting approximately 1450 μm lateral and 300 μm caudal to the junction between the midline of the tectal lobes and the dorsal thalamic region. Penetrations were approximately 1000 μm deep, and were continued medially until units were encountered which spiked as a result of light in the room being turned on and off (See Figure 11).

Data was collected in multi-unit form, and single-unit data isolated later using a window discriminator and computer-assisted analysis (See below). The screen in front of the frog was first illuminated by a 100 watt tungsten bulb, filling a 100° portion of the frog's frontal field of view. Responsiveness to small targets

filling less than 100° of the frontal field of view, either stationary or moved across the field, was not determined in this experiment. Baseline unit activity occurring during a 10-second interval was recorded first under binocular conditions and then under monocular conditions with the ipsilateral eye (i.e. ipsilateral to the unit being recorded) covered with an opaque cover. Then, a stationary pattern of horizontal black and white stripes, produced by the strip projector was presented on the screen for four consecutive 10- second intervals. These baseline response levels were recorded with brief intervals (3 sec.) of darkness interposed. The moving OKN stimulus pattern was then presented once in each of 3 different planes; vertical (up and down), horizontal (right and left), and oblique (45° left- up and down, 45° right- up and down). Thus, the following trajectories of stimulus movement were presented to each unit: 0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°. At each angle, three different stimulus velocities were presented (6, 15, 24°/sec), for 10- second intervals with shorter (5 sec.) intervals of darkness interposed. This whole procedure was then repeated to test monocular, contralateral responses by covering the eye ipsilateral to the unit with an opaque cover, leaving the other eye uncovered. Unit activity was amplified using an EG&G Parc Model 113 pre-amplifier and displayed on a Tektronix 5113 dual-beam storage oscilloscope. Activity was simultaneously recorded on a Sony Stereo Tape Recorder. The duration of the stimulus (and stimulus onset/offset) was marked by the input of a 100 Hz oscillating signal into an alternate recording channel on the tape recorder during the

recording intervals. This signal was provided by a tone generator which was attached to the recorder.

After all stimulating conditions and corresponding responses were obtained, a small electrolytic lesion was produced by passing a current from a lesion maker of 5 μamps for 5 seconds (electrode positive). After a post-lesion survival time of about 3-4 days, the frog was again anesthesized with tricaine (1:500), and perfused with saline, followed by Carnoy's Solution (60 ml absolute alcohol, 10 ml glacial acetic acid). The brain was excised, dehydrated with a series of cellosolve followed by chloroform, and embedded in paraffin. The brain was then sectioned in 10-micron thick sections coronally, on a rotary microtome. Serial sections were saved from the thalamus through the anterior tectum, and stained with the Kluver-Barerra stain.

Recorded data from approximately 80 units in nLM were analyzed: 50 from normal experiments (30 under binocular and monocular conditions, 20 under monocular conditions only),and 30 from picrotoxin experiments (all 30 under monocular conditions). One unit, histologically identified as being located in the optic tectum, was also analyzed. After multi-unit activity was recorded on tape, the data were replayed and displayed on the oscilloscope, while simultaneously using a Frederick Haer Spike Enhancer and Window Discriminator modules to aid in selecting one spike amplitude for analysis. The Spike Enhancer was employed to enhance the signal-to-noise ratio and effectively reduced the amount of baseline "noise", allowing firing units to be seen more clearly on the

oscilloscope screen. The window discriminator was set so that only the spike(s) exceeding the boundaries determined by 2 lines on the oscilloscope screen would be "counted" by a computer. Thus, each processed spike that met the amplitude criteria of the window discriminator triggered a standard pulse output from the discriminator (See Figure 9). In most cases, the largest amplitude spikes were selected for analysis, although in other cases, the window boundaries were reset to allow analysis of a second unit from the same recorded data.

Computer analysis was performed using software developed for the experiment under an MS-DOS operating system. A Zenith 150 computer was interfaced with an analog-to-digital converter circuit (Data Translation 2805), which allowed the conversion of neural data to a form recognizable by the computer. Thus, the total number of spikes from each and every recording interval were "counted up" and stored onto a disk under a specific file name denoting the animal number, hemisphere being recorded from, binocular vs. monocular conditions, and specific stimulus conditions. Data were then accessed from disk to determine how many spikes occurred under the various stimulus directions and velocities.

A computer analysis of multi-unit activity was also carried out for comparison using the same methods as in single-unit analysis. The major difference involved the specific setting of the upper and lower boundaries of the window discriminator. Instead of selecting only one unit which spiked across the window boundaries, 2-4 units were chosen for analysis. The comparison of multi-unit analysis

versus single-unit analysis was performed to determine if both analyses were similar with regard to the stimulus direction resulting in the greatest increase in unit response activity.

Picrotoxin Experiments

The same procedures were followed as in the normal experiments except for the following modifications: after the frog was immersed in tricaine methanesulfonate (1:500), one eye was injected intravitreally with 30 µl of picrotoxin (5×10^{-3} M) using a microsyringe (method of Bonaventure et al., 1983). Picrotoxin takes effect about one-half hour after injection (Bonaventure et al., 1983). During this time, surgery was performed on the frog to expose the brain. The same stimuli and equipment were used as in the normal experiments, and with the same order of stimulus presentation. 30 units from 16 frogs were recorded and analyzed. In four of these animals, normal data were taken before the injection of picrotoxin. Also, a comparison was made of changes in response activity, before and after injection of picrotoxin, of the same unit (8 units total). Recording from the same unit was achieved by placing the syringe containing the picrotoxin in a position so that the tip of the needle was already inserted into the eye before unit recording began, but the picrotoxin not injected until after normal responses were recorded. After data were taken from the frog under normal conditions, the picrotoxin was then injected without jarring the animal or apparatus (See Fig 10). (Note: Although it is hoped that

these recordings were indeed from the "same" units, this was not conclusively proven. Thus, it cannot be assumed that the data were taken from the same units, before and after the injection of picrotoxin).

After data were obtained, the recording site was marked with a lesion as in the normal experiments (5 μamps for 5 sec.). The frog was sacrificed after 3-4 days, and the brain processed in the manner outlined previously (See Normal Experiments).

Data Analysis

Normal experiments

Spike-frequency data were recorded for single units (in 10-second stimulation intervals), under conditions of both monocular and binocular stimulation. The variable of stimulus direction was further analyzed to determine which direction of movement produced the greatest response from the unit being examined, under either monocular or binocular stimulating conditions. Increases in the response rate were determined by comparing the average unit activity level during baseline trials (i.e. average number of spikes/ 10 sec. interval, over four trials) to unit activity seen during stimulus presentation trials. The amount of increase was often quite variable, but occasionally would change by as much as a factor of 2. The "most-preferred" stimulus direction was defined as the stimulus direction resulting in the highest response rate of the unit being recorded.

An analysis of multi-unit activity (2-4 units/frog) from 8 normal animals was carried out for direct comparison with single unit data on the same frog. The analysis procedure was the same as for single-unit recordings, except that more than one unit was included in each analysis. The analysis of multi-unit activity enabled a determination of that stimulus direction which produced the greatest increase in spike frequency over baseline conditions. Multi-unit data was then compared to the corresponding single-unit analysis done previously to determine if both analyses (Multi- and Single unit) were similar with regard to the stimulus direction resulting in the greatest increase in unit response activity.

Picrotoxin experiments

Spike frequency data were recorded for single-units (from the hemisphere ipsilateral to the injected eye), in terms of monocular responses. Results were compared both within and across animals with respect to stimulus direction to determine which direction was "most preferred" by the unit being examined. Data was also examined to determine any effect of stimulus velocity on response rate.

Combined data from this group was compared to monocular responses obtained from the normal animals (monocular stimulation) to determine if there were any changes in rates of responding or preferences for stimulus direction and velocity which were attributable to the picrotoxin manipulation.

Histology

The location of recording sites for 60 electrolytic lesions, 44 from normal experiments and 16 from picrotoxin experiments, relative to the position of nLM, were determined by examination of tissue. One unit was identified as being located in the optic tectum (See Fig.1,2). nLM is composed of neurons and optic axonal terminal arborizations located along the inner (medial) margin of the anterior tectum (Montgomery et al., 1985). Most of the lesions were discrete (sizes ranged from .06mm to .2 mm), allowing comparisons to be made of lesion sites with location within nLM, according to an atlas of the frog brain (expanded version of Scalia, 1976)(See Fig. 1,2) and detailed comparisons with HRP-labelled brain sections (standard series reference material) which delineated clearly the pretectal optic fields (See Figure 1). An examination of the tissue also revealed that the area being considered as nLM was usually located between 375-525 μm caudal to the location of the posterior thalamic nucleus. It was often possible to identify the cells remaining which surrounded the lesion site. Commonly, cells of the large neuron classification (25 μm diameter soma) were seen which are unique to nLM in the pretectum. This type of neuron tends to cluster around the central, dense-core area of nLM (Montgomery et al., 1985).

C H A P T E R III

RESULTS

Control Experiments

One unit was identified as being located in the optic tectum. This unit demonstrated a preference for the 0^{o} stimulus angle under binocular conditions and for 180^{o} under monocular conditions. The preferred stimulus direction was vertical and preferred stimulus velocity 15^{o}/ sec., under both conditions (See Table 1).

Normal Experiments

Unit responses in nLM

Eighty units, obtained from 29 animals, were histologically identified as having originated in nLM (See Fig.1,2). In the normal group, 30 units were recorded under both binocular and monocular stimulating conditions. Twenty other units from the normal group were obtained under monocular stimulating conditions only. Thus, 50 units, in total, were analyzed monocularly. There were 30 units obtained in the picrotoxin experiments, all obtained under monocular stimulating conditions (See Table 1).

All of the units in nLM were responsive to changes in background illumination, especially to on-off changes in general room illumination. There was a significant difference in unit firing rate (normals) in response to a "blank screen" presentation, when

comparing binocular versus monocular conditions. In this comparison, units demonstrated a tendency to decrease firing rates with the monocular blank screen condition as opposed to the higher rates of response obtained with the binocular blank screen condition for the same unit (X^2=11.4, p< .01). This type of result was also found in the normal group for the binocular versus monocular, stationary pattern condition (X^2=10.4, p< .01)(See Table 2).

A comparison of unit responses (normals), obtained under monocular conditions, to blank screen versus stationary pattern stimuli, revealed no significant pattern of differences. Approximately half of the units demonstrated an increased response rate to the stationary pattern, while approximately half did not demonstrate this change. This type of result was also found under binocular stimulating conditions. A comparison of unit responses to binocular, moving, stimuli revealed that only 31% of the units increased their activity levels. Unit responses to monocular, moving, stimulus conditions, however, demonstrated that 97% of the units demonstrated an increase in unit activity over baseline levels (Table 1, Fig. 4-5).

Spontaneous activity was a consistent property of all units recorded and could be used to identify units specifically in nLM. The spike rate (about 2-16/sec), did not fluctuate appreciably during the blank screen baseline interval. Also, unit activity appeared to be independent of stimulus velocity, demonstrating no pattern over the three stimulus velocities employed (6, 15, 24^{o}/sec)(See Table 3).

Changes in unit response rates were divided into three categories: An increase in response rate was defined for this study as a 50% or greater increase in firing rate in response to moving stimuli over the stationary pattern baseline level. The second category included units with a response rate increase of less than 50% over the stationary pattern level. The third category included units whose response rate to moving stimuli was less than that to the stationary pattern level. These criteria were determined by an analysis of percentage increase in unit activity (Table 4, Fig. 4-6).

Monocular stimulation (50 units)

Under monocular stimulus conditions, 28 units (56%) met the criterion of a $\geq$ 50% increase in response rate over the baseline rate in response to moving stimuli, 18 (36%) demonstrated a <50% increase, 2(4%) showed 0% increase and 2 (4%) demonstrated less than the baseline level of unit activity (See Table 5, Fig. 5). These results are significant (X^2= 59.3, $p < .001$), demonstrating that units in nLM did show increased activity in response to the moving stimuli. Of the 28 units demonstrating the greatest increase in unit activity, 7(25%) were most responsive to vertical stimulus angles ($0,180^{o}$), 9(32%) to oblique, upward angles ($45,315^{o}$), 6(21%) to horizontal angles ($90,270^{o}$), and 6(21%) to oblique, downward angles ($135,225^{o}$) (See Table 6). Of these unit preferences, 8(29%) were for nasotemporal stimulus directions, 13(46%) were for temporonasal directions, and 7(25%) were for vertical directions (See Table 7).

The unit preferences for stimulus angles and directions were not statistically significant. Also, an analysis of unit responsiveness to upward versus downward stimulus angles demonstrated a preference, although not statistically significant, for upward moving stimuli (13 units, 59%).

A comparison of binocular stimulation vs. monocular stimulation response rates for the same 30 units

A binocular analysis was also made of the 30 units recorded under <u>both</u> binocular and monocular conditions (See Table 1). Recordings under binocular conditions showed that of these 30 units, 13(43%) demonstrated a $\geq$ 50% increase in response rate, under binocular conditions, to moving stimuli, over baseline rates. 9(30%) demonstrated <50% increase, 1(3%) demonstrated 0% increase and 7(23%) demonstrated less than the baseline rate of activity (See Table 5, Fig. 2,4). Of the 13 units with a $\geq$50% increase in activity over baseline levels, 3(23%) were most responsive to $0,180^{\circ}$ stimulus angles, 2(15%) to $45,315^{\circ}$, 6(46%) to $90,270^{\circ}$, and 2(15%) to $135,225^{\circ}$ (See Table 6). Four of the 13 units (31%) were most responsive to nasotemporal stimulus directions, 6(46%) preferred temporonasal directions, and 3(23%) preferred vertical directions (See Table 7). The unit preferences for stimulus angles and directions were not statistically significant.

Picrotoxin Experiments

Unit responses recorded in nLM after intraocular injection of picrotoxin

This group included 16 animals (30 units), 12 of which were anesthesized, injected monocularly with picrotoxin, and then used for neurophysiological analysis. In the other four animals, recordings were also taken from contralateral nLM units under monocular, normal conditions, before the injection of picrotoxin (See Table 1). In these 4 cases, (8 units), an attempt was made to compare any changes in response activity, of the same unit, before and after injection of picrotoxin. (See Table 1, Fig. 7,10).

After intravitreal injection of picrotoxin, 19 units (63%) demonstrated a $\geq$50% increase in response rate over the stationary pattern baseline level, 8(27%) demonstrated <50% increase in response rate, 0 units demonstrated a 0% increase and 3(10%) demonstrated less than the baseline level of activity (See Table 5, Fig. 6,8). These results are significant ($X^2 = 30$, $p < .001$), demonstrating that units were responsive to the moving stimuli. Of the 19 units showing the greatest increases in unit activity, 5 units (26%) were most responsive to the stimulus angles $0,180^{\circ}$, 6 (32%) to $45,315^{\circ}$, 3(16%) to $90,270^{\circ}$, and 5(26%) to $135,225^{\circ}$. (See Table 6). Also, 6 of the units (32%) demonstrated a preference for nasotemporal stimulus directions, 8(42%) for temporonasal directions, and 5(26%) for vertical directions (See Table 7). These results were not statistically significant.

A comparison of monocular normal data and picrotoxin data demonstrates that a higher percentage of units recorded in the picrotoxin experiments showed a two-to threefold magnitude increase in response rate (i.e. $\geq$100% increase) for specific stimulus directions over the baseline level (40%), than in normal experiments (34%) (See Table 5, Fig. 8,9). Also, after injection of picrotoxin, units seemed to demonstrate greater response rates over all directions, instead of to one stimulus angle.

A Comparison of Multi-Unit Analysis and Single-Unit Analysis

Both multi-unit responses and single-unit responses (1 unit/animal) from eight normal animals were analyzed and compared from previously taped data in order to determine whether or not multi-unit analysis would correspond to results obtained with single-unit analysis with regard to the stimulus direction corresponding to the greatest increase in single-unit response activity. Each multi-unit analysis included between 2-4 units (one of which was the unit used for single-unit analysis), which was then compared to the single-unit analysis obtained from the same animal.

In 3 animals, the stimulus direction yielding the greatest increase in response activity was the same when comparing multi-unit and single-unit responses, but in the other 5 animals, this was not the case. An analysis of stimulus direction preferences revealed a 75% agreement (6/8), which was not statistically significant, while the analysis of stimulus velocity preferences demonstrated a 37%

agreement (3/8) (See Table 8). These results show that multi-unit data and single unit data did not concur. Hence, multi-unit analysis was not an acceptable method of analysis in this experiment.

Histological Results

Recordings were taken from the caudal portions of nLM (35 units, 79%) and rostral portions of nLM (9 units, 21%), in normal animals (See Figure 2). Of the 35 units located caudally, 22(63%) demonstrated a $\geq$50% increase in response rates over the stationary pattern baseline level (See Table 1). Of the 9 units located rostrally, 6(67%) met this criterion (See Table 1). The 22 units located caudally demonstrated the following stimulus angle preferences: 7(30%) were most responsive to 0,180^{o}, 6(27%) were most responsive to 45,315^{o}, 5(22%) were most responsive to 90,270^{o}, and 4(18%) were most responsive to 135,225^{o} (See Table 9). Six (27%) of these units preferred nasotemporal stimulus directions, 9(41%) preferred temporonasal directions, and 7(32%) preferred vertical directions (See Table 10).

Of the 6 units located rostrally demonstrating the greatest increase in response rate: 0% were most responsive to 0,180^{o}, 1(20%) was most responsive to 45,315^{o}, 2(40%) were most responsive to 90,270^{o}, and 2(40%) were most responsive to 135,225^{o} (See Table 9). Two of the units preferred nasotemporal directions (33%), and 3(66%) preferred temporonasal direction (See Table 10). These results were not statistically significant.

Of the picrotoxin experiments, 19 met the criterion of a ≥50% increase in rate of response over the stationary pattern baseline level (See Table 1). Ten of the units were located caudally and demonstrated the following preferences for stimulus angles: 4(40%) preferred $0,180^{o}$, 2(20%) preferred $45,315^{o}$, 1(10%) preferred $270,90^{o}$, and 3(30%) preferred $135,225^{o}$ (See Table 9). Also, 5 of the units (50%) preferred nasotemporal stimulus directions, 1(10%) preferred temporonasal directions and 4(40%) preferred vertical directions (See Table 10). The 9 rostrally located picrotoxin units demonstrated the following stimulus angle preferences: 1(10%) preferred $0,180^{o}$, 4(40%) preferred $45,315^{o}$, 2(20%) preferred $90,270^{o}$, and 2(20%) preferred $135,225^{o}$ (See Table 9). Of the 9 units, 1(11%) demonstrated maximal response to a nasotemporal stimulus direction, 7(78%) to temporonasal directions and 1(11%) to vertical directions (See Table 10). The preference seen for temporonasal directions in the rostrally located picrotoxin units is significant ($X^2 = 8$, $p < .02$).

Summary of Results

1. All recorded units in nLM were responsive to changes in background illumination (i.e. on-off changes).
2. Spontaneous activity was a consistent property of all units recorded in nLM.
3. Unit activity appeared to be independent of stimulus velocity over the range tested.

4. Units under monocular conditions tended to show a decrease in firing rates in response to the "blank screen" and "stationary pattern" baseline stimuli, as compared to the same unit responses under binocular conditions.

   Units recorded under monocular OKN stimulus conditions were responsive to the moving stimuli, but no significant preferences were noted for stimulus angles or directions.

   The units also recorded under binocular conditions demonstrated no significant preferences for stimulus angle or direction, and did not show the same significant responsiveness to moving stimuli as did the units under monocular conditions.

5. After intraocular injection of picrotoxin: A higher percentage of these units demonstrated a two-to threefold magnitude increase in response rate over the baseline level than units in normal experiments.

6. Multi-unit analyses do not correspond to results obtained in single-unit analyses regarding the stimulus angle, direction or velocity resulting in the greatest increase in single-unit response rates.

7. An analysis of unit responses by unit location in nLM revealed no significant results for normal experiments. In the picrotoxin experiments, rostrally located units in nLM demonstrated a preference for temporonasal stimulus directions.

C H A P T E R IV

DISCUSSION

In this study, an electrophysiological examination was made of the nucleus lentiformis mesencephali (nLM) in the pretectal optic complex of the frog, Rana pipiens. Some of the properties of pretectal units discussed in this study have been described by other investigators. The response of pretectal units to sudden dimming of the visual field is a property discussed by von Wietersheim and Ewert (1978), and spontaneous activity of all pretectal units was previously described in other studies (Katte and Hoffmann, 1980, Manteuffel, 1984, Cochran et al.,1984). However, these studies included recordings from a wide area of the pretectum, not just from nLM, therefore, it is difficult to make precise comparisons with their findings. Pretectal visual units were also found to have response rates relatively independent of stimulus velocity both in this study and in one by Katte and Hoffmann (0.02-75^{o}/sec.)(1980). These results of Katte and Hoffmann differ from those found by Cochran et al. (1984), where units were responsive only to relatively lov stimulus velocities (5-10^{o}/sec.).

Direction Selectivity

Most of the research done on the optic pretectum has described a pronounced unit selectivity for certain stimulus orientations (Cochran et al., 1980, Katte and Hoffmann, 1980, Cochran et al.,

1984, Manteuffel, 1984); specifically for horizontal movement in a temporonasal direction. Although the units demonstrated a small preference for temporonasal directions in the present study, it was not found to be statistically significant (See Table 7). Also, in this study, there was no consistent pattern of data seen to support previous fingings of "null directions" (See Table 1). The null direction is usually 180^{o} apart from a preferred direction, has been reported for nasotemporal (stimuli) movements (in frogs) and the presentation of stimuli in this direction results in a decrease or total inhibition of responses from units being recorded. Evidence in this experiment for a null direction was not expected, though, as directional selectivity for stimulus angle or stimulus direction was not found. It is possible, however, that if different units in nLM "prefer" different stimulus angles and directions, they would not be considered directionally selective, but could be considered directionally "sensitive". This would mean that the units are not selective for just one type of stimulus movement, but for a wider or even wide range of movements. The data has indeed demonstrated that many units in nLM show directional preferences, and that as a whole, they show a range of preferences. It is believed that unit preferences are partially dependent upon unit loci in nLM and neuron size, and that if this is true, a generalization for nLM as a whole in terms of the units being <u>selective</u> cannot be made.

It is still unclear, however, as to the reasons for the difference in results between this experiment and previous studies. One possibility is the fact that other experiments have examined the

pretectum as a whole and not just nLM. Also, in the experiment by Cochran et al. (1984), the units recorded in the pretectum seemed to be the more medially located tegmental gray cell groups, a location which was different from the unit loci found in the present experiment. Even in previous experiments not limited to nLM, though, there were visual units reportedly responsive to stimulus directions other than horizontal, temporonasal ones. Cochran et al. (1984), for example, found that a small number of pretectal units were responsive to nasotemporal stimuli (7/61) or to vertical stimuli (5/61). It must also be mentioned that only two stimulus orientations were used in Cochran's study; horizontal and vertical. Thus, none of the oblique angles were investigated. Also, one of the criteria established by Cochran for localizing pretectal cells was responsiveness to horizontal stimuli. This means, however, that only units which were "horizontally" selective were selected to determine if pretectal units preferred horizontal stimuli. In Katte and Hoffmann's study (1980)(32 units total), units in the pretectal region were predominantly sensitive to horizontal stimulation while units located closer to the basal optic region were sensitive to more vertical stimulation.

Also, in Hoffmann and Schoppmann's study (1975), "horizontal" was defined in much broader terms than in the present experiment. As mentioned earlier, they considered the term "horizontal" to include oblique directions, and exclude only up and down vertical directions. This grouping of units resulted in many more units being described as directionally sensitive for horizontal stimuli, and

makes comparisons between that experiment and the present one more difficult. When the data in this experiment is analyzed in a similar manner, 74% of the units prefer "horizontal" directions as defined by Hoffmann and Schoppmann. This method of analysis would result in a significant number ($X^2 = 7$, $p < .01$) of units preferring "horizontal" stimuli (Table 7).

Researchers have also described physiological properties of areas such as the basal optic nucleus and optic tectum, both of which, along with nLM, are important in visual functions. Units in the basal optic nucleus are responsive to large stimuli and very slow stimulus velocities (less than 10^{o}/sec.). These units demonstrate directional preferences for the following types: 1) upward movement, 2) downward movement, 3) upward and nasotemporal movement and 4) downward and nasotemporal movement. The units are not responsive to temporonasal movements (Cochran et al., 1984). Research on the optic tectum in frogs has demonstrated the following unit properties: 1) habituation of units is overcome by a pause or a new stimulus, 2) units respond to an on-off change in general illumination, 3) units do not demonstrate directional selectivity and 4) response rates range from 5-80 spikes/sec. (Grusser and Grusser-Cornehls, 1976, Katte and Hoffmann, 1980). (Data from the one tectal unit obtained in this study was considered insufficient for comparison with the properties listed). From the results stated above, it is clear that units in nLM have different properties in comparison to those of units in the basal optic nucleus or optic tectum, but also have some properties which <u>are</u> similar, supporting

the belief that the three structures mediate some behavior(s) in common (ex. OKN) but they each perform a different role.

If directionally selective cells exist which are not located within nLM, then they must be located in another, or other areas. In the study by Cochran et al.(1984), directionally selective units were found in the medially located tegmental gray cell groups. This area, then, is a strong possibility for the location of direction selective cells. Another study by Grigonis (1982) also examined unit responses from various areas such as nLM, pretectal gray, posterodorsal division of the lateral thalamic nucleus and the anterior margin of the ventromedial optic tectum. Results demonstrated that units in the three areas other than nLM seemed to demonstrate limited directional selectivity. Interestingly, the area which seemed to be most responsive to horizontal stimulus directions was the posterodorsal division of the lateral thalamic nucleus. Unit responses in this region were reported to resemble those of class- 3 ganglion cells (Grusser and Grusser-Cornehls, 1976), and were active during hOKN stimulus presentations. Unfortunately, in the study by Grigonis (1982), recordings were taken from only one unit in this region which demonstrated sensitivity to hOKN stimuli. Thus, it appears that there could be two (or more) areas mediating hOKN responses. Due to the ambiguity of reported unit loci in many of the previous experiments, however, evidence for direction selective units in the tegmental gray or lateral thalamic nucleus is not yet definitive.

Note: It is possible that the methodology employed in this study was sensitive enough to allow more complete and objective analyses of nLM pretectal units than in previous studies. Indeed, the methodology was designed to eliminate experimenter bias in selecting units for analysis. Thus, this may also be a reason for the differences found between this experiment and other experiments.

Lesion Studies

Unfortunately, as mentioned before, previous neurophysiological studies concentrating on the frog pretectum usually have not specified exact lesion sites in the brain of the units reported. In the studies by Katte and Hoffmann (1980) and Cochran et al. (1984), for example, there was a great deal of ambiguity as to the loci of pretectal units recorded. Thus, it is much more difficult to determine to what extent other areas in the pretectum, besides nLM, are involved in the mediation of the OKN response. Lesions of nLM in frogs, however, have been shown to have a substantial effect on horizontal OKN; namely, eliminatng the OKN response (Montgomery et al., 1982). Pretectal neurons in frogs also seem to play a role in detecting stationary objects (Ingle, 1980), and in salamanders, lesions of the thalamic-pretectal region results in disinhibition of prey catching behaviors (Finkenstadt, 1980). In rats and cats, bilateral lesions of the pretectal area results in impaired visual avoidance (Harutiunian-Kozak et al., 1970), while in the rabbit, lesions in the lateral pretectum abolished OKN (Collewijn, 1975). It

is known, also, that areas other than nLM (or the pretectum as a whole) are involved in the mediation of OKN, and that these areas have neuronal connections with the pretectum. For example, lesions of the accessory optic tract and nBOR (in pigeons and turtles) (Fite et al., 1979), nBOR, basal optic nucleus, peri-nBOR, anterior, dorsal tegmental grey, and of the dorsal caudal thalamic pretectal gray in frogs, all reduce the OKN response at mid- to high pattern velocities (Fite et al., 1980, Montgomery et al., 1985). The optic tectum also demonstrates connections with the pretectum, and it plays a major role in prey catching behavior (Brown and Ingle, 1973) and motion detection in frogs (Ingle, 1980). In frogs, tectal ablation results in impaired avoidance responses (Brown and Ingle, 1973).

Hence, it can be hypothesized that structures such as the pretectum, accessory optic system and optic tectum work together in the mediation of OKN responses. It is believed that the caudal thalamus influences the responsivity of tectal neurons (Brown and Ingle, 1973), and that accessory optic neurons influence pretectal cell responses (Montgomery et al., 1985). Behaviorally, it has been proposed (Montgomery et al., 1985) that when a stimulus is observed in the peripheral visual field, the accessory optic area is activated (nBOR), which in turn influences nLM neurons. Neurons of nLM, in turn, could influence tectal response (and be influenced by tectal units) as pertains to detection of motion and then prey catching behavior.

Possible Role of nLM

As stated in the results section, units were found in nLM which were responsive to OKN stimuli, but were not directionally selective and not selective for stimulus velocities between 6-24°/sec. If nLM is not primarily involved in the mediation of hOKN behaviors specifically, then it may have some related role. It is possible that nLM is involved in the detection and location of stimuli with contrasting features, such as edges, spots or bars. This might provide some explanation for why lesions of the pretectum will result in an impaired ability in salamanders to detect prey (Finkenstadt, 1980) and in frogs to avoid objects (Ingle, 1980). In rats, rabbits and cats, lesions of the pretectum will result in similar impairments (Harutiunian-Kozak et al., 1970, Collewijn, 1975). It is also possible that nLM is involved in the startle response, where the frog is responding to movement and to change in environmental cues.

It is also known that in rabbits and cats, W-fibers provide input to the nucleus of the optic tract (Collewijn, 1975, Hoffmann and Schoppmann, 1975). W-fibers have centers which can be aroused by light or dark spots, or in other words, are cells responsive to stimulus contrasts. Therefore, units in nLM and units in NOT may be responding to stimulus contrasts rather than to horizontal, temporonasal movements exclusively.

Effects of Binocular Versus Monocular Stimulation

As noted in the Summary of Results, there were units which demonstrated differences in response rate seemingly dependent upon whether the stimulus condition was binocular versus monocular. There is some evidence, at least in salamanders, (Manteuffel, 1984) to suggest that response rates may differ according to whether the recorded unit was binocularly or monocularly influenced, and whether there was some influence from the eye ipsilateral to the recorded unit. Hence, binocularly influenced units responded most vigorously when stimulated binocularly, less so when only the contralateral eye is stimulated, and not at all if only the ipsilateral eye is stimulated. Monocularly influenced units responded in the same way whether or not the stimulus is presented binocularly or only to the contralateral eye. One other type of binocularly influenced unit, found only in salamanders thus far (Manteuffel, 1984), is responsive only to binocular stimulation. The ipsilateral eye can also contribute inhibitory influences on response rate, possibly derived from the contralateral pretectum via pretecto-pretectal fibers (Hoffmann, 1981).

As stated in the Results section, a significant percentage of the units recorded under monocular conditions with the moving pattern demonstrated a $\geq$ 50% increase in response rate over the baseline rate. This result was not seen for units recorded under binocular conditions. Also, of the units recorded under monocular conditions, only 4% demonstrated less than the baseline level of

response, while 56% demonstrated a ≥50% increase in response rate. Of the units recorded under binocular conditions, 23% demonstrated less than the baseline level of response, and only 43% demonstrated a ≥50% increase in response rate (See Table 4). Also, from an examination of the normal data in this experiment (See Table 1), and a comparison of the unit activity percentage increases over baseline rates (binocular vs. monocular conditions), it would seem that approximately 43% of the units recorded were binocularly influenced. This implies that data were taken from postsynaptic recordings in the case of binocularly influenced units. Although it is believed that the other 57% were monocularly influenced, this is unclear, as it appears that an inhibitory mechanism was in effect under the binocular stimulus conditions. Some possible explanations for these results include: 1) Recordings were taken from more than a few monocularly influenced units, 2) Ipsilateral inhibition was a factor, or 3) Inhibition may have been mediated via the contralateral nLM in binocular conditions. In this study, there seemed to be little or no "additive effect" (i.e. more unit activity seen) of binocular, moving stimulation, and the data do suggest that suppression/inhibition was much more likely to occur under binocular, moving stimulus conditions than under monocular, moving stimulus conditions.

The examination of binocular and monocular responses of the same unit to the blank screen and stationary pattern stimuli, however, revealed exactly the opposite results (See Table 2). It is possible that there do exist some units which demonstrate an

"additive effect" in response to binocular, non-moving, stimulus conditions, resulting in higher binocular response rates than for those units under monocular, stationary stimulus conditions. In contrast, an examination of these unit activity rates in response to binocular, moving, stimulus conditions demonstrates that only 31% of the units increased their activity levels. When the data are examined as to the response rates of these units under monocular, moving stimulus conditions, 97% demonstrated some increase in unit activity. Again, there seems to be some suppression/inhibition present, which affected the unit response rates.

It is interesting that the $\geq$50% criteria set in this experiment, measuring increases in unit response rate, did not exclude the majority of units (normals or picrotoxin cases; there was only one unit under control conditions). Indeed, of the units (normal and picrotoxin) included in the group with a $\geq$50% increase, greater than 50% demonstrated a 100% increase or more (See Table 4). Thus, it appears that when units in nLM are found which are responsive to OKN stimuli, they often demonstrate very large effects.

The large effects seen in this experiment may have been influenced, in part, by the types of cells located within nLM. As reported by Montgomery et al. (1985), four types of neurons were observed in this nucleus: large, medium, stellate and small (possibly glial). In looking at the present data, the large neurons are of particular interest. These neurons have long dendrites (250 μm) which extend through the whole nucleus, and may summate activity

over the center portion of the retina. If this is so, and if the large cells are direction sensitive, then they may represent at least some of the units which demonstrated the large increases in activity found in the data. In this experiment, it must be mentioned again that the largest spike in a given recording was often chosen for analysis, and that the majority of units under monocular and picrotoxin conditions showed $\geq$50% increases in rates. The large spikes may represent the activity of the large cells, and although it cannot be proven in this study that the large cells always demonstrated large increases in response rates, it is very likely that many of the units with large spikes fell into this category. Another possible explanation for the large effects is that there was probably electrode bias present, resulting in a tendency for the larger units to be recorded. These cells may also be oriented across different axes (at least two: ventrolateral and dorsomedial (See Montgomery et al., 1985)). This would help explain why units in nLM did not demonstrate selectivity for just one stimulus direction or angle.

By the hypothesis stated above, it seems possible that the medium and stellate cells in nLM are responsible for some of the smaller increases in response rates seen in this study. The smaller cells, which may be glial, may be responsive to very small portions of the visual field- i.e. to one particular spot in the visual field oriented spatially in a particular way.

Picrotoxin Experiments

From an analysis of the experiments using picrotoxin, it seems that picrotoxin does produce some change in the responsiveness of nLM visual units. In frog, GABA reduces the receptive field area of both sustained and ON-OFF ganglion cells (Bonaventure and Wioland, 1981). Picrotoxin increases the receptive field area by abolishing the inhibition exerted on the center of the field by the surround (Bonaventure and Wioland, 1981). Picrotoxin also causes the appearance of spontaneous discharges and an increase in the duration of ON and OFF discharges. This leads to an increase in the total number of spikes recorded in response to visual stimulation (Bonaventure et al., 1983).The assertion that GABA inhibits the nasotemporal component of OKN (Bonaventure et al., 1983) could not be corroborated in this study as no unit preferences for nasotemporal or temporonasal presentations of stimuli were observed in nLM in normal experiments or in those using picrotoxin. There did seem to be, however, some evidence in the picrotoxin experiments for increased unit activity, sometimes substantial. As is seen in Table 4, the number of units in the picrotoxin experiments which demonstrated large increases in response rate ($\geq$50%) was greater than the number of units meeting this criteria in the normal experiments.

Receptive Field Sizes

Pretectal units have been described as having large receptive fields (> 60^{o}) (Brown and Marks, 1977, Manteuffel, 1984), and being sensitive to large-field moving stimuli (Cochran et al., 1980, Katte and Hoffmann, 1980). In this study, there was no determination made of the minimum stimulus size necessary to cause units to fire. This question would undoubtedly be one of interest for further investigation.

Multi-Unit vs. Single Unit Analysis

Another question which was examined in this study was that of single-unit versus multi-unit analysis to determine if multi-unit analysis was as accurate in determining unit preferences as was single-unit analysis. Analysis of data, however, did not demonstrate a concurrence of results (See Table 8). For nLM, single-unit analysis was found to be preferable, as it was possible that multi-unit analysis included unit activity from units with different directional selectivities. The results suggested that neighboring cells in nLM may demonstrate different unit preferences and multi-unit analysis alone would not be able to specify where each unit was located.

Unit Loci and Responses

Although the analysis of data did not reveal significant findings for single-unit preferences for stimulus angle based upon unit location in nLM, there seemed to be a slight preference of caudally located units for oblique, upward or vertically moving stimuli. For units located more rostrally, there seemed to be more of a preference for horizontal or oblique, downward moving stimuli. Examination of the picrotoxin experiments, however, showed no pattern as to similar or opposite preferences for stimulus angle compared to the normal units. The analysis of picrotoxin data for stimulus direction, though, did demonstrate a preference for temporonasal directions for rostrally located units.

It is possible that differential patterns of unit responses do exist, based upon the unit location in nLM. This could be influenced, hypothetically, by the fact that retinal afferents to nLM originate from two major branches of the optic tract: the axial and marginal branches (Levine, 1980), each of which influences different parts of nLM. There is also the possibility that there are differences between unit responsivity in the "dense core" region of nLM and units outside of this core region (See Montgomery et al., 1985). Since contralateral fibers project to the core region and ipsilateral fibers to the peripheral or surround region, this pattern may have a direct influence upon unit "preferences" for stimulus direction and angle.

Homology: nLM vs. NOT

Many of the previous studies examining the pretectal complex have stated that there is a possible homology between the pretectum and the nucleus of the optic tract (NOT) (Wilczynski and Northcutt, 1977, Cochran et al., 1980, Katte and Hoffmann, 1980, Montgomery et al., 1985). This hypothesis is based on anatomical similarities between the anuran pretectum and NOT, and on similarities of the single-unit responses recorded in these nuclei. In this study, no particular preference for a specific stimulus direction was found in nLM, as is found in NOT in rabbits and cats (Oyster and Barlow, 1967, Harutiunian-Kozak et al., 1970, Wyatt and Daw, 1974, Kanaseki and Sprague, 1974, Collewijn, 1975, Hoffmann and Schoppmann, 1975, Schoppmann and Hoffmann, 1979, Ballas et al., 1981, Ariel and Daw, 1982). Thus, this experiment cannot support the hypothesis of homology between the frog nLM and NOT, especially when looking at functional criteria alone. There is, however, at least one difference between frogs and mammals which should be mentioned. As mentioned above, studies on mammals such as rabbits and cats have all demonstrated the existence of directionally selective cells in NOT. They have also pointed out that there are many directionally selective retinal ganglion cells in these animals. One study on the frog (Backstrom et al., 1978), though, showed that only a small proportion of frog retinal ganglion cells (29 out of 171) were directionally selective. Thus, it becomes apparent that attempting to demonstrate homology between frogs and mammals, in this instance,

is more difficult, due to this difference. Nevertheless, it is very possible that other pretectal structures besides nLM do contain directionally selective cells, which would warrant further experimentation. It is possible that nLM is homologous to a mammalian structure other than NOT, but this would require much more research, as it is unclear what structure would qualify. Neuroanatomically, nLM and NOT have been considered homologous. A functional analysis, however, demonstrates important differences. The functional properties of nLM units, instead, are possibly more similar to another pretectal nucleus besides NOT, in mammals.

APPENDIX

Table 1

Average Unit Response Rates/ 10 sec.to Baseline and Moving Stimuli: Normal, Control, Picrotoxin Cases (*=TN,#=NT-Direction of Preferred Stimulus Angle, C= Caudal, R= Rostral)

Normals

Binocular Stimulation

Unit # Hemis. Loci	Baseline Blank Screen	Baseline Stat. Pattern	Moving Stimulus 0	180	270	90	45	315	135	225
1L C*	5	17	44	7	25	46	33	11	6	8
1R C	66	62	52	59	57	56	58	53	57	56
2L R	1	3	4	2	1	1	2	2	1	1
2R C	47	35	16	10	8	10	14	10	11	6
3L C#	23	6	4	4	3	4	3	2	4	5
3R C*	7	8	11	10	12	17	11	12	12	8
8L C*	66	58	67	50	49	54	65	63	48	50
8R C	32	27	29	27	25	28	31	23	28	25
16L C*	66	58	67	50	49	54	65	63	48	50
16R C*	34	20	12	20	20	21	20	18	18	19
17L R#	1	2	2	2	6	3	4	2	3	2
17R R*	30	35	31	42	45	35	43	39	38	47
18L C#	10	105	61	107	99	70	76	117	96	127
19L C*	14	29	16	7	17	14	35	21	19	6
19R R#	16	15	11	11	13	11	12	9	16	9

Monocular Stimulation

1L C*	8	7	19	17	12	22	17	12	15	16
1R C*	54	70	66	45	90	37	18	135	47	20
2L R	1	1	1	1	2	1	1	1	1	1
2R C*	11	8	8	9	7	7	7	3	8	10
3L C	5	3	3	9	6	5	8	8	1	6
3R C#	1	12	18	4	4	5	6	6	3	5
8L C	19	24	26	16	22	20	23	23	23	22
8R C*	35	51	42	42	44	44	48	53	38	51
16L C#	18	20	20	36	43	28	29	50	35	37
16R C#	77	65	67	54	55	50	60	50	62	54
17L R*	1	2	3	1	2	3	2	2	4	2
17R R#	44	44	45	41	40	50	48	42	45	40
18L C*	102	130	141	143	113	149	147	148	144	135
19L C	16	16	15	12	10	10	12	8	11	6
19R R*	13	7	4	3	4	5	3	9	6	5

Table 1, cont'd.

Normals
Binocular Stimulation

Unit # Hemis. Loci	Baseline Blank Screen	Baseline Stat. Pattern	Moving Stimulus 0	180	270	90	45	315	135	225
20L C	6	6	7	3	4	6	6	3	2	5
6L C	38	54	45	37	36	31	31	31	40	35
9L C	7	6	17	6	9	4	7	2	4	2
9R C*	3	5	6	5	5	7	7	4	6	8
5L C	9	5	8	2	1	7	4	1	3	1
5R C*	10	16	23	17	16	25	20	13	20	18
10L C	10	8	12	6	4	7	9	6	7	11
10R C	15	14	10	4	3	4	9	2	2	3
12R C*	16	17	24	8	17	25	30	50	36	21
12L C*	13	29	6	7	11	45	5	2	4	7
14R C*	15	16	6	16	18	5	3	15	6	24
22L R#	63	67	41	48	58	51	45	61	52	44
22R C*	29	41	60	52	97	54	51	110	54	70
28R C	2	3	3	1	1	1	1	1	1	2
29R C*	8	5	4	12	11	16	12	10	11	9

Monocular Stimulation

20L C#	2	4	2	1	4	1	2	3	2	3
6L C	24	21	21	18	16	17	18	113	18	12
9L C	2	2	8	3	5	2	2	2	3	4
9R C#	4	2	5	4	2	3	3	2	3	4
5L C	1	5	2	7	5	1	2	5	1	5
5R C#	21	16	19	16	18	20	26	20	22	16
10L C#	2	3	5	5	5	4	7	22	5	3
10R C*	1	2	5	4	5	2	3	10	4	4
12R C#	8	6	16	9	10	9	13	10	4	4
12L C*	27	16	8	1	3	24	13	5	9	1
14R C#	18	23	19	19	13	26	27	13	29	15
22L R*	37	43	50	50	48	45	64	46	56	52
22R C*	81	88	103	98	122	94	103	104	84	118
28R C#	1	1	1	1	1	1	2	1	1	1
29R C#	14	6	7	8	7	12	7	6	8	6

Table 1, cont'd.

Normals
Monocular Stimulation

Unit # Hemis. Loci	Baseline Blank Screen	Baseline Stat. Pattern	Moving Stimulus 0	180	270	90	45	315	135	225
21R C*	34	22	17	15	25	15	18	14	16	21
21L C	21	22	25	35	27	23	18	30	25	24
35L2C#	10	12	6	10	18	16	9	9	16	9
36L2C*	4	4	5	1	6	5	11	8	12	3
37L2R*	14	4	10	17	12	14	18	14	15	15
39L2C	8	13	4	22	16	11	17	7	11	16
30R C*	7	6	11	8	7	7	7	4	6	12
31R C#	11	19	24	26	19	29	33	22	30	28
33R C#	17	18	15	22	17	19	21	17	19	15
34R C*	19	17	15	14	20	11	20	23	15	33
35L1C#	12	13	8	14	18	13	8	16	16	9
35R C#	33	38	37	40	37	30	31	37	28	31
36L1C*	4	5	6	4	6	5	7	7	8	6
36R R*	20	17	16	25	26	25	21	20	20	19
37L1R*	15	15	12	13	14	14	16	14	14	14
37R R*	9	7	13	17	12	9	11	18	13	15
38R C#	20	25	25	22	26	30	25	26	19	25
39L1C	9	13	8	18	16	13	15	12	13	14
39R C#	14	20	18	16	10	10	191	18	11	17
27R R#	4	9	9	13	18	24	4	22	27	17

Control

Unit # Hemis. Loci	Baseline Blank Screen	Baseline Stat. Pattern	Moving Stimulus 0	180	270	90	45	315	135	225
					Monocular Stimulation					
13L C	8	7	6	8	6	3	5	4	5	5
					Binocular Stimulation					
13L C	3	4	11	3	6	8	10	7	8	5

Table 1, cont'd.

Picrotoxin
Monocular Stimulation

Unit # Hemis. Loci	Baseline		Moving Stimulus							
	Blank Screen	Stat. Pattern	0	180	270	90	45	315	135	225
25R1C#	7	5	22	7	2	18	14	3	21	6
23R R*	2	4	4	4	4	4	5	6	4	4
26R C#	10	10	1	10	7	3	4	7	11	5
24R1C#	5	2	3	1	2	2	2	1	1	1
27R1R#	1	3	7	6	2	10	6	7	1	4
28R1R*	2	4	5	12	12	5	6	12	7	17
29R1C*	21	20	15	14	16	14	13	17	12	18
30R1R*	2	4	1	1	3	1	1	2	1	1
31R1R*	40	35	58	90	99	70	74	88	84	97
32R1R*	24	29	33	73	75	52	52	76	65	71
33R1R#	39	37	42	53	32	44	42	41	42	46
34R1R*	21	22	28	26	30	28	22	27	25	28
35L1C#	15	13	15	24	28	11	14	30	16	33
36L1C#	10	21	9	9	10	14	8	15	27	5
37L1R*	17	14	14	17	14	15	18	17	14	12
39L1C*	8	23	18	19	11	9	16	20	21	12
27R2R#	4	8	10	9	21	32	5	19	39	15
28R2R*	1	5	3	5	7	5	3	6	1	5
29R2C#	18	13	17	17	16	18	22	14	21	21
30R2C	7	7	17	10	9	8	5	3	7	9
31R2R*	40	38	50	105	111	61	70	91	71	97
32R2R*	23	30	34	77	74	54	45	93	56	84
33R2R	38	37	38	57	35	43	30	40	41	43
34R2C	20	20	25	36	26	22	26	27	20	27
35L2C#	14	13	12	32	24	11	17	37	10	33
36L2C*	9	20	10	3	8	16	9	30	35	2
37L2R*	16	4	16	19	11	16	21	15	15	12
39L2C	7	24	16	25	12	15	15	22	16	13
24R2C#	1	4	6	4	6	6	5	5	7	5
25R2C#	13	5	3	10	3	51	18	3	20	5

Table 2

A Comparison of Responses to "Blank Screen" and "Stationary Pattern" Stimulation: Binocular vs. Monocular Changes for the Same Unit (n=30)

Unit Response Rate Changes as Stimulation is Changed from Binocular to Monocular Conditions

Stimulation	Increase		No Change		Decrease	
	#	%	#	%	#	%
Blank Screen	11	37	2	7	17	56
Stationary Pattern	8	27	4	13	18	60

TABLE 3

Responses of Directionally Sensitive Neurons Recorded Under Monocular, Binocular and Monocular Picrotoxin Conditions at Stimulus Velocities 6, 15 and 25° /second

Monocular Unit	Stimulus Angle	Velocity 6°	15°	25°
1L	0	16	20	22
	45	17	21	12
	90	18	19	28
	135	17	18	11
	180	4	25	21
	225	26	16	7
	270	7	24	16
	315	14	22	11
1R	0	79	89	29
	45	0	54	1
	90	19	44	48
	135	34	46	61
	180	39	48	48
	225	0	0	0
	270	102	67	101
	315	120	130	154
2L	0	1	1	0
	45	1	0	1
	90	0	0	1
	135	0	1	1
	180	1	1	1
	225	1	1	0
	270	0	3	3
	315	1	1	1
3L	0	0	2	8
	45	9	6	9
	90	7	7	1
	135	0	1	2
	180	17	7	3
	225	6	8	4
	270	2	9	7
	315	10	5	12

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
3R	0	11	26	18
	45	5	7	5
	90	3	7	6
	135	0	4	4
	180	0	8	4
	225	4	5	7
	270	3	1	7
	315	3	8	7
5R	0	12	19	27
	45	32	23	24
	90	18	27	16
	135	24	19	23
	180	13	18	17
	225	18	17	13
	270	18	16	20
	315	25	15	19
9L	0	5	19	0
	45	4	2	1
	90	2	1	2
	135	3	4	1
	180	8	0	2
	225	5	4	3
	270	7	6	2
	315	3	2	2
9R	0	9	3	3
	45	3	2	3
	90	4	3	1
	135	6	3	0
	180	7	3	3
	225	4	2	6
	270	0	3	3
	315	2	4	1

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
10L	0	9	2	3
	45	6	3	11
	90	4	3	4
	135	4	5	5
	180	6	5	4
	225	5	0	3
	270	4	9	1
	315	15	25	25
10R	0	7	7	1
	45	5	1	3
	90	2	2	2
	135	2	2	7
	180	7	1	3
	225	3	5	3
	270	9	1	4
	315	15	4	10
12L	0	3	14	7
	45	7	0	33
	90	59	0	13
	135	5	9	12
	180	2	1	2
	225	2	0	2
	270	1	1	6
	315	0	6	8
12R	0	16	16	16
	45	13	10	17
	90	9	14	3
	135	7	5	8
	180	6	11	10
	225	8	8	17
	270	9	8	12
	315	13	5	13

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
16L	0	26	15	20
	45	31	29	27
	90	35	21	28
	135	35	34	36
	180	28	32	49
	225	32	30	48
	270	44	49	37
	315	45	47	57
17L	0	1	3	4
	45	2	0	3
	90	0	4	4
	135	4	4	2
	180	0	1	1
	225	3	1	2
	270	0	4	1
	315	1	4	1
21L	0	15	25	34
	45	14	16	23
	90	21	18	29
	135	30	18	26
	180	40	27	37
	225	29	27	16
	270	32	29	21
	315	30	33	27
27R	0	10	9	9
	45	5	2	6
	90	32	23	17
	135	39	23	18
	180	9	16	14
	225	15	10	27
	270	21	18	17
	315	19	12	36

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
28R	0	1	1	0
	45	1	2	3
	90	1	1	0
	135	0	1	0
	180	0	1	0
	225	0	2	0
	270	3	1	0
	315	0	2	0
29R	0	8	6	7
	45	7	3	10
	90	13	9	14
	135	10	5	10
	180	5	16	3
	225	7	6	6
	270	11	10	2
	315	5	10	2
30R	0	17	7	8
	45	5	10	7
	90	8	6	8
	135	7	5	7
	180	10	8	5
	225	9	10	17
	270	9	5	7
	315	3	1	7
31R	0	14	36	23
	45	35	32	33
	90	38	31	17
	135	30	31	29
	180	29	25	24
	225	26	26	33
	270	19	23	14
	315	24	25	17

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
34R	0	17	14	14
	45	24	22	14
	90	10	13	11
	135	15	13	18
	180	13	13	16
	225	32	34	35
	270	20	20	19
	315	20	29	18
36L1	0	5	8	6
	45	11	5	6
	90	4	6	4
	135	13	8	5
	180	1	5	8
	225	3	6	10
	270	7	6	7
	315	8	10	3
36R	0	15	14	19
	45	24	24	16
	90	13	31	31
	135	15	18	26
	180	27	29	20
	225	22	19	15
	270	25	22	30
	315	18	17	24
37R	0	3	15	20
	45	8	17	9
	90	10	8	10
	135	19	11	8
	180	19	20	13
	225	17	19	10
	270	12	13	12
	315	19	21	12

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
35L2	0	7	8	4
	45	8	17	9
	90	10	8	10
	135	19	11	8
	180	19	20	13
	225	17	19	10
	270	12	13	12
	315	19	21	12
36L2	0	4	6	5
	45	13	9	12
	90	4	5	6
	135	18	12	8
	180	1	1	1
	225	1	2	6
	270	5	4	7
	315	9	8	6
37L2	0	10	8	11
	45	20	19	14
	90	13	16	15
	135	17	13	16
	180	17	14	20
	225	13	17	15
	270	10	18	9
	315	20	11	11
39L2	0	6	4	3
	45	1	20	22
	90	7	14	13
	135	8	12	15
	180	20	22	24
	225	16	16	18
	270	14	18	16
	315	16	3	4

TABLE 3, cont'd.

Binocular Unit	Stimulus Angle	Velocity 6°	15°	25°
1L	0	56	56	20
	45	30	33	27
	90	38	52	48
	135	5	3	11
	180	8	8	6
	225	8	9	7
	270	15	10	51
	315	2	17	15
3R	0	10	12	11
	45	14	13	7
	90	14	26	13
	135	10	17	8
	180	7	13	10
	225	10	6	8
	270	9	6	22
	315	7	14	14
9L	0	9	5	38
	45	7	11	3
	90	9	2	2
	135	4	2	6
	180	8	5	5
	225	4	1	1
	270	1	24	1
	315	2	0	5
9R	0	4	5	8
	45	5	7	8
	90	3	4	13
	135	8	6	5
	180	6	2	7
	225	11	4	8
	270	3	6	6
	315	6	6	0

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
5L	0	8	6	11
	45	5	6	1
	90	6	6	12
	135	3	4	2
	180	2	1	4
	225	0	2	1
	270	0	1	3
	315	1	1	1
5R	0	17	22	30
	45	19	25	17
	90	19	29	28
	135	15	22	24
	180	19	13	20
	225	14	30	11
	270	16	13	18
	315	6	20	13
10L	0	10	16	11
	45	5	15	7
	90	9	7	5
	135	4	6	10
	180	8	3	6
	225	15	11	8
	270	8	4	1
	315	7	3	8
12L	0	1	11	5
	45	2	8	6
	90	101	32	3
	135	2	8	2
	180	2	11	7
	225	7	8	5
	270	10	12	0
	315	3	1	1

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
12R	0	24	2	9
	45	1	33	38
	90	30	0	5
	135	25	46	37
	180	4	10	11
	225	7	35	21
	270	9	18	25
	315	44	153	153
14R	0	14	2	2
	45	4	2	2
	90	7	2	7
	135	5	1	12
	180	14	14	19
	225	21	24	28
	270	25	18	12
	315	10	19	15
17L	0	3	2	2
	45	0	2	9
	90	1	7	2
	135	2	4	2
	180	0	4	3
	225	1	4	2
	270	5	7	6
	315	2	2	1
22R	0	57	69	53
	45	58	48	47
	90	57	47	57
	135	52	46	64
	180	54	47	54
	225	54	91	64
	270	79	109	103
	315	123	87	121

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
29R	0	3	4	5
	45	9	5	22
	90	18	26	4
	135	8	13	12
	180	7	19	9
	225	14	7	7
	270	10	14	9
	315	7	9	13
Picrotoxin 27R2	0	10	9	12
	45	5	4	6
	90	38	26	32
	135	34	40	45
	180	6	9	12
	225	17	14	14
	270	19	18	26
	315	22	16	19
29R2	0	14	21	17
	45	24	12	31
	90	18	15	20
	135	21	27	15
	180	12	25	15
	225	17	26	22
	270	15	14	19
	315	9	17	17
30R2	0	18	19	14
	45	5	5	6
	90	8	10	6
	135	6	8	7
	180	10	11	10
	225	6	12	9
	270	8	9	10
	315	3	4	2

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
31R2	0	50	60	41
	45	68	70	72
	90	61	64	58
	135	68	74	70
	180	100	104	110
	225	90	105	96
	270	108	114	111
	315	83	98	92
32R2	0	38	35	30
	45	47	44	44
	90	57	54	50
	135	57	54	55
	180	81	77	74
	225	84	85	84
	270	76	74	72
	315	91	95	92
33R2	0	40	37	36
	45	30	31	30
	90	38	43	48
	135	39	40	43
	180	57	59	55
	225	46	38	45
	270	30	38	37
	315	40	40	41
34R2	0	30	22	23
	45	25	28	25
	90	22	22	23
	135	30	10	20
	180	39	34	35
	225	30	25	26
	270	21	28	29
	315	17	32	32

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
35L2	0	10	3	5
	45	6	12	9
	90	14	20	14
	135	16	12	20
	180	12	9	9
	225	10	7	8
	270	16	19	19
	315	7	10	9
36L2	0	7	4	5
	45	9	13	11
	90	7	5	3
	135	15	11	10
	180	1	0	1
	225	3	4	3
	270	4	10	3
	315	8	12	4
37L2	0	18	12	18
	45	21	24	18
	90	10	18	20
	135	20	15	16
	180	21	18	18
	225	11	10	15
	270	8	11	14
	315	17	12	16
24R2	0	7	7	4
	45	4	6	5
	90	7	8	4
	135	9	5	8
	180	6	1	5
	225	6	3	6
	270	8	7	3
	315	4	9	2

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
25R2	0	0	10	0
	45	0	20	34
	90	40	52	60
	135	38	10	12
	180	12	8	11
	225	6	5	4
	270	0	10	0
	315	0	10	0
25R1	0	36	11	19
	45	24	16	3
	90	15	21	17
	135	29	20	14
	180	4	11	5
	225	7	10	2
	270	5	10	2
	315	4	6	0
23R	0	4	1	7
	45	3	6	5
	90	4	6	3
	135	6	4	4
	180	2	5	5
	225	4	5	4
	270	6	2	4
	315	6	4	7
24R1	0	4	4	2
	45	4	3	1
	90	3	1	3
	135	1	0	1
	180	1	0	2
	225	1	0	0
	270	3	2	0
	315	0	0	0

TABLE 3, cont'd.

Unit	Stimulus Angle	Velocity 6°	15°	25°
28R1	0	9	5	0
	45	18	8	2
	90	10	0	5
	135	8	5	8
	180	15	6	17
	225	15	15	22
	270	16	9	11
	315	11	13	11
31R1	0	50	60	65
	45	70	86	66
	90	61	64	84
	135	71	85	96
	180	105	101	65
	225	97	101	93
	270	111	60	97
	315	91	100	74
32R1	0	34	24	42
	45	45	48	62
	90	54	53	50
	135	56	73	66
	180	77	79	63
	225	84	73	56
	270	74	78	73
	315	93	74	62
35L1	0	12	18	14
	45	17	14	10
	90	11	13	10
	135	10	20	19
	180	32	20	21
	225	33	35	30
	270	24	37	22
	315	37	23	30

Table 4

Greatest Percentage Increase in Unit Response Rate to Moving Stimuli over Stationary Pattern Rate: Normals, Picrotoxin Experiments

Percent Increase	Control		Normals		Picrotoxin
	Binoc	Monoc	Binoc	Monoc	
<0			7 (23%)	2 (4%)	3 (10%)
0			1 (3)	2 (4)	0 (0)
1-49		1	9 (30)	18 (36)	8 (27)
50-99	1		6 (20)	11 (22)	7 (23)
100 & UP			7 (23)	17 (34)	12 (40)

Percent Increase	Normals		Picrotoxin
	Binoc	Monoc	
<0	7	2	3
0	1	2	0
1-9	2	5	1
10-19	3	3	1
20-29	2	5	3
30-39	2	3	1
40-49	0	2	2
50-59	4	5	3
60-69	2	3	1
70-79	0	1	2
80-89	0	0	1
90-99	0	2	0
100 & UP	7	17	12

Table 5

Greatest Percentage of Increase in Unit Spike Frequency Rate in Response to Moving Stimuli over Stationary Pattern Baseline Rate: Normal and Picrotoxin Experiments

	Normals				Picrotoxin	
Increase	Binocular Stimulation (n=30)		Monocular Units (n=50)		Units (n=30)	
	#	%	#	%	#	%
≥ 50%	13	43	28*	56	19	63
< 50%	9	30	18	36	8	27
0%	1	3	2	4	0	0
< Baseline Rate	7	23	2	4	3	10

Table 6

Units in nLM with ≥50% Increases in Response Rates Over Stationary Pattern Rate: Number and Percentage Most Responsive to Particular Stimulus Angles

	Normals				Picrotoxin	
Stimulus Angle (Degrees)	Monocular Units (n=28)		Binocular Stimulation (n=13)		Units (n=19)	
	#	%	#	%	#	%
0	4	14	3	23	3	16
180	3	11	0	0	2	10
45	4	14	0	0	2	10
315	5	18	2	15	4	21
90	3	11	5	39	1	5
270	3	11	1	8	2	10
135	4	14	0	0	3	16
225	2	7	2	15	2	10

Table 7

Units with ≥50% Increases in Response Rates
Nasotemporal vs. Temporonasal vs.
Vertical Stimulus Direction Preferences:
Normal Experiments, Picrotoxin Experiments

		Normals				Picrotoxin	
Stimulus Direction Preference		Monocular Units (n=28)		Binocular Stimulation (n=13)		Monocular Units (n=19)	
		#	%	#	%	#	%
Horizontal Angles	Naso-temporal	2	7	3	23	1	5
	Temporo-nasal	4	14	2	15	2	10
Oblique Angles	Naso-temporal	6	21	3	23	5	26
	Temporo-nasal	9	32	2	15	6	32
Vertical Angles	0^{o}	4	14	3	23	3	16
	180^{o}	3	11	0	0	2	10

Table 8
Multi-Unit Analysis versus Single-Unit Analysis:
Preferred Stimulus Direction, Angle and Velocity

Unit	Stimulus Direction		Stimulus Angle		Stimulus Velocity	
	Single	Multi	Single	Multi	Single	Multi
16 R	Vertical	Vertical	0^{o}	0^{o}	25^{o}/sec	25^{o}/sec
19 R	TN	TN	315	225	25	15
18 L	TN	NT	90	270	6	6
16 L	NT	NT	315	315	6	25
20 L	NT	NT	270	270	6	15
17 L	TN	NT	135	225	15	25
30 R	TN	TN	225	270	25	25
17 R	NT	NT	90	45	6	15

Table 9

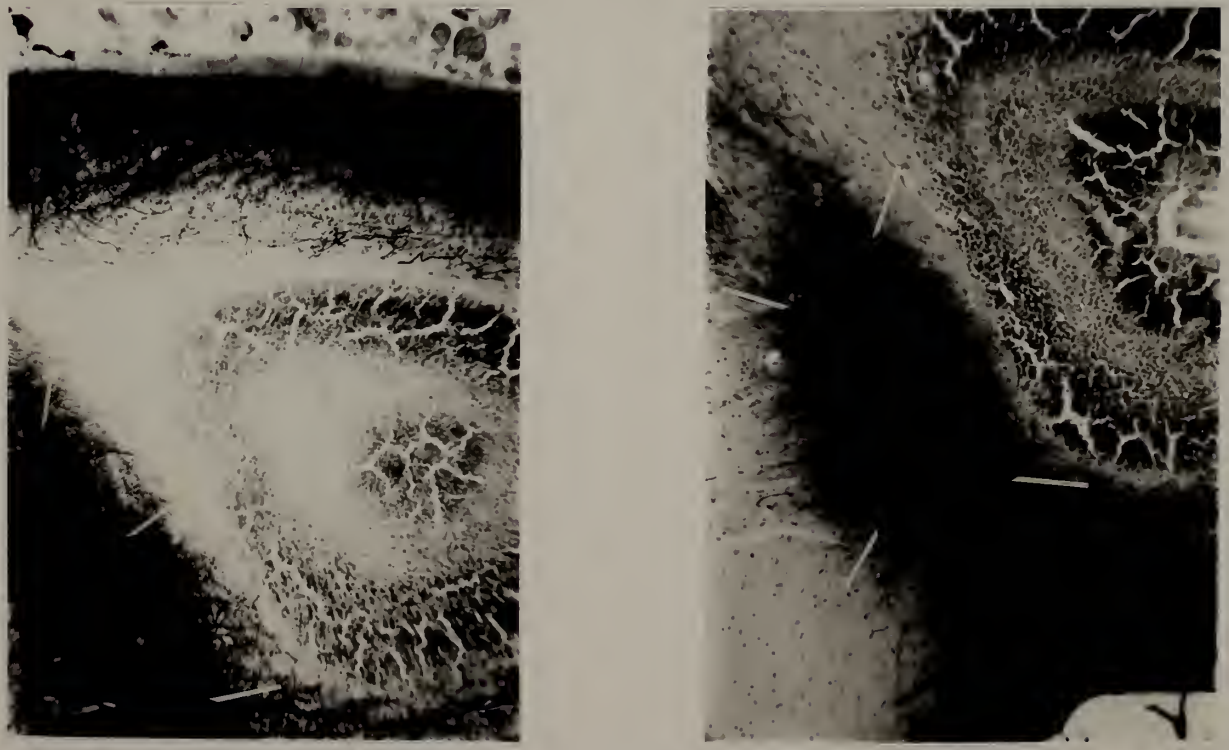
Units with ≥50% Increases in Response Rates
Location of Unit in nLM (Caudal vs. Rostral) and
Preferred Stimulus Angle of Unit:
Normal and Picrotoxin Cases (Monocular Conditions)

	Normals				Picrotoxin			
Stimulus Angle	Caudal (n=22)		Rostral (n=6)		Caudal (n=10)		Rostral (n=9)	
	#	%	#	%	#	%	#	%
0	4	18	0	0	3	30	0	0
180	3	14	0	0	1	10	1	11
45	3	14	1	17	1	10	1	11
315	4	18	1	17	1	10	3	33
270	1	4	2	33	1	10	2	22
90	3	14	0	0	1	10	0	0
135	2	9	2	33	2	20	1	11
225	2	9	0	0	1	10	1	11

Table 10

Units with ≥50% Increases in Response Rates
Nasotemporal vs. Temporonasal vs.
Vertical Stimulus Direction Preferences:
A Comparison of Caudal vs. Rostral nLM Units

Stimulus Direction		Normals				Picrotoxin			
		Caudal (n=22)		Rostral (n=6)		Caudal (n=10)		Rostral (n=9)	
		#	%	#	%	#	%	#	%
Horizontal Angles	Naso-temporal	2	9	1	16	1	10	0	0
	Temporo-nasal	2	9	1	16	0	0	2	22
Oblique Angles	Naso-temporal	4	18	1	16	4	40	1	11
	Temporo-nasal	7	32	3	50	1	10	5	56
Vertical Angles	0^{o}	4	18	0	0	3	30	0	0
	180^{o}	3	14	0	0	1	10	1	11



A nLM labelled with HRP B

Figure 1. Location of Units in nLM and Optic Tectum: A) Rostral Areas of nLM, B) Caudal Areas of nLM.

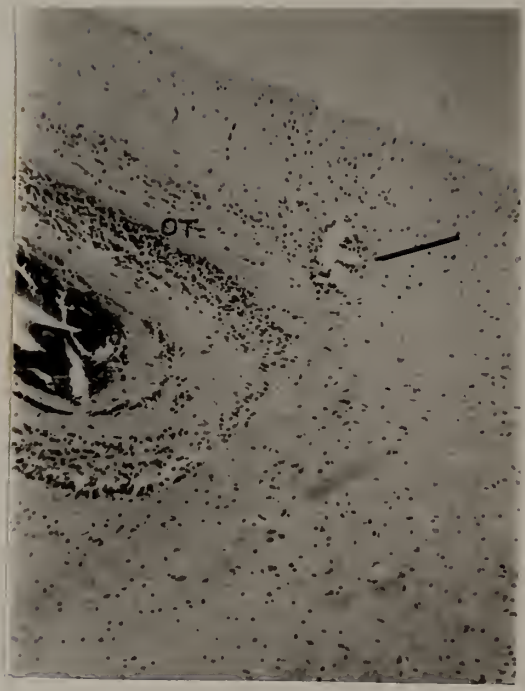


Fig. 1 (cont'd) Lesion in Optic Tectum

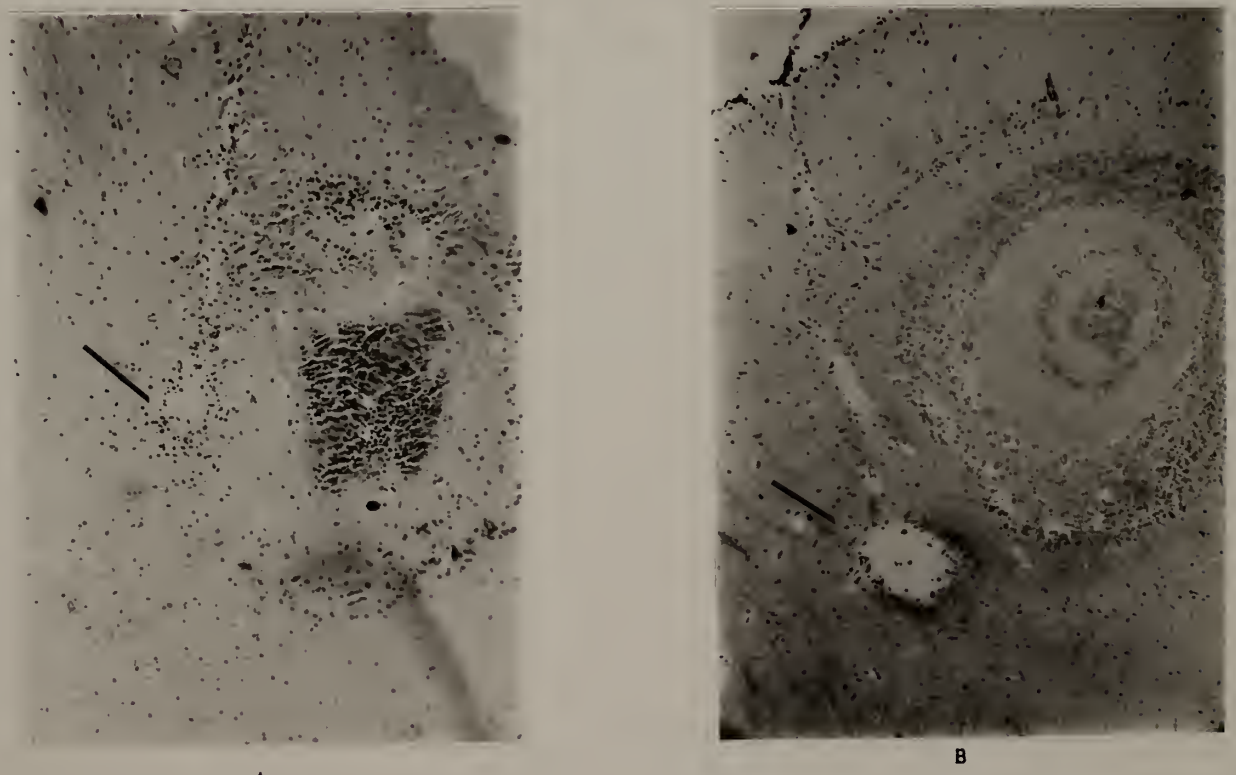
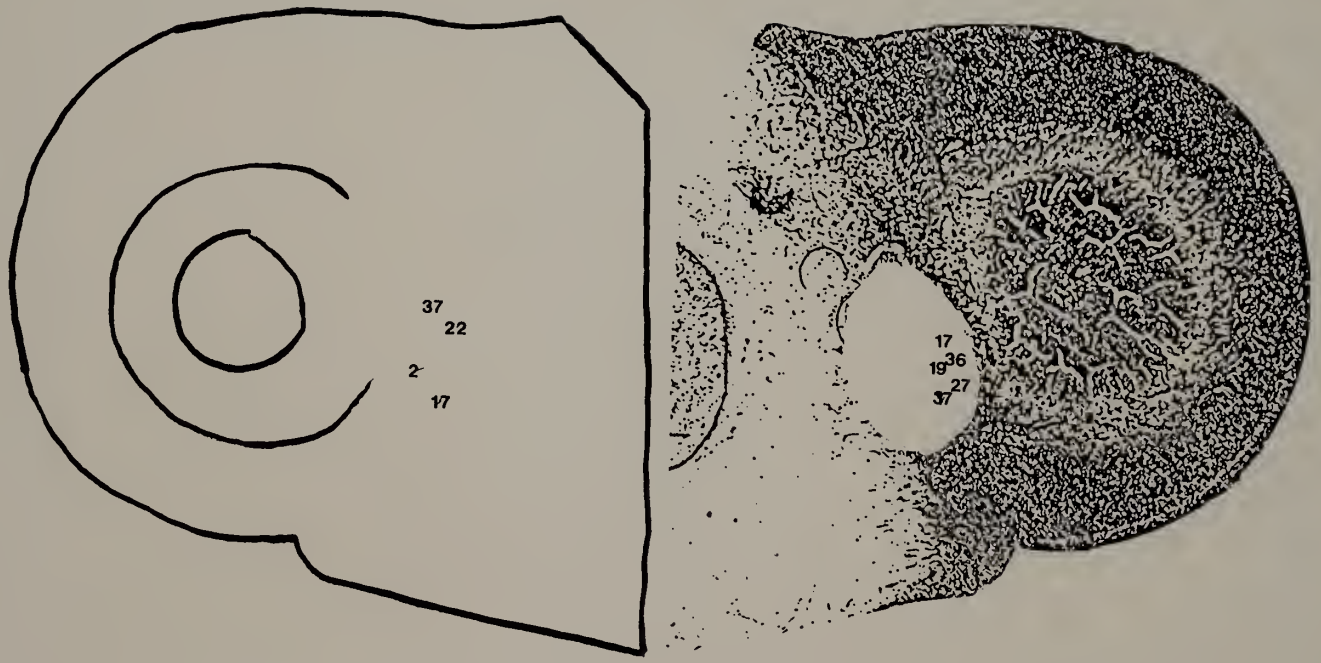
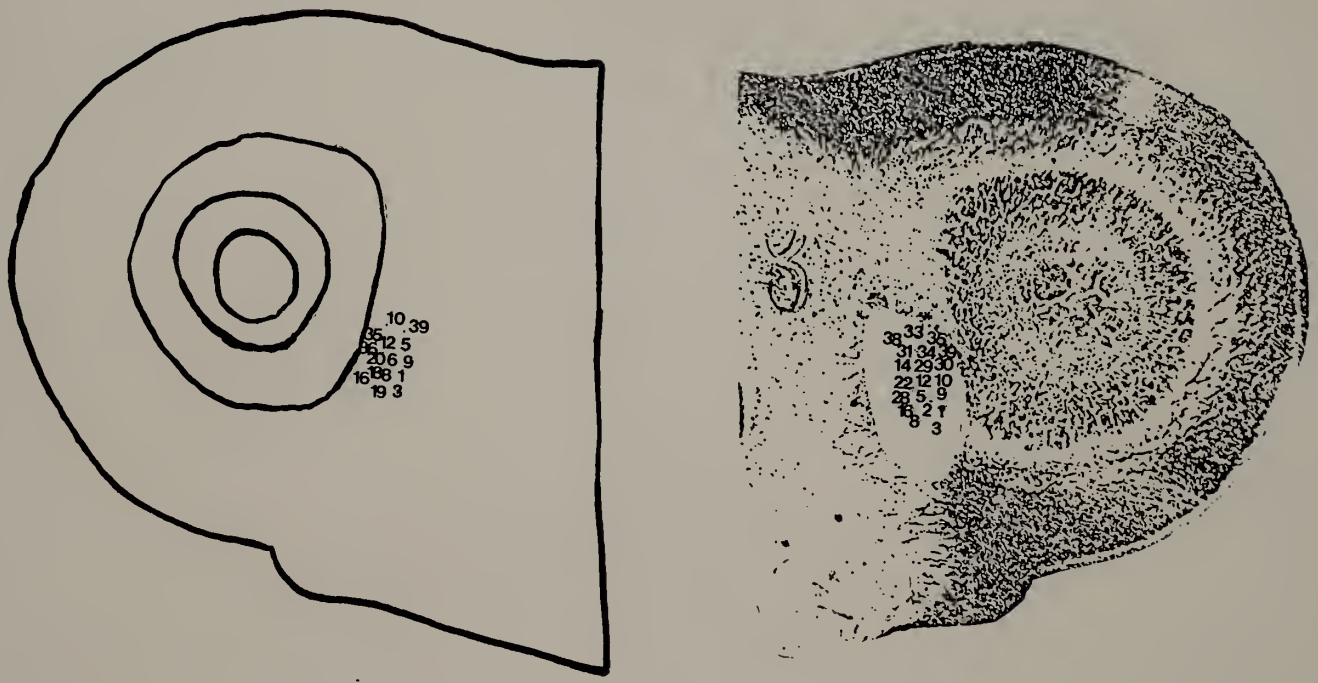


Figure 2. Lesions in nLM: A) Rostral nLM, B) Caudal nLM.



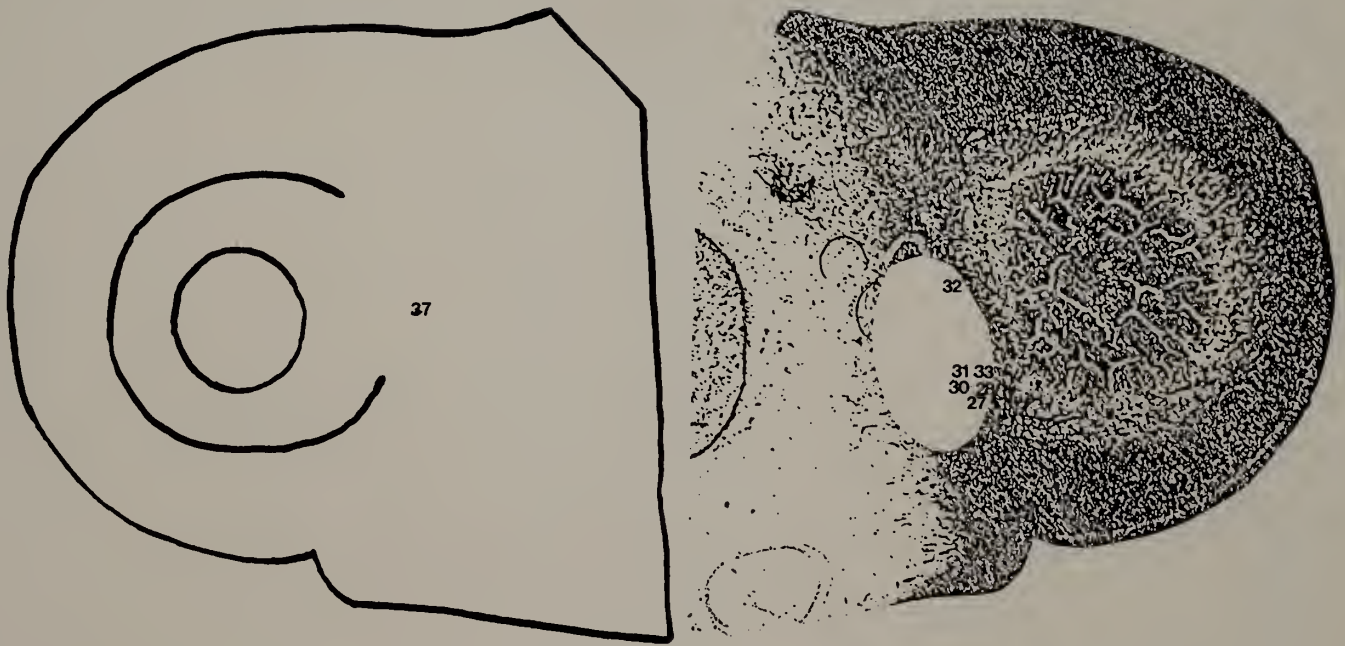
A

Fig. 2 (cont'd) Lesion Loci in Normals


10 39
35 12 5
20 6 9
16 8 1
19 3
38 33 35
31 34 36
14 29 30
22 12 10
28 5 9
16 2 1
8 3

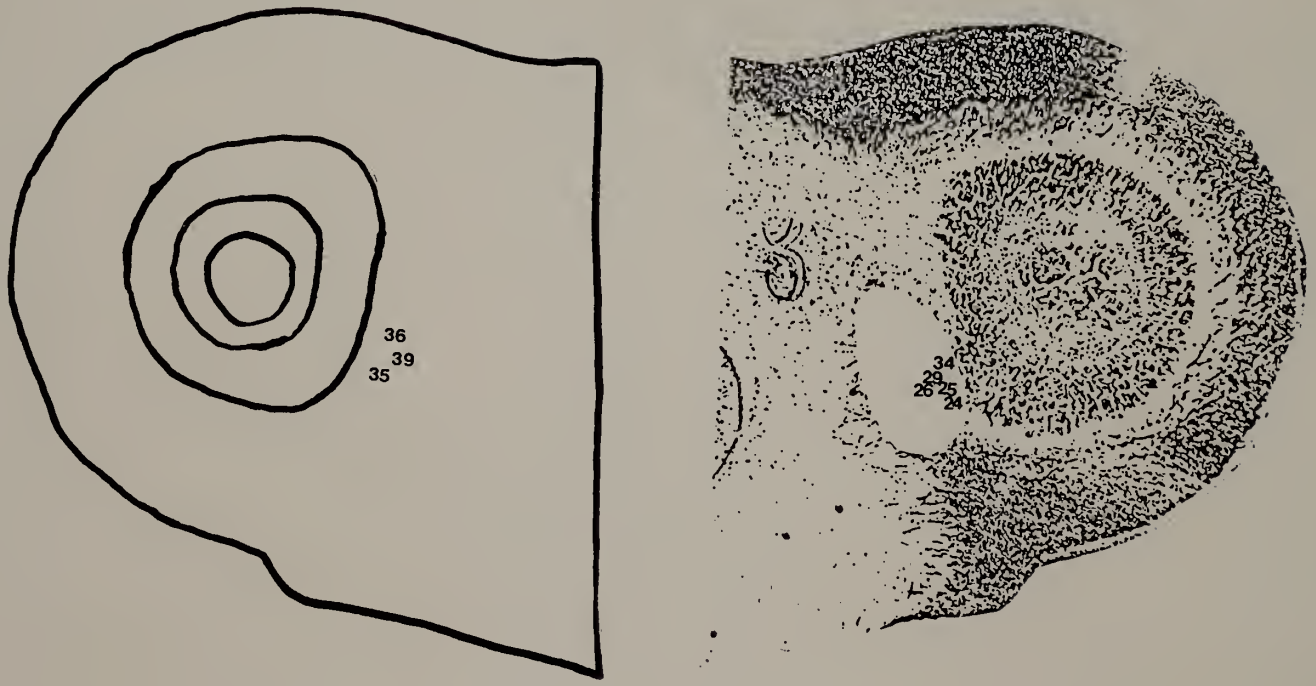
B

Fig. 2 (cont'd)



A

Fig. 2 (cont'd) Lesion Loci in Picrotoxin Cases



B

Fig. 2 (cont'd)

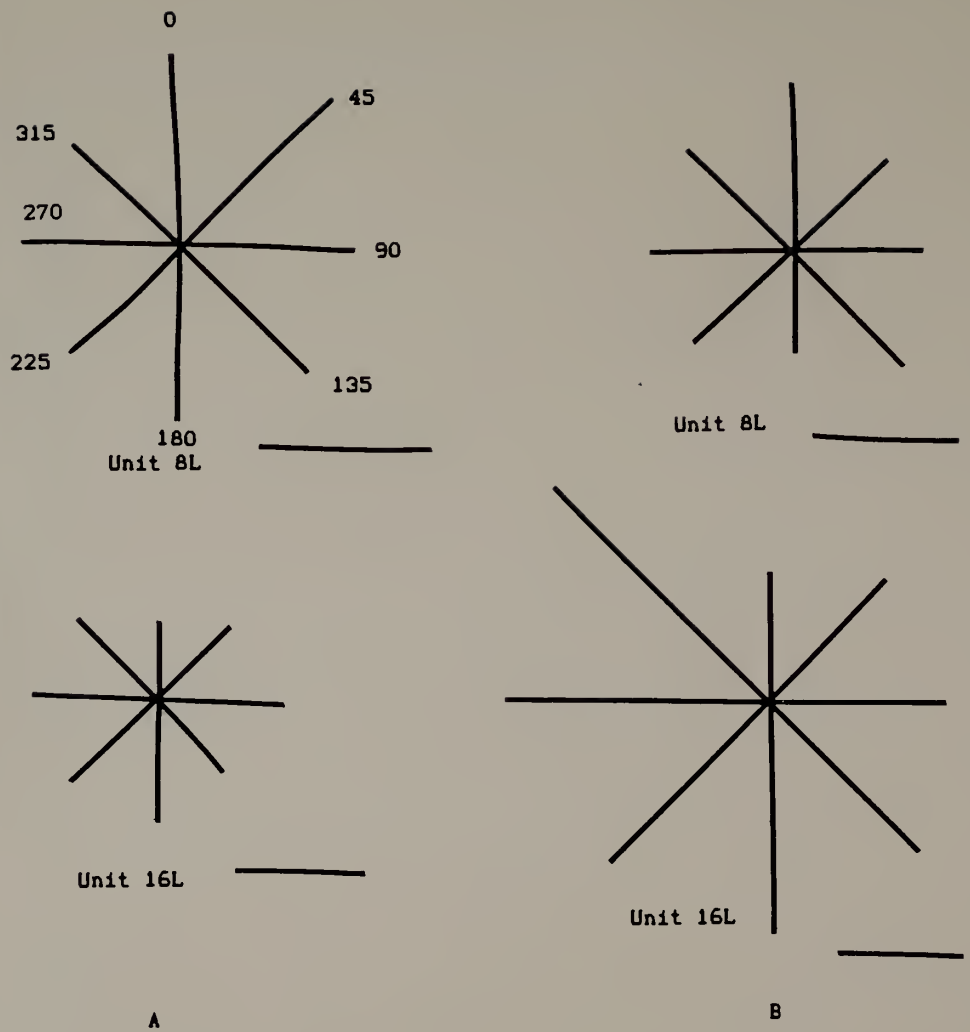
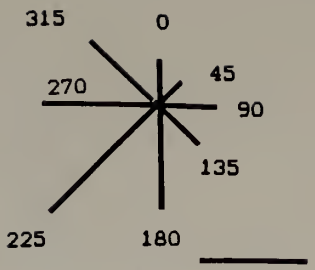
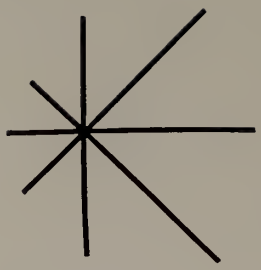


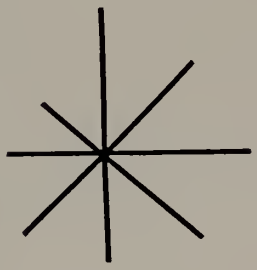
Figure 3. A Comparison of Unit Responses: A) Binocular vs. B) Monocular Stimulation of Same Unit (n=8) (1 cm= 10 spikes/10 sec., avg. unit response rate was measured over the 3 stimulus velocities, ——— = stationary pattern rate).



Unit 14R

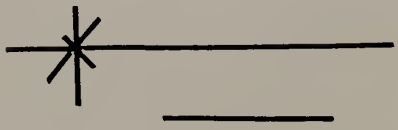


Unit 14R



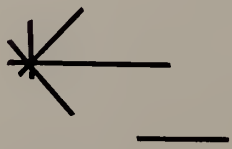
Unit 5R

Unit 5R



Unit 12L

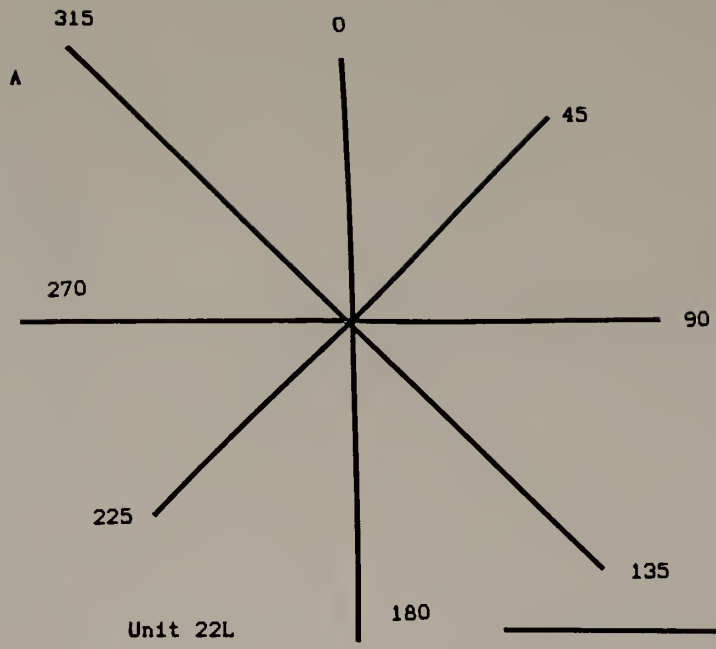
A



Unit 12L

B

Fig. 3 (cont'd)



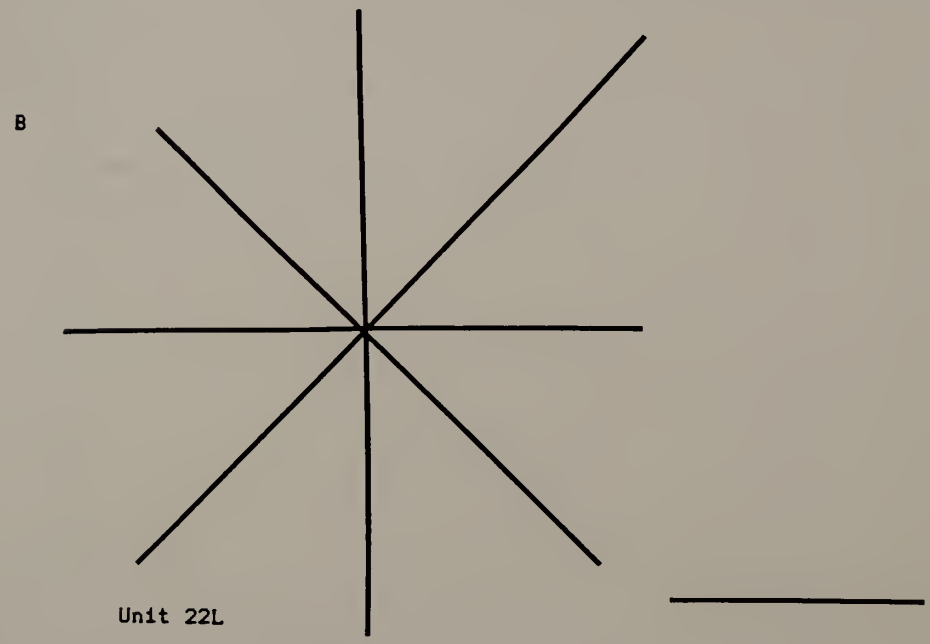
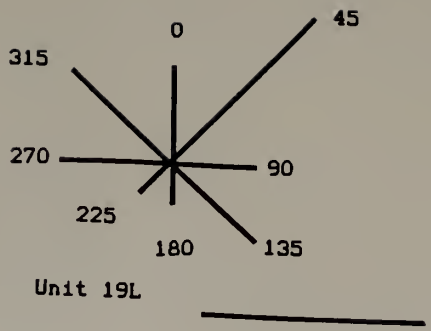
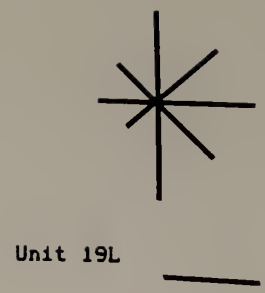
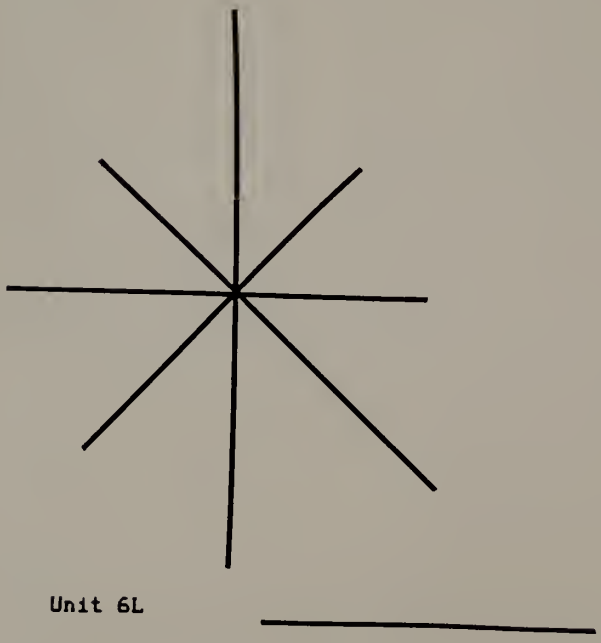


Fig. 3 (cont'd)







A

B

Fig. 3 (cont'd)

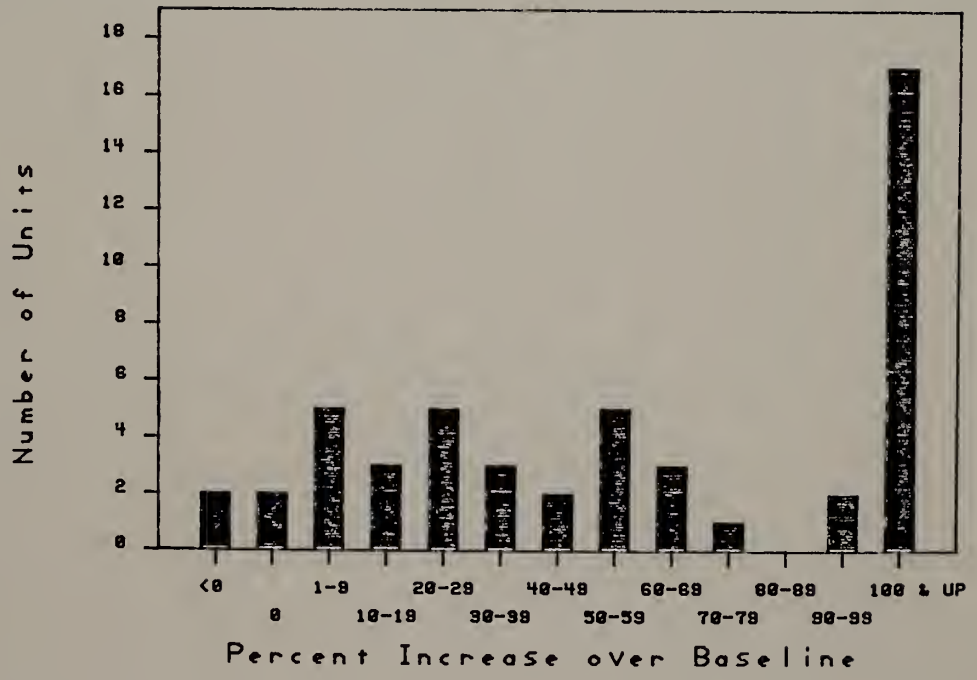


Figure 4. Response Rate Increases for Units Recorded Under Binocular Conditions.

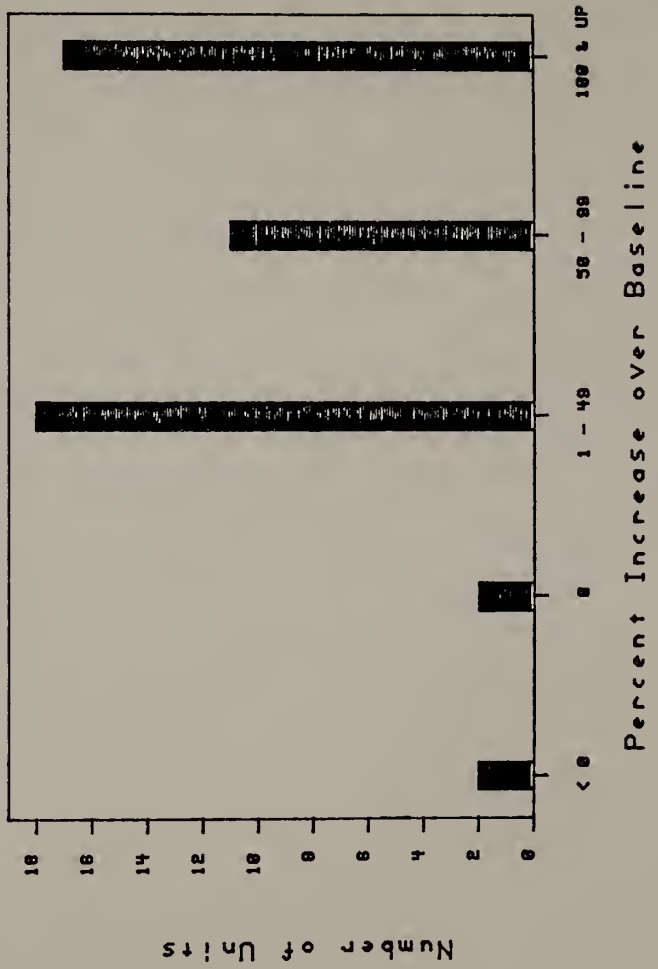

Number of Units
18
16
14
12
10
8
6
4
2
0
< 0
0
1 - 49
50 - 99
100 & UP
Percent Increase over Baseline

Fig. 4 (cont'd)

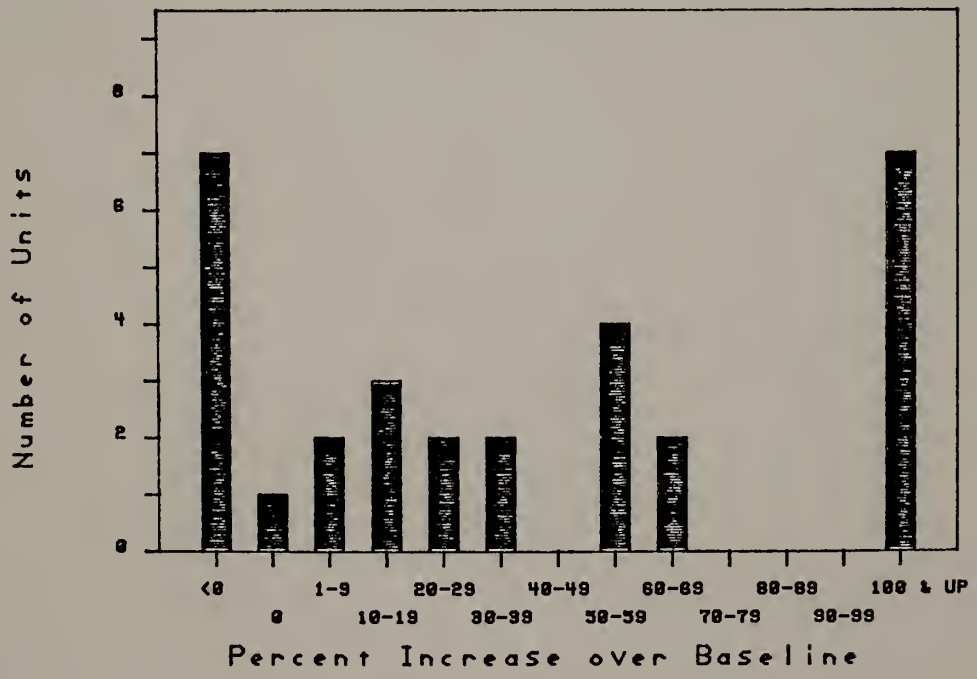


Figure 5. Response Rate Increases for Units Recorded Under Monocular Conditions.

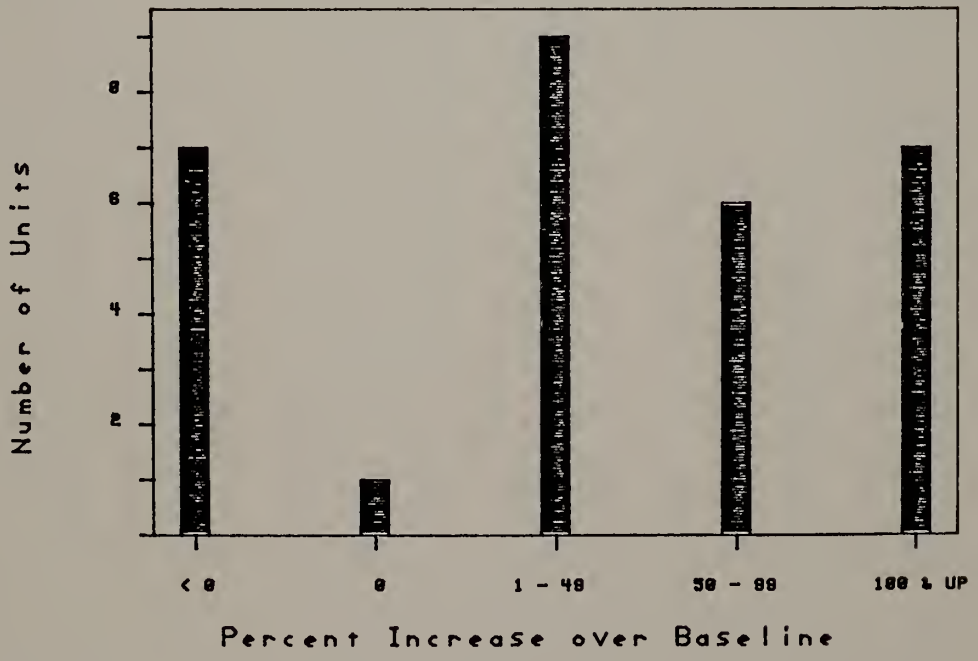

Number of Units
2
4
6
8
< 0
0
1 - 48
50 - 99
100 & UP
Percent Increase over Baseline

Fig. 5 (cont'd)

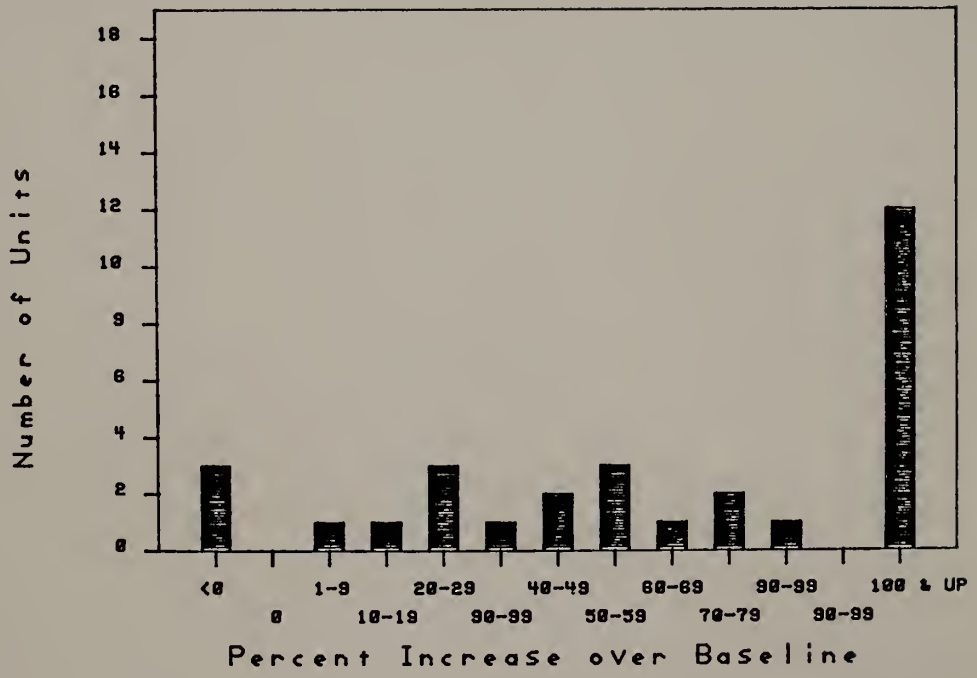


Figure 6. Response Rate Increases for Picrotoxin Units.

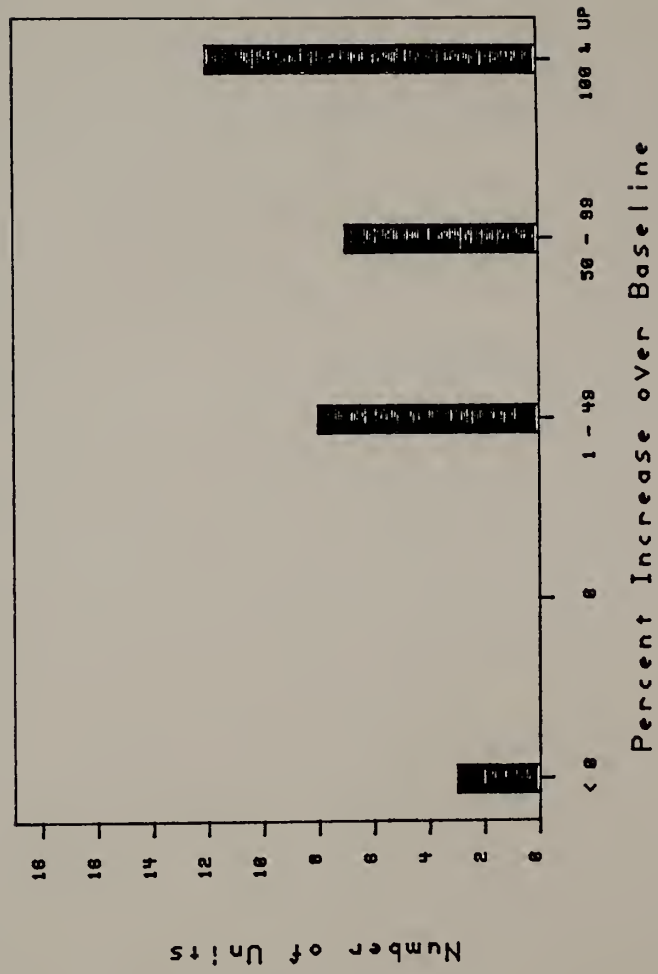
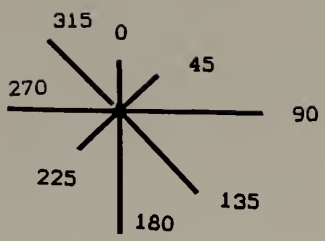
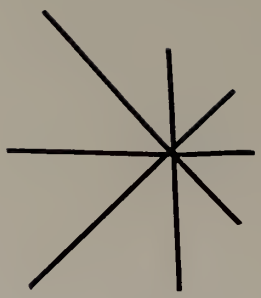

Number of Units
18
16
14
12
10
8
6
4
2
0
< 0
0
1 - 49
50 - 99
100 & UP
Percent Increase over Baseline

Fig. 6 (cont'd)



Unit 35L



Unit 35L

Unit 36L

Unit 36L

Unit 39L

A

Unit 39L

B

Figure 7. A Comparison of Unit Responses: A) Before and B)After Picrotoxin Injection (1 cm= 10 spikes/10 sec., avg. unit response rate was measured over the 3 stimulus velocities).

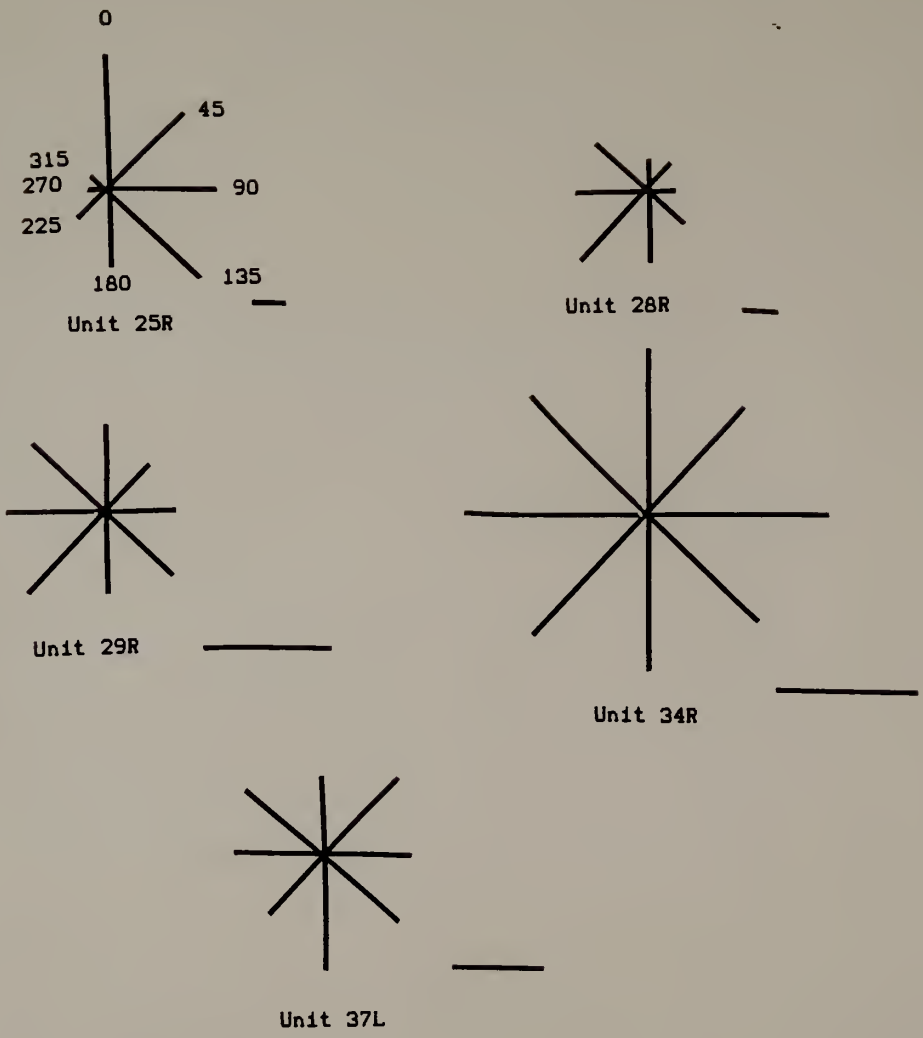
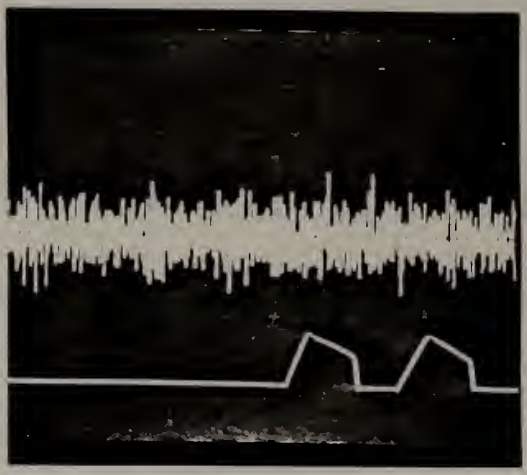


Figure 8. Rate of Responding for 5 Picrotoxin Cases (1 cm= 10 spikes/ 10 sec., avg. response rate was measured over the 3 stimulus velocities).



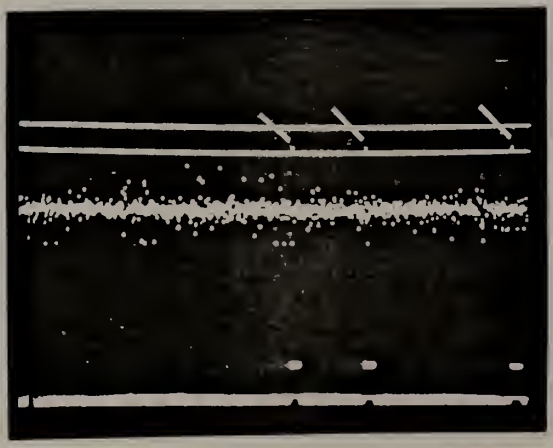
1

Figure 9. Unit Analysis from Oscilloscope: 1) Multi-Unit Data with Onset of Signal Marker, 2) Single unit Data- A) Control Data, B) Picrotoxin Data.

Window with Spike

Computer Representation of Spike

A



B

.5 mv

2 msec

Fig. 9 (cont'd) 2. Single Unit Data

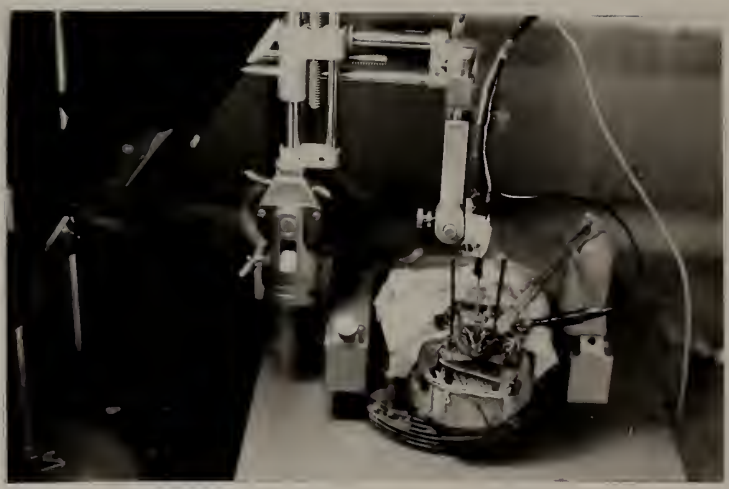


Figure 10. Frog in Stereotaxic Apparatus: Preparation for Picrotoxin Injection.

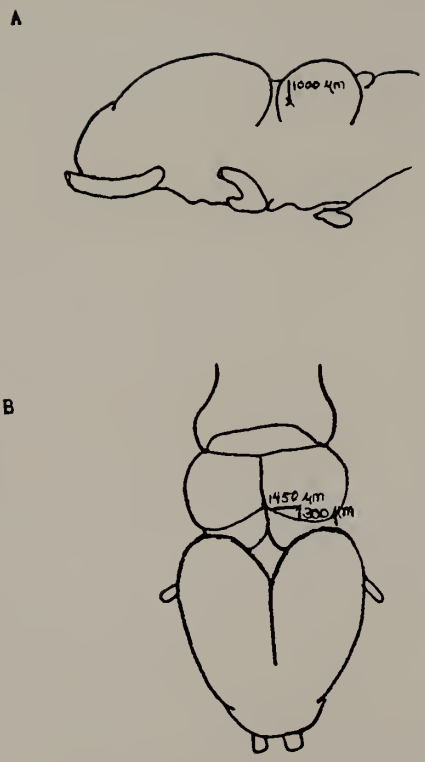


Figure 11. Diagrammatic Representation of nLM Recording Sites:
A) Lateral View, B) Dorsal View.

REFERENCES

Abols, I.A. and Basbaum, A.I. The posterior pretectal nucleus: evidence for a direct projection to the interior olive of the cat. Neurosci. Letters, 13, 1979, 111-116.

Baarsma, E.A. and Collewijn, H. Vestibulo-ocular and optokinetic reactions to rotation and their interaction in the rabbit. J. Physiol., 238, 1974, 603-625.

Bellonci, J. Uber die centrale Endiguing des nervus Opticus bei den Vertebraten. Zeitsch. F. Wissensch. Zool., B.d., 47, 1888, 51.

Benevento, L.A., Rezak, M. and Santos-Anderson, R. An autoradiography study of the projection of the pretectum in the rhesus monkey (Macaca mulatta): Evidence for sensorimotor links to the thalamus and oculomotor nuclei. Brain Res., 129, 1977, 197-218.

Berman, N. Connections of the pretectum in the cat. J. Comp. Neurol., 174, 1977, 227-254.

Birukow, G. Untersuchungen uber den optischen Drehnystagmus und uber die Sehscharfe des Grasfrosches (Rana temporaria). Z. Vergl. Physiol., 25, 1937, 92-142.

Bon, L., Corazza, R. and Inchingolo, P. Neuronal activity correlated with eye movement in cat's pretectum. Neurosci. Letters, 5, 1977, 69-74.

Bonaventure, N. and Wioland, N. Involvement of GABA in ganglion cell receptive field organization in the frog retina. Vis. Res., 21, 1981, 1653-1655.

Bonaventure, N. Wioland, N. and Bigenwald, J. Involvement of GABAergic mechanisms in the optokinetic nystagmus of the frog. Exp. Brain Res., 50, 1983, 433-441.

Brown, W.T. and Ingle, D. Receptive field changes produced in frog thalamic units by lesions of the optic tectum. Brain Res., 59, 1973, 402-409.

Brown, W.T. and Marks, W.B. Unit responses in the frog's caudal thalamus. Brain Behav. Evol., 14, 1977, 274-297.

Burkhardt, D.A. Effects of picrotoxin and strychnine upon electrical activity of the proximal retina. Brain Res. 43, 1972, 246-249.

Carpenter, H.R.S. Cerebellectomy and the transfer function of the vestibulo-ocular reflex in the decerebate cat. Proc. Roy. Soc., B, 181, 1972, 353-374.

Cochran, S.L., Precht, W. and Dierenger, N. Direction-selective neurons in the frog's visual system. Soc. Neurosci. Abstr., 6, 1980, 121.

Cochran, S.L., Dierenger, N. and Precht, W. Basic optokinetic-ocular reflex pathways in the frog. J. Neurosci. 4, 1984, 43-57.

Collewijn, H. Direction-selective units in the rabbit's nucleus of the optic tract. Brain Res. 100, 1975, 489-508.

Collewijn, H. Eye and head movements in freely moving rabbits. J. Physiol., 266, 1977, 471-498.

Collewijn, H. and Kleinschmidt, H.J. Vestibulo-ocular and optokinetic reactions in the rabbit: changes during 24 hours of normal and abnormal interaction. In Basic Mechanisms of Ocular Motility and their Clinical Interpretations, Lennerstrand, G. and Bach-y-Rita (Eds.), Pergamon Press, Oxford, 1975, 477-483.

Conley, M. and Fite, K.V. Optokinetic mystagmus in the domestic pigeon. Effects of foveal lesions. Brain Behav. Evol., 17, 1980, 89-102.

Daw, N.W. and Ariel, M. Effect of synaptic transmitter drugs on receptive fields of rabbit retinal ganglion cells. Vis. Res., 21, 1981, 1643-1647.

Dowben, R.M. and Rose, J.E. A metal filled microelectrode. Science, 118, 1953, 22.

Dubois, M.F.W. and Collewijn, H. The optokinetic reactions of the rabbit: relation to the visual streak. Vis. Res., 19, 1979, 9-17.

Dufosse, M., Ito, M., Jastreboff, P.J. and Miyashita, Y.A. Neuronal correlate in rabbit's cerebellum to adaptive modification of the vestibulo-ocular reflex. Brain Res., 150, 1978, 611-616.

Ebbesson, S.O.E. and Meyer, D.L. The visual system of the guitar fish (Rhinobatos productus). Cell Tissue Res., 206, 1980. 243-250.

Erickson, R.G. and Barmack, N.H. A comparison of the horizontal and vertical optokinetic reflexes of the rabbit. Exp. Brain Res., 40, 1980, 448-456.

Ewert, J.P. Neural mechanisms of prey-catching and aviodance behavior in the toad (Bufo bufo L.). Brain Behav. Evol., 3, 1970, 36-56.

Ewert, J.P. Single unit response of the toad's (Bufo americanus) caudal thalamus to visual objects. Z. Vergl. Physiol., 74, 1971, 81-102.

Ewert, J.P. The visual system of the toad: Behavioral and physiological studies on a pattern recognition system. In The Amphibian Visual System, K.V. Fite (Ed.), 141-202. New York, Academic Press, 1976.

Ewert, J.P. and von Wietersheim, A. Pattern analysis by tectal and thalamus/pretectal nerve nets in the visual system of the toad (Bufo bufo L.). J. Comp. Physiol., 92, 1974a, 131-148.

Ewert, J.P. and von Wietersheim, A. Influence of thalamus/pretectal lesions on the response of tectal neurons to visual objects on the toad (Bufo bufo L.). J. Comp. Physiol., 92, 1974b, 149-160.

Ewert, J.P., Hock, F.J. and von Weitersheim, A. Thalamus, pretectum, tectum: retinal topography and physiological interactions in the toad (Bufo bufo L.). J. Comp. Physiol., 92, 1974, 343-356.

Fite, K.V., Carey, R.G. and Vicario, D. Visual neurons in frog anterior thalamus. Brain Res., 127, 1977, 283-290.

Fite, K.V., Montgomery, N., Wojcicki, C. and Bengston, L. Visuomotor correlates of the anuran accessory optic system. Soc. Neurosci. Abstr., 6:839, 1980.

Fite, K.V., Reiner, A. and Hunt, S.P. Optokinetic nystagmus and the accessory optic system of the pigeon and turtle. Brain Beh. Evol., 16, 1979, 192-202.

Fite, K.V. and Scalia, F. Central visual pathways in the frog. In The Amphibian Visual System, K.V. Fite (Ed.), 87-118. New York, Academic Press, 1976.

Finkenstadt, Th. Disinhibition of prey-catching in the salamander following thalamic-pretectal lesions. Naturwissenschaften, 67, 1980, 471.

Fukuda, T. The unidirectionality of the labrynthine reflex in relation to the unidirectionality of the optokinetic reflex. Acta Oto. Laryngol., 50, 1959, 507-516.

Fukuda, T. and Tokita, T. Uber die Bezeihung der Richtung der optischen Reize zu den Reflextypen der Augen- und Skelett-muskeln. Acta Oto. Laryngol., 48, 1957, 415-424.

Gaillard, F. and Galand, G. Diencephalic binocular wide field neurons in the frog. Exp. Brain Res., 34, 1979, 511-520.

Galifret, Y. Les diverses aires fonctionelles de la retine du pigeon. Z. Zellforsch, 86, 1968, 535-545.

Gioanni, H., Rey, J., Villalobos, J., Bouyer, J. and Gioanni, Y. Optokinetic nystagmus in the pigeon (Columba livia). I. Study in monocular and binocular vision. Exp. Brain Res., 44, 1981, 362-370.

Gioanni, H., Rey, J., Villalobos, J., Richard, D. and Dalbera, A. Optokinetic nystagmus in the pigeon (Columba livia). II. Role of the pretectal nucleus of the accessory optic system (AOS). Exp. Brain Res., 50, 1983, 237-247.

Glickman, R.D., Adolph, A.R. and Dowling, J.E. Inner plexiform

circuits in the carp retina: effects of cholinergic agonists, GABA and Substance P on the ganglion cells. Brain Res., 234, 1982, 81-99.

Grahm, J. and Berman, N. Origins of the pretectal and tectal projections to the central lateral nucleus in the cat. Neurosci. Letters, 26, 1981, 209-214.

Grigonis, A. Neurobiological investigation of the pretectal region of the leopard frog, Rana pipiens. Doctor of Philosphy Dissertation, Psychology, Univ. of Massachusetts, Amherst, Ma., 1982.

Grover, B.G. and Sharma, S.C. Organization of extrinsic tectal connections in goldfish (Carassius auratus). J. Comp.Neurol., 196, 1981, 471-478.

Grusser, O.J., Pause, M. and Schreiter, U. Three methods to elicit sigma-optokinetic nystagmus in Java monkeys. Exp. Brain Res., 35, 1979, 519-526.

Grusser, O.J., Grusser-Cornehls. Neurophysiology of the anuran visual system. Frog Neurobiology, Llinas, R. and Precht, W. (Eds.), Springer Verlag, 1976, 297-385.

Hayes, W.N. and Ireland, L.C. A study of visual orientation mechanisms in turtles and guinea pigs. Brain Behav. Evol., 5, 1972, 226-239.

Harris, L.R., Lepore, F., Guillemot, J.P. and Cynader, M. Abolition of optokinetic nystagmus in the cat. Science, 210, 1980, 91-92.

Hepp, K., Henn, V. and Jaeger, J. Eye movement related neurons in

the cerebral nuclei of the alert monkey. Exp. Brain Res., 45, 1982, 253-264.

Herrick, C.J. The amphibian forebrain. III. The optic tracts and centers of amblystoma and the frog. J. Comp. Neurol., 39, 1925, 433-489.

Hertzler, D.R. and Hayes, W.N. Cortical and tectal function in visually guided behavior of turtles. J. Comp. Physiol. Psych., 63, 1967, 444-517.

Hodos, W. and Bonbright, J.C. Intensity and pattern discrimination after lesions of the pretectal complex, accessory optic nucleus and ventral geniculate in pigeons. J. Comp. Neurol., 161, 1975, 1-18.

Hoffmann, K.P. Naso-temporal vs. temporal-nasal OKN in the cat. Neurosci. Abstr. 7:23, 1981.

Hoffmann, K.P., Behrend, K. and Schoppmann, A. A direct afferent visual pathway from the nucleus of the optic tract to the inferior olive in the cat. Brain Res., 115, 1976, 150-153.

Hoffmann, K.P. and Schoppmann, A. A quantitative analysis of the direction-specific response of neurons in the cat's nucleus of the optic tract. Exp. Brain Res., 42, 1981, 146-157.

Ingle, D. Some effects of pretectum lesions on the frog's detection of stationary objects. Behav. Brain Res., 1, 1980, 139-163.

Itoh, K. Efferent projections of the pretectum in the cat. Exp. Brain Res., 30, 1977, 89-106.

Kanaseki, T. and Sprague, J.M. Anatomical organization of pretectal

nuclei and tectal laminae in the cat. J. Comp. Neurol., 158, 1974, 319-338.

Karten, H.J. and Brecha, N. Localization of neuroactive substances in the vertebrate retina: evidence for lamination in the inner plexiform layer. Vis. Res., 23, 1983, 1197-1205.

Katte, O. and Hoffmann, K.P. Direction specific neurons in the pretectum of the frog (Rana esculenta). J. Comp. Physiol., 140, 1980, 53-57.

Kicliter, E. Flux, wavelength, and movement discrimination in frogs: forebrain and midbrain contributions. Brain Behav. Evol., 8, 1973, 340-365.

Kirby, A.W. and Enroth-Cugell, C. The involvement if gamma-aminobutyric acid in the organization of cat retinal ganglion cell recetive fields. J. Gen. Physiol., 68, 1976, 465-484.

Lazar, Gy. and Szekely, Gy. Distribution of optic terminals in the different optic centers of the frog. Brain Res., 16, 1969, 1-14.

Lazar, G. Role of the accessory optic system in the optokinetic nystagmus of the frog. Brain Behav. Evol., 5, 1973, 443-460.

Legg, C.R. Do pretectal lesions impair visual discrimination acquisition in rats? Physiol. Behav. 18, 1977, 781-786.

Levine, R.L. An autoradiography study of the retinal projection in Xenopus laevis with comparisons to Rana. J. Comp. Neurol., 189, 1980, 1-29.

McKenna, O. and Wallman, J. Metabolic mapping of avian brain areas responsive to retinal slip. Soc. Neurosci. Abstr. 6:840, 1980.

Maekawa, K. and Kimura, M. Electrophysiological study of the nucleus

of the optic tract that transfers optic signals to the nucleus reticularis tegmenti pontis- the visual mossy fiber pathway to the cerebellar flocculus. Brain Res., 211, 1981, 456-462.

Manteuffel, G. Electrophysiology and anatomy of direction-specific pretectal units in Salamandra salamandra. Exp. Brain Res., 54, 1984, 415,525.

Manteuffel, G. Petersen, J. and Himstedt, W. Optic nystagmus and nystagmogen in the european fire salamander (Salamandra salamandra). Zool. Jb. Physiol., 87, 1983, 113-125.

Miles, F.A. and Fuller, J.H. Adaptive plasticity in the vestibulo-ocular responses in the rhesus monkey. Brain Res. 80, 1974, 516.

Montarolo, P.G. Precht, W. and Strata, P. Functional organization of the mechanisms subserving the optokinetic nystagmus in the cat. Neurosci., 6, 1981, 231-246.

Montgomery, N., Fite, K.V. and Bengston, L. The accessory optic system of Rana pipiens: Neuroanatomical connections and intrinsic organization. J. Comp. Neurol., 302, 1981, 595-612.

Montgomery, N., Fite, K.V., Taylor, M. and Bengston, L. Neural correlates of optokietic nystagmus in the mesencephalon of Rana pipiens: A functional analysis. Brain Behav. Evol., 21, 1982, 137-150.

Montgomery, N., Fite, K.V. and Grigonis, A.M. The pretectal nucleus (Lentiformis Mesencephali) of Rana pipiens. J. Comp. Neurol., 234, 1985, 264-275.

Neverov, V.P., Sterc, J. and Bures, J. Electrophysiological

correlates of the reversed postoptokinetic nystagmus in the rabbit: Activity of vestibular and floccular neurons. Brain Res., 189, 1980, 355-367.

Oyster, C.W. and Barlow, H.B. Direction-selective units in rabbit retina: distribution of preferred directions. Science, 155, 1967, 841-842.

Pasik, P. and Pasik, T. Oculomotor functions in monkeys with lesions of the cerebrum and superior colliculi. The Oculomotor System. Harper and Row, New York, 1964.

Pasik, T. and Pasik, P. Optokinetic nystagmus. An unlearned response altered by section of chiasma and corpus callosum in monkeys. Nature, 203, 1964, 609-611.

Pasik, T., Pasik, P. and Bender, M.B. The pretectal syndrome in monkeys: II. Spontaneous and induced nystagmus and "lighting" eye movement. Brain, 92, 1977, 871-884.

Reperant, J., Rio, J.P. and Amouzou, M. Radiographic analysis of the retinofugal pathways in the primitive bony fish, Polypterus senegalus, C.R. Hegd. Seances. Acad. Sci. Ser. D. Sci. Nat., 289, 1979, 947-950.

Robertson, R.T., Kaitz, S.S. and Robards, M.J. A subcortical pathway links sensory and limbic systems of the forebrain. Neurosci. Letters, 17, 1980, 161-166.

Rubinson, K. Projections of the tectum opticum of the frog. Brain Behav. Evol., 1,1968, 529-561.

Scalia, F. and Gregory, K. Retinofugal projections in the frog:

Location of the postsynaptic neurons. Brain Behav. Evol., 3, 1970, 16-29.

Scalia, F. and Fite, K.V. A retinoscopic analysis of the central connections of the optic nerve in the frog. J. Comp. Neurol., 158, 1974, 455-478.

Scalia, F. The optic pathway of the frog: Nuclear organization and connections. In Frog Neurobiology, Llinas, R. and Precht, W. (Eds.), Springer Verlag, 1976, 394.

Scalia, F. and Arango, V. Topographic organization of the projections of the retina to the pretectal region in the rat. J. Comp. Neurol., 186, 1979, 271-292.

Schoppmann, A. and Hoffmann, K.P. A comparison of visual responses in two pretectal nuclei and in the superior colliculus of the cat. Exp. Brain Res., 35, 1979, 495-510.

Simpson, J.I., Soodak, R.E. and Hess, R. The accessory optic system and its relation to the vestibulo-cerebellum. In Reflex Control of Posture and Movement. Granit, R. and Pompeiano, O. (Eds.), Progress in Brain Research, 50, 1979, Elsevier, North Holland.

Thoden, V., Dichgans, J. Doerr, M. and Savides, T. Direction specific vestibular and visual modulation of fore- and hind limb reflexes in cats. In Reflex Control of Posture and Movement. Granit, R. and Pompeiano, O. (Eds.), Progress in Brain Research, 50, 1979, 211-218.

Van Hof-Van Duin, J. Direction preference of optokinetic responses in monocularly tested normal kittens and light deprived cats. Arch. Ital. Biol., 116, 1978, 471-477.

Vesselkin, N.P., Agayan, A.L. and Nomokonova, L.M. A study of thalamo-telencephalic afferent systems in frogs. Brain Behav. Evol., 4, 1971, 295-306.

von Wietersheim, A. and Ewert, J.P. Neurons of the toad's (Bufo bufo L.) visual system sensitive to moving configurational stimuli: A statistical analysis. J. Comp. Physiol., 126, 1978, 35-42.

Weber, J.T. and Harting, J.K. The efferent projections of the pretectal complex: An autoradiographic and horseradish peroxidase analysis. Brain Res., 194, 1980, 1-28.

Wilczynski, W. and Northcutt, R.G. Afferents to the optic tectum of the leopard frog: An HRP study. J. Comp. Neurol., 173, 1977, 219-230.