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An electrophysiological study of the primary retinal fibers of the retino-tectal and retino-thalamo-cortical visual systems of the frog, rana pipiens

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AN ELECTROPHYSIOLOGICAL STUDY OF THE PRIMARY RETINAL FIBERS OF THE RETINO-TECTAL AND RETINO-THALAMO-CORTICAL VISUAL SYSTEMS OF THE FROG, RANA PIPIENS

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ABSTRACT

An electrophysiological study was made of the primary retinal projections in the retino-tectal and retino-thalamo-cortical visual system of the frog (Rana pipiens). In twenty-two medium sized frogs, response latencies to photic and optic nerve stimulation were recorded from various depths and areas of the tectal and forebrain structures.

The data obtained from optic nerve stimulation indicated that the optic fibers (i.e. fast and slow components) are trimodally distributed in the surface layers of the contralateral tectum. Also, the high frequency with which fiber responses were recorded in the anterior region of the tectum, suggested that the anterior tectal region receives the majority of afferent retinal fibers. In addition, the direction in which most of the responses recorded in the contralateral tectum were distributed, suggested that the afferent retinal fibers entered anteriorally and projected longitudinally, along the surface of the tectal lobe.

The fact that little electrophysiological data were obtained from the ipsilateral tectum, and none from the forebrain areas, indicated that the major retinal pathways to these visual structures were probably polysynaptic. Also, because of the short latencies of the few ipsilateral responses obtained, it was thought that possibly these responses came from small direct retinal projections.

Data from the photic stimulation experiments were not obtained

readily. The reason for the low percentage of success may be partly the result of the anesthetic that was used in the study.

AN ELECTROPHYSIOLOGICAL STUDY OF THE PRIMARY RETINAL FIBERS OF THE RETINO-TECTAL AND RETINO-THALAMO-CORTICAL VISUAL SYSTEMS OF THE FROG, *RANA PIPIENS*

by

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CBL	Cerebellum
Ch	Contralateral hippocampus
C. lat. gen.	Lateral geniculate body
Ct or ct	Contralateral tectum
Fore	Forebrain
Ih	Ipsilateral hippocampus
It	Ipsilateral tectum
LOT	Lateral optic tract
MOT	Medial optic Tract
nuc Bell	Nucleus of Bellonci
nuc pret.	Pretectal nucleus
OB	Olfactory bulb
ON	Optic nerve
op. ch.	Optic chiasma
OT	Optic tract
P or P. Pyr	Pallial cortex or pallium pyriform
PH	Primordium hippocampus
Tec	Tectum
Thal	Thalamus

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An electrophysiological study was made of the primary retinal projections in the retino-tectal and retino-thalamo-cortical visual system of the frog (Rana pipiens). In twenty-two medium sized frogs, response latencies to photic and optic nerve stimulation were recorded from various depths and areas of the tectal and forebrain structures.

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Data from the photic stimulation experiments were not obtained

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INTRODUCTION

The following experiment is an electrophysiological study of the primary retinal projections in the retino-tectal and retino-thalamo-cortical systems of the frog (figure 1).

After crossing at the optic chiasma, the majority of the optic tract fibers (i.e. marginal tract) in the amphibian are found to project along the surface of the diencephalon to the broad antero-ventral rim of the contralateral tectum. At that point, the optic tract divides into two smaller tracts which branch out and travel along the medial and lateral perimeter of the tectum (Herrick, 1925, Amblystoma; Mat urana, Lettvin, McCulloch, and Pitts, 1960, frog; Potter, 1969, bullfrog) (figure 2). Due to the optic ventricle that is located beneath the tectal layers, it has been hypothesized (Potter, 1969) that all afferent and efferent fibers must enter and exit from the tectum along the tectal perimeter. Moreover, the parallel and longitudinal manner in which the retinofugal fibers have been observed to project across the tectal surface, (and terminate at different points in the various fiber layers) (Herrick, 1925; Lazar and Szekely, 1967; Potter, 1969), and the high degree of fiber density that has been found in the anterior region of the tectum, have suggested that the principal site of fiber entry is along the tectum's anteroventral rim (Potter, 1969). However, some histological findings have not been in agreement with this contention (Scalia, Knapp, Halpern and Riss, 1968). These investigators found no evidence of retinofugal fibers being present

FIGURE 1. BLOCK DIAGRAM OF RETINOTECTAL AND RETINO-THALAMO-CORTICAL VISUAL SYSTEMS IN THE FROG.

The arrows represent the two areas of the frog brain in which retinal fibers project after crossing the optic chiasma. The larger arrow represents the major group of optic fibers projecting to the posterior diencephalon (i.e. thalamus) and contralateral tectum. The smaller arrow represents the small group of optic fibers terminating in the dorsal thalamus.

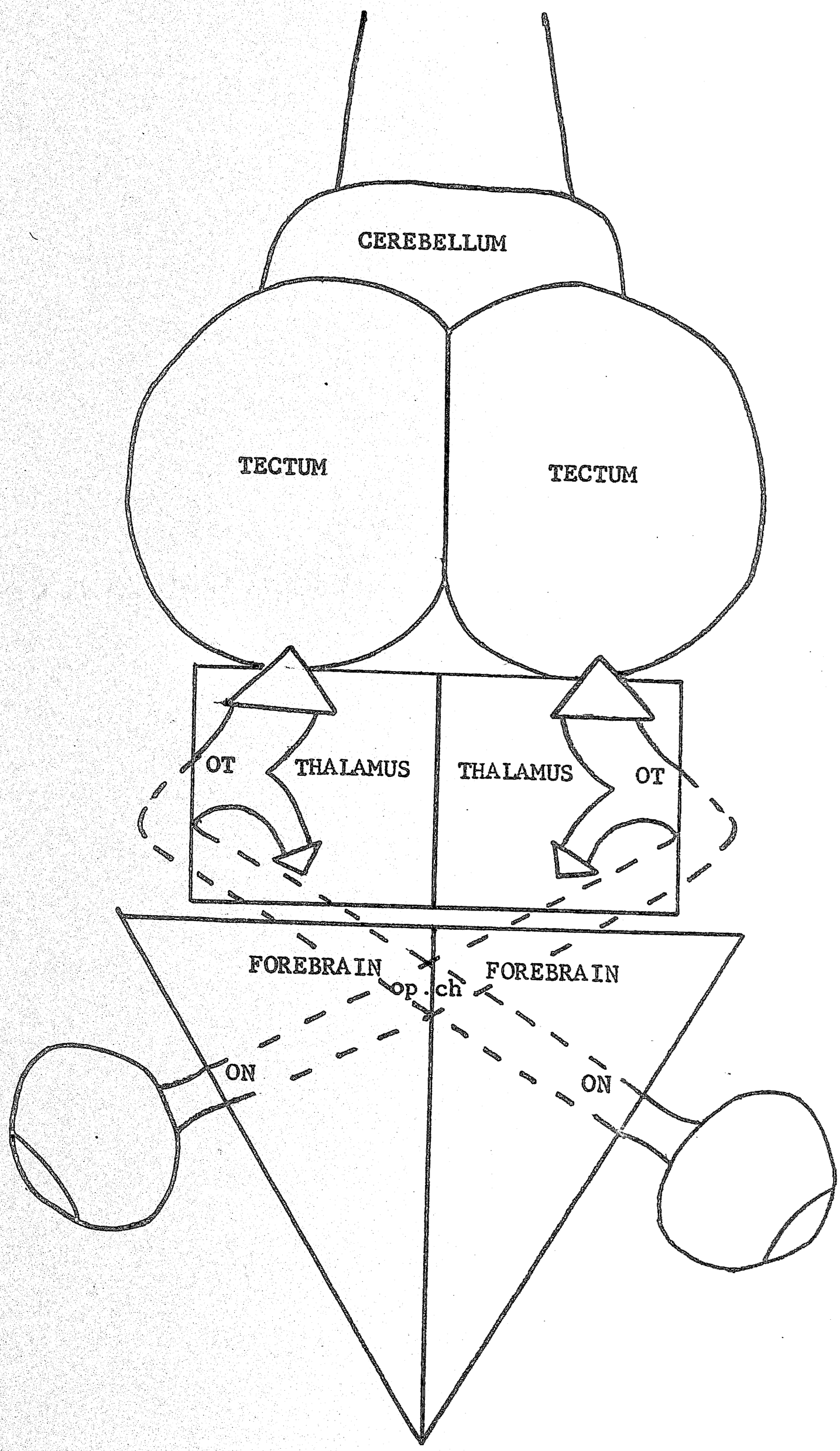
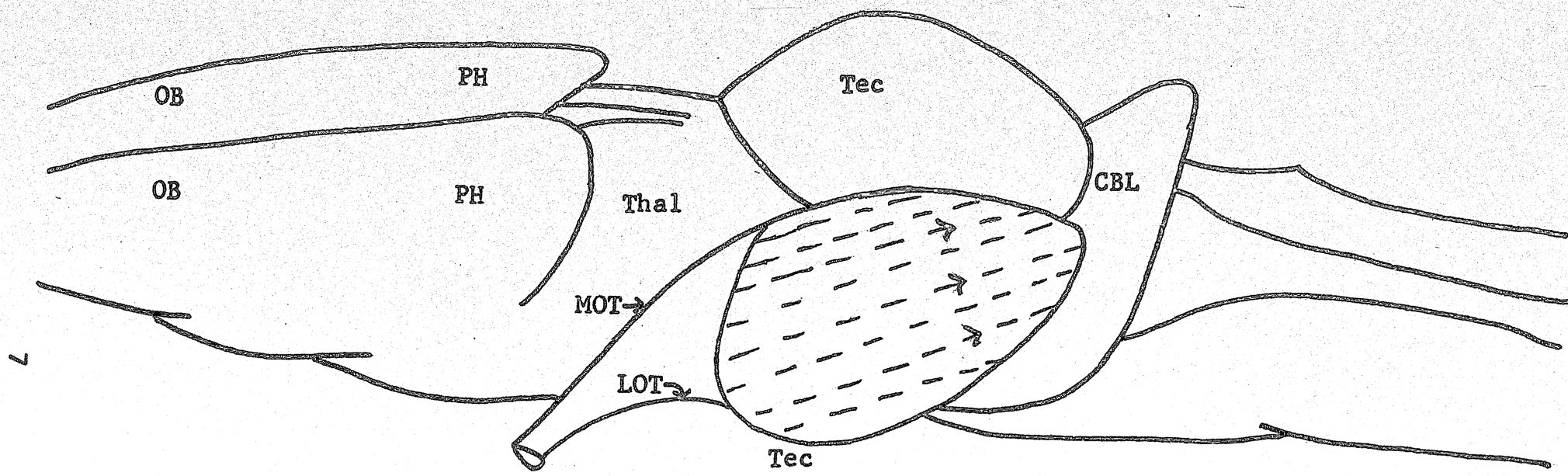

CEREBELLUM
TECTUM
TECTUM
OT
THALAMUS
THALAMUS
OT
FOREBRAIN
op.ch
FOREBRAIN
ON
ON

FIGURE 2. MEDIAL AND LATERAL OPTIC TRACTS IN THE BULLFROG

Dorso-lateral view of the bullfrog's brain showing the division of the ascending optic tract into a medial optic tract (MOT) and a lateral optic tract (LOT). Arrows indicate the direction in which retinal fibers enter and project across the surface of the contralateral tectum. (Adapted from Potter, 1969.)


OB
PH
Tec
OB
PH
Thal
CBL
MOT
LOT
Tec

in the superficial layer of the anteroventral tectum. But it is not clear whether this fiber free band was primarily lateral or medial. In addition, there were differences in the species of frogs that were used in the studies by Lazar and Szekely (Rana esculenta), Potter (Rana catesbeiana), and Scalia et al. (Rana pipiens).

Phylogenetically, the retino-tectal system in the vertebrate is an ancient system with its greatest representation of anatomical dominance in the submammalian vertebrate, particularly, in the frog and reptile (Karamian, Vesselkin, Belekhova, Zagorulko, 1966; Nauta and Karten, 1970). In the lower order amphibian, Necturus, the underdeveloped optic tract fibers do not reach the extreme posterior tectum (Herrick, 1933). Moreover, the poorly differentiated tectum of the Necturus (i.e. lacking nerve cell groups and fiber systems) was observed to be innervated by other sensory systems (eg. gustatory, olfactory, visceral) and to have efferents connected to the higher (thalamus, hypothalamus) and lower (tegmentum, medulla, cerebellum) brain structures. In the Amblystoma (an amphibian which is between the lower order Necturus and higher order Rana), the tectum is found to be larger and more differentiated in tectal organization. The optic fibers extend into the caudal tectum, but are found to share terminal loci with other sensory afferents. Thus, it is thought (Herrick, 1925, 1933) that the tectum in the lower amphibian is involved, primarily, in gross bodily reactions (i.e. reflexes) to external stimuli.

In the Rana (i.e. frog), however, the optic tectum is the principal structure for the integration of visual information (Cajal, 1911;

Herrick, 1925; Gaze, 1958; Maturana et al., 1960). It is homologous to the superior colliculus in the visual system of mammalian vertebrates (Lettvin, Maturana, McCulloch, and Pitts, 1959).

In general, the optic tectum is a multilayered structure as was illustrated in an early study by Cajal (1911) (figure 3). However, only the inner eight layers could be identified clearly.

The scheme of stratification described in this paper is based primarily on the findings of Scalia et al. (1966) in the frog (Rana pipiens) and Potter (1969) in the bullfrog (Rana catesbeiana) (figure 4a).

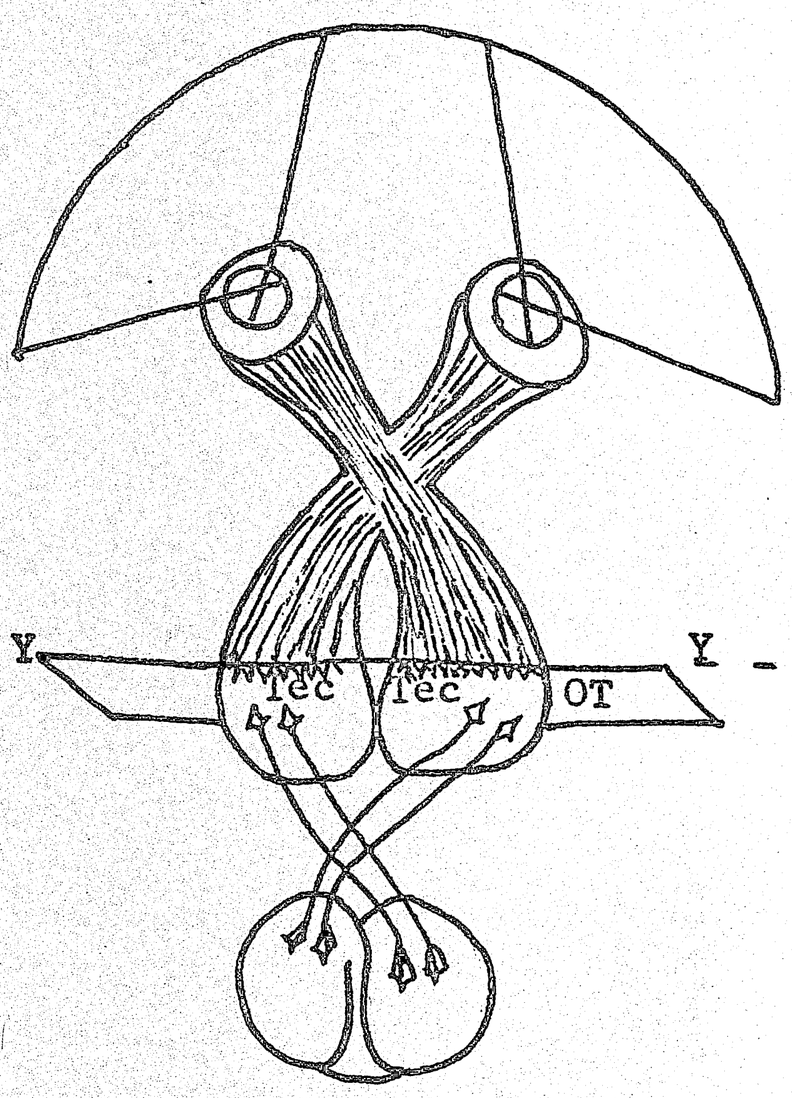
The tectum consists of two principal zones, the superficial zone which consists of layers of optic fibers and some tectal neurons, and a deep zone of tectal cells (stratum periventriculare, Potter, 1969). The fiber and cellular zones are separated by an intermediate fiber system, the stratum album centrale, an efferent pathway for tectal neurons which runs in a direction perpendicular to the fibers in a superficial neuropil (i.e. zone) (Lazar and Szekely, 1967; Potter, 1969).

The superficial neuropil (which is approximately 220u to 250u in thickness, Maturana et al., 1960; Lazar and Szekely, 1967) (figure 4b, c) is located immediately beneath the pial surface and is made up of three distinct strata (stratum opticum, stratum fibroseum et griseum superficiale, and stratum griseum centrale, Scalia et al., 1968) (figure 4a). These afferent strata of fibers were found to be in register with the retinal operations reported by Maturana et al. (1960) (figure 4b). (These findings will be discussed in more detail later in this section.)

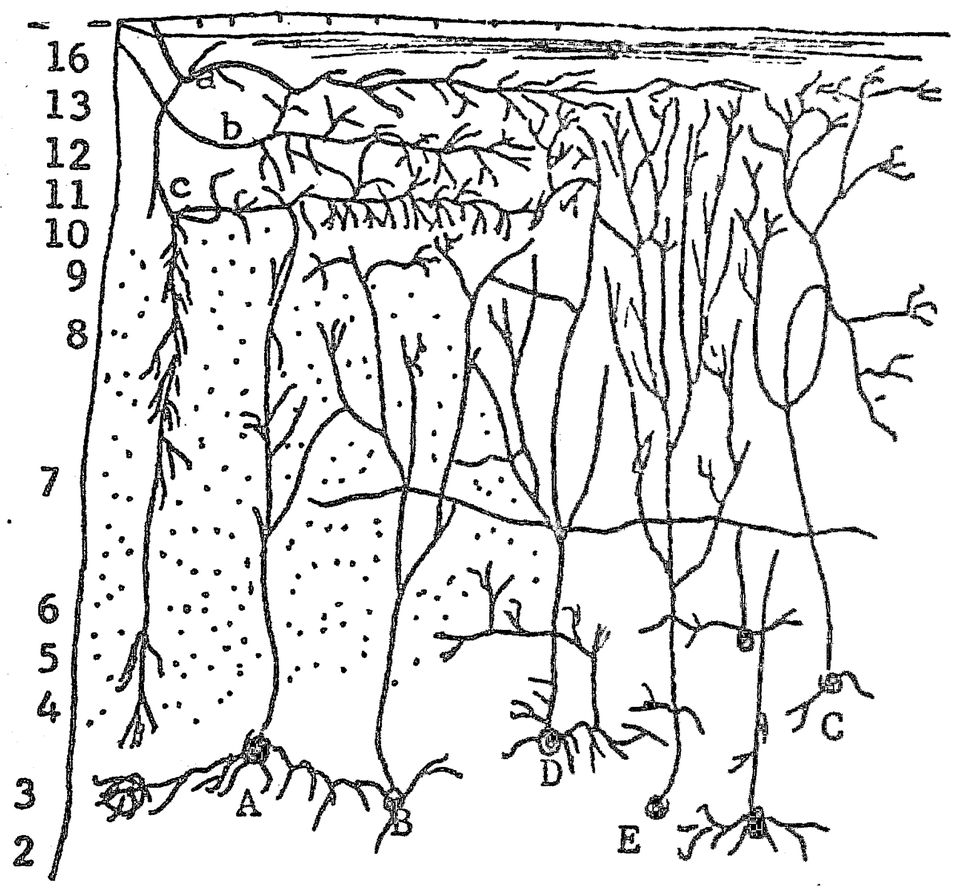
FIGURE 3. CAJAL'S ILLUSTRATION OF TECTAL ORGANIZATION IN THE FROG

a. Ramon y Cajal's (1911) illustration of retinal fibers decussating completely to the surface of the contralateral tectum (tec).

b. This diagram represents a cross-section of the multilayered tectum of the frog as conceived by Cajal (1911). Numerals to the left correspond to the layers of optic fibers (8-14) and cells (2-6). Layer 7 is the pathway of efferent fibers from the various layers of tectal cells. The layers of optic terminals are indicated by the letters a, b, and c. Some examples of tectal cells are labelled in capital letters. (Note, layers 8-16 were not identified clearly by Cajal.)



a



b

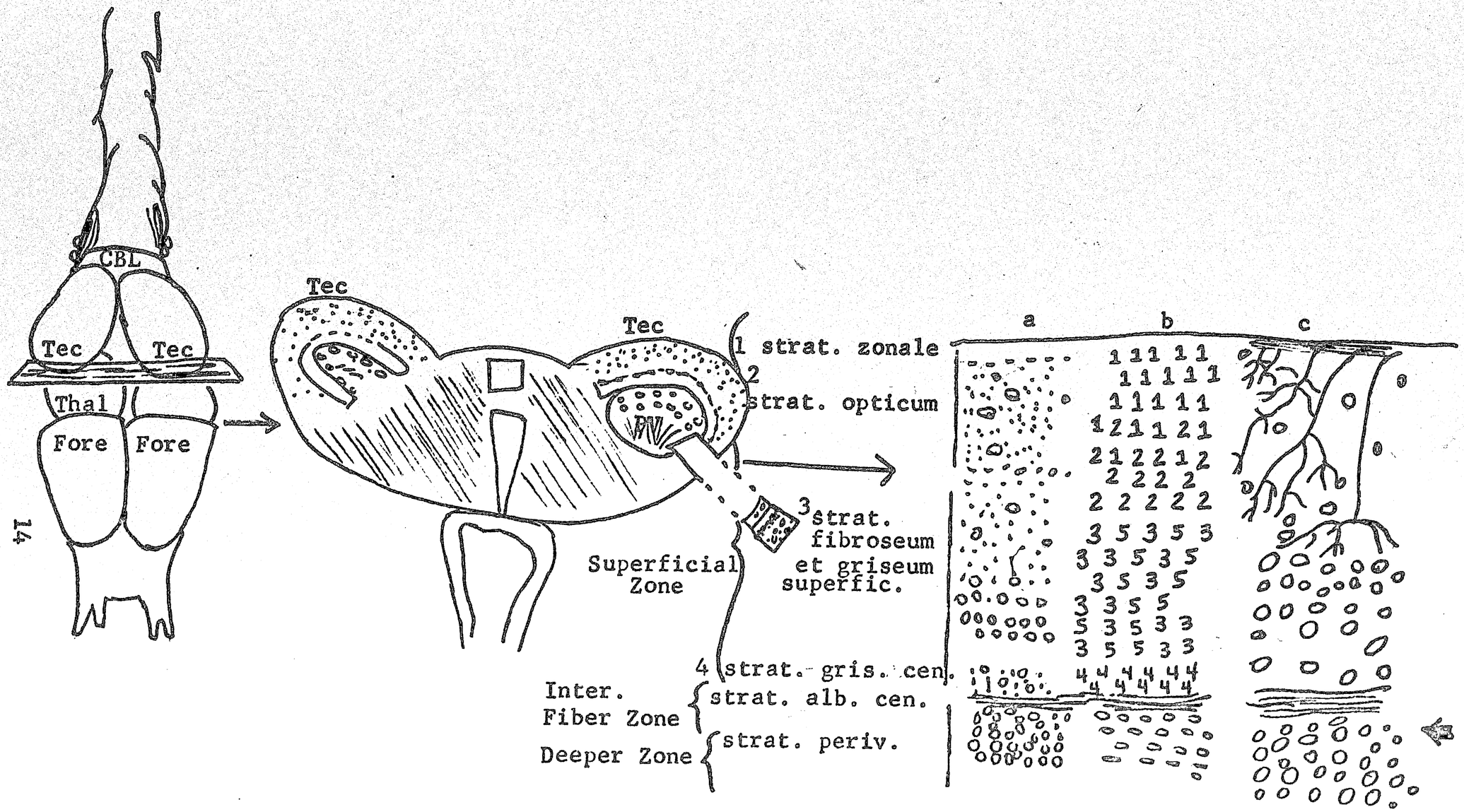
FIGURE 4. TECTAL ORGANIZATION IN THE FROG

a. The cross-section of the tectum shown in this figure represents a view of tectal stratification after a coronal cut was made in the anterior region of the tectum. In the superficial zone, there are four strata, three of which are made up of the terminals from optic fibers. (1)Stratum zonale is the most superficial stratum in the tectum, it is fiber free. (2) Stratum opticum consists of many small myelinated and unmyelinated fibers (represented by small dots) and some tectal cells. This layer of fibers extends down to the outer part of (3) the stratum fibroseum et griseum superficiale. This stratum is made up of larger myelinated fibers (larger dots). Between stratum 3 and 4 there are no optic fibers. Along the outer border of stratum album centrale is a band of large myelinated fibers making up stratum 4, stratum griseum centrale. Stratum album centrale, efferent pathway for tectal axons, separates the superficial zone from the deeper zone of tectal cells (stratum periventriculare).

b. Numerals in this figure represent the five retinal operations (see text) that were recorded by Maturana et al.(1960) from the various tectal layers. The number of times that each operations was represented was arbitrary. It can be seen that the slowest (i.e. small fibers) conducting opera-

tions were in the surface fiber layers and the fastest (large fibers) conducting operations were in the deepest fiber layers. Also, there was an interval of electrophysiological silence between operations three and four. These strata of physiological operation were in register with 4a.

c. Schemata of the optic fibers descending from various points along the tectal surface and terminating in different strata of the tectum, reported by Lazar and Szekely (1967). Open circles represent tectal cells in the fiber layers, as well as in the deeper stratum periventriculare. The largest number of tectal cells are located approximately 400u below the tectal surface (see arrow in figure). (Adapted from Scalia et al., 1968.)


CBL
Tec
Tec
Tec
Thal
Fore
Fore
14
Tec
Tec
1 strat. zonale
2
strat. opticum
3 strat. fibroseum et griseum superfic.
Superficial Zone
4 strat. gris. cen.
Inter. Fiber Zone
strat. alb. cen.
Deeper Zone
strat. periv.
a
b
c

The stratum zonale, the most superficial tectal stratum is fiber free. Its broad edge which is along the anteroventral rim of the tectum thins out significantly along the dorsal side of the tectal lobe. In contrast, the stratum opticum is packed densely with small myelinated and unmyelinated fibers that extend into the outer region of the next stratum. A broad zone of larger sized myelinated fibers are found throughout the inner layer of the stratum fibroseum et griseum superficiale, and also in the outer layer of the stratum griseum centrale. But, no fibers are found in the inner stratum griseum centrale which corresponds to the silent area (electrophysiologically) reported by Maturana et al. (1960) in the deeper fiber layers. Along the outer border of the stratum album centrale is a thin band of large myelinated fibers that make up the deepest layer of optic fibers.

Most of the estimated two hundred fifty thousand tectal cells have been located in the deeper layers of the tectum with their axon and dendritic processes extending vertically and laterally to the surface layers (Maturana et al., 1960; Lazar and Szekely, 1967; Potter, 1969). The tectal axons terminate in the surrounding layers or exit via the main efferent pathway (i.e. stratum album centrale). The largest number of tectal cells (212,000) have been reported to be in a densely packed cellular layer, approximately 400μ below the tectal surface (Lazar and Szekely, 1967)(fig 4c). Because of the vertical orientation in which tectal axons, dendrites, and

retinofugal fibers, were found in the surface layers of the tectum, Lazar and Szekely (1967) proposed that the frog's tectal organization was arranged in columns similar to that which was described to be characteristic of the visual cortex of cats (Hubel, Wiesel, 1959)

Most of the 450,000 optic nerve fibers (29,000 of which are myelinated, Polyak, 1957) in the frog have been found to make up many small unmyelinated fiber bundles (Maturana et al., 1960). Bishop (1933) identified three different fiber groups (A,B,C) in the optic nerve of the bullfrog, on the basis of differential conduction velocities. These velocities were directly related to the fiber diameter. The relative conduction speeds of the fast, A and B components, were found to be 16 and 3 meters per second (mps), respectively. The most representative fiber component in the optic nerve was the slow C fiber group (.5 mps) with a fiber population equal to approximately half that of the fast fibers.

In his electrophysiological study of the frog's retino-tectal visual system, Gaze (1958) found the retina and contralateral tectum to be in a point to point (i.e. receptor field to receptor field) relationship with each other, a phenomenon which has been observed in the visual system of higher mammalian vertebrates, (eg. in birds, cats, goats; Gaze, 1958). The optic fibers which emanated from the receptor fields in each of the four retinal quadrants of the eye (eg. the naso-inferior quadrant), were found to be projected to a particular region of the contralateral tectum (i.e. the posterior part of the optic lobe along the midline), producing a topographical

map of the retina.

Also, this retinotopographical representation was found to be present in the rostral part of the ipsilateral tectum (Gaze and Jacobson, 1962, 1962a; Fite, 1969). Binocularly driven visual responses, that were recorded from corresponding points in the anterior contralateral and ipsilateral tecta, were found to differ in latency by 20-40 (i.e. longer in the ipsilateral tectum) milliseconds (msec.) (Andrews, 1955; Gaze and Jacobson, 1962a). The difference in response latencies was attributed to a synaptic delay in the pathway connecting the contralateral and ipsilateral tecta. Substantial electrophysiological evidence in favor of an intertectal pathway has been presented by Gaze and Jacobson (1962a) and more recently by Fite (1969). However, histological studies (Rubinson, 1968) have not yet determined the exact neuro-anatomical route of the pathway.

In addition, five different classes of retinal operations (previously mentioned on page 9) (1. sustained edge detection, 2. convex edge detection, 3. changing contrast detection, 4. dimming detection, 5. dark detection) have been identified by Lettvin et al. (1959), Maturana et al. (1960) and Grusser-Cornehls, Grusser, and Bullock (1963) in various fiber layers (i.e. of each retinal point) of the frog's tectum. For example, in the surface and lower layers of the stratum opticum, classes 1 and 2 respectively, were found to be mediated by slow conducting fibers. Also, the small retinal receptor field (RRF, 1-5°, for these responses) suggested

that these responses were transmitted via small unmyelinated fibers. The third (on-off responses) and fifth (darkness response) classes of fibers made up the (thickest) stratum of optic fibers (stratum fibroseum et griseum superficiale) in the superficial zone. The large RRF's (7-12°) for these retinal operations (particularly class 3) were mediated by fast conducting myelinated fibers. Between this fiber stratum and the next stratum, (stratum griseum centrale), there was an interval of electrophysiological silence. In the deepest layers of the superficial zone, dimming responses were recorded from a narrow band of large myelinated fibers, (conduction velocity of 8m/sec.), which had the largest RRF (15°) of all retinal operations.

Scalia et al.'s (1968) neuroanatomical model of tectal organization is in close agreement with the tectal layers in which the retinal operations were reported to be found by Maturana et al. (1960) and Grusser - Cornehls et al. (1963). The fast and slow fiber components mediating these retinal responses were similar to those identified in the optic nerve by Bishop (1933). Also, the orderly arrangement of the different retinal operations in successive layers of the tectum was consistent with the notion of a columnar organization in the tectum.

In addition to the direct retinal projections to the contralateral tectum in the amphibian, numerous optic fibers have been observed to terminate in almost all areas (except the caudal area)

of the contralateral thalamus (Herrick, 1925, 1933). After crossing the optic chiasma, three sets of fiber collaterals were found to branch off from the marginal optic tract, and terminate in the anterior (dorsal thalamus and hypothalamus) and posterior regions of the thalamus (figure 5).

In the amphibian, Amblystoma, large fields of optic fibers were found in three areas of the thalamus, the pretectal nucleus, the lateral geniculate body, and the anterior nucleus of Bellonci (figure 6). These neural structures in the Amblystoma were not well differentiated. That is, the pretectal nucleus and lateral geniculate body were partly diencephalic-mesencephalic structures.

However, in the frog, the optic thalamic organization was found to be more advanced (Herrick, 1925). In particular, the anterior nucleus of Bellonci is located in the rostral thalamus, dorsal to a well-defined lateral geniculate body. These two neural structures were found to have cell bodies in the peripheral layers of the thalamus with fiber processes extending into the dorso-thalamic layer of optic terminals (figure 6). Also, the lateral geniculate body and the nucleus of Bellonci were reported to receive and send efferent fibers to the optic tectum (Herrick, 1925; Muntz, 1962).

In addition, electrophysiological data has shown these optic thalamic fibers to be responsive to the onset of photic stimulation (i.e. on-responses) but not to the offset of light (i.e. off-responses) as has been found in the surface fiber layers of the optic tectum (Muntz, 1962).

Moreover, axons from the posterior part of the lateral geniculate

FIGURE 5. OPTIC TRACT COLLATERALS IN THE ANTERIOR AND POSTERIOR THALAMUS

A sagittal view of the optic collaterals branching from the ascending marginal optic tract and terminating in the anterior (nucleus of Bellonci) and posterior (corpus lateral geniculate and pretectal nucleus) thalamus of the Amblystoma. Dotted circles represent the approximate areas in which the undifferentiated nuclei are located. In the Amblystoma, the corpus lateral geniculate (c.lat. gen.) and pretectal nucleus (pret. nuc.) are partly diencephalic-mesencephalic.

(Modified from Herrick, 1925.)

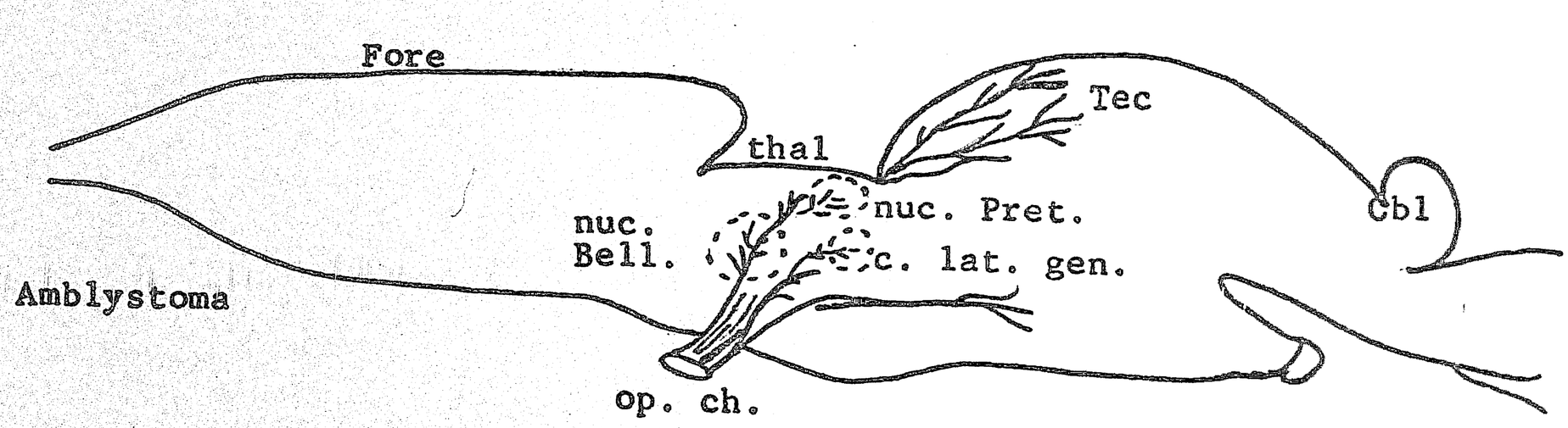
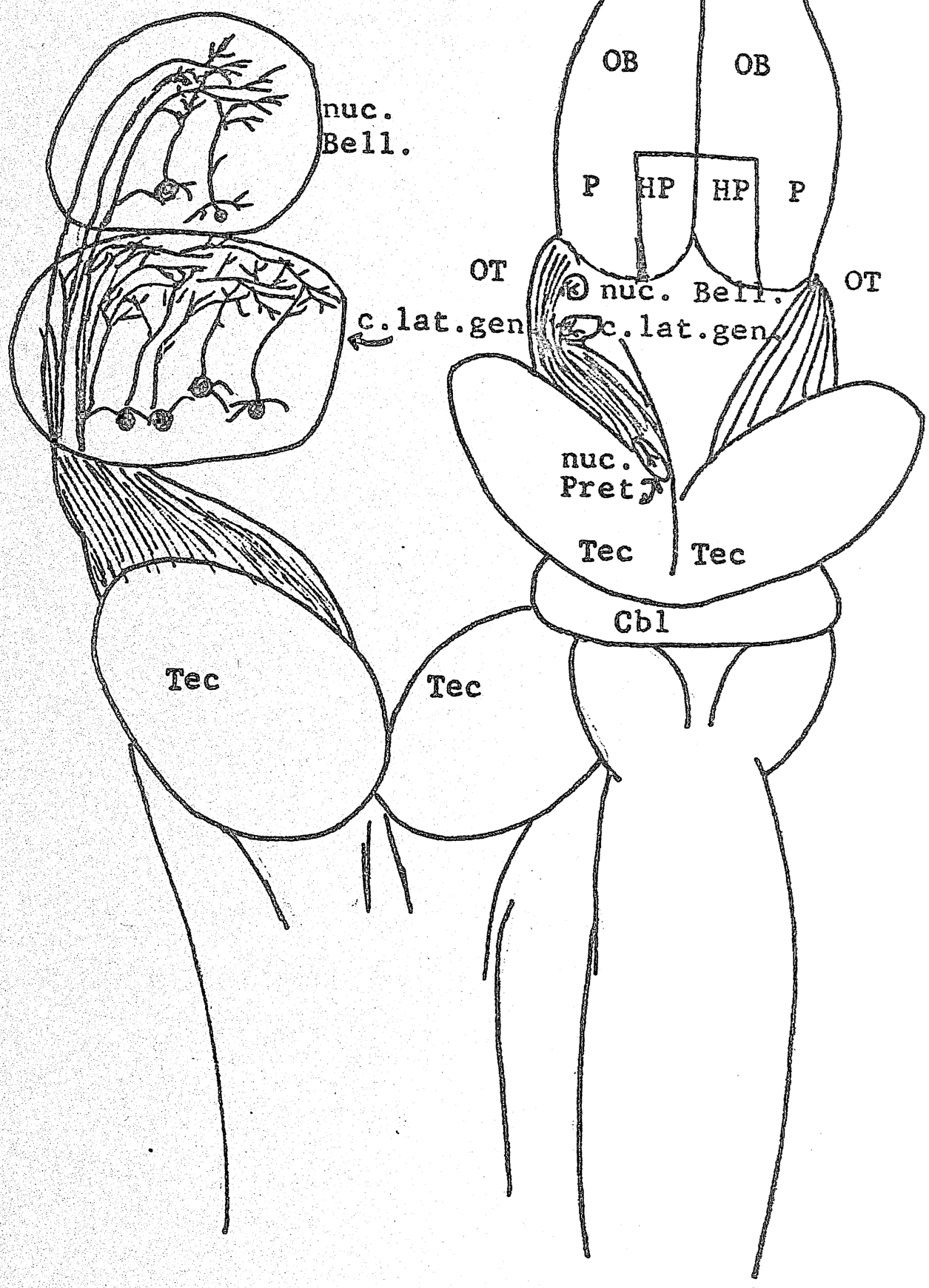

Fore
thal
Tec
nuc.
Bell.
nuc. Pret.
c. lat. gen.
Cbl
Amblystoma
op. ch.

FIGURE 6. PRIMARY RETINAL PROJECTIONS IN THE DORSAL THALAMUS.

Dorsal view of the primary retinal projections to the dorsal thalamus, particularly, the nucleus of Bellonci (nuc. of Bell.) and lateral geniculate body (c. lat. gen.) and to the posterior thalamus (i.e. pretectal nucleus) and tectum.

On the left side of figure 6, there is a magnified view of the dorsal thalamus, illustrating the intermingling of optic terminals with the dendritic processes of the thalamic nuclei.

(Modified from Herrick, 1925).


nuc.
Bell.
OB
OB
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HP
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nuc. Bell.
OT
c.lat.gen
c.lat.gen
nuc.
Pret
Tec
Tec
Cbl
Tec
Tec

body extended anteriorly to the cerebral hemispheres via the medial forebrain bundle (Herrick, 1925). These dorso-thalamic fiber connections to the frog's forebrain were interpreted to be homologous to the cortical projections that originate from the postero-dorsal side of the lateral geniculate body in mammals (Herrick, 1925).

In support of Herrick's early studies, more recent histological (Scalia et al., 1968) and histochemical (Goldberg and Kotani, 1970) examinations of the frog's visual system have also shown three sets of collateral fibers from the marginal optic tract, terminating in approximately the same anterior (nucleus of Bellonci, nucleus lateralis tegmenti of Herrick) and posterior (posterior thalamic nuclei and pretectal nucleus) regions of the thalamus.

Also, Goldberg and Kotani (1970) have reported evidence of very small retinal fibers projecting ipsilaterally to the terminal loci corresponding to those of the decussated fibers.

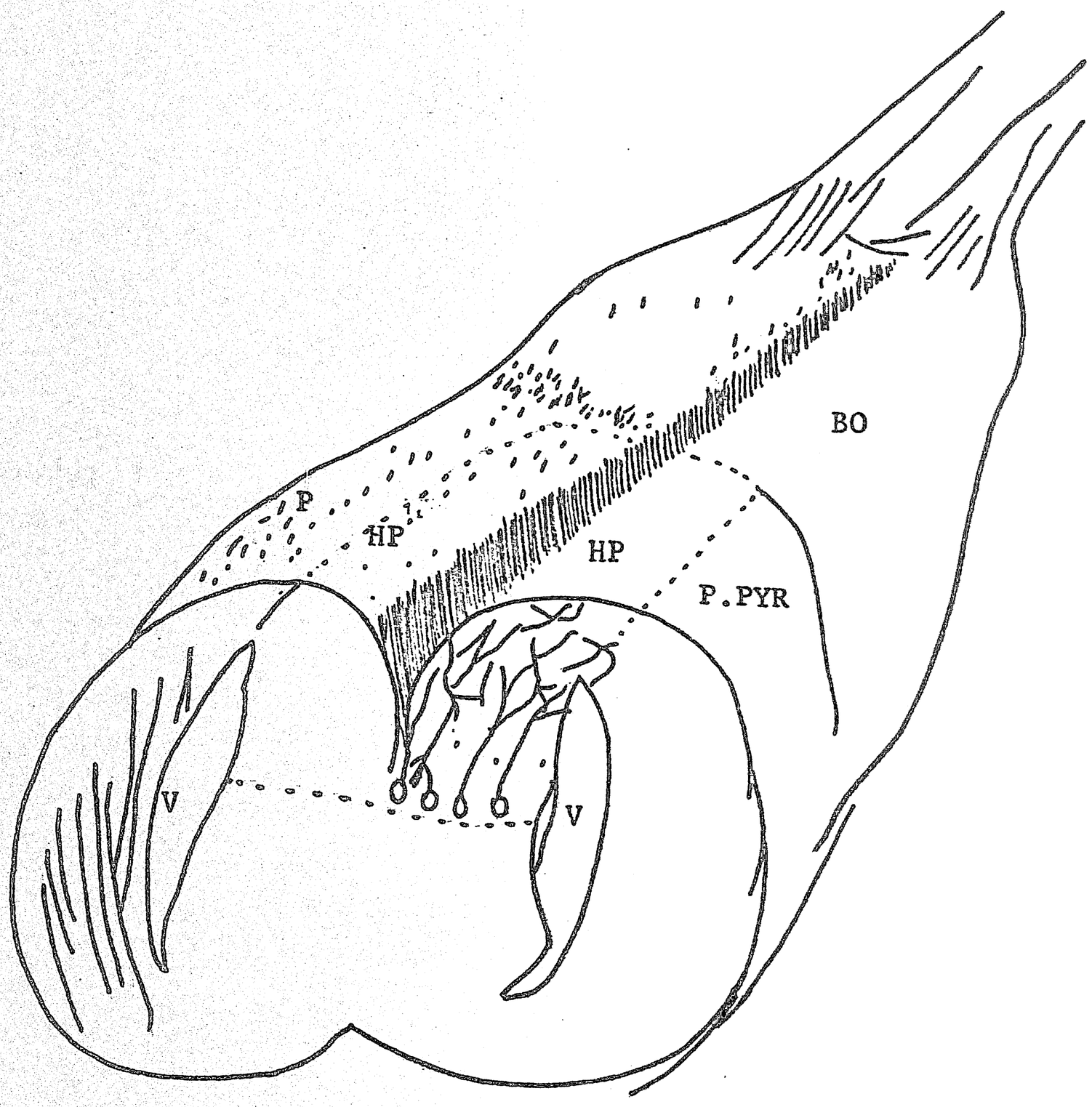
In the lower submammalian vertebrates, the cerebral hemispheres are predominantly under the influence of the olfactory bulb. For example, the olfactory bulb, in the amphibian, extends (along the lateral wall) half the length of the forebrain (Herrick, 1933).

In the frog, the cerebral hemispheres (figure 7) are more differentiated (Herrick, 1933). In the dorso-medial section of the primordium pallium, there is located the relatively simple two-layered structure, the hippocampus primordium. The outer molecular layer (which is approximately 300μ - 400μ thick) consists of the

FIGURE 7. HIPPOCAMPUS PRIMORDIUM IN THE FROG

Coronal view of the frog's forebrain (reader views posterior side of the cut). The hippocampus primordium (HP) which is found in the dorso-medial hemisphere of the forebrain, is the most differentiated of the frog's cortical structures. It receives sensory input, primarily, from the diencephalon (not shown in this figure).

(Taken from Servit and Strejckova, 1970.)


BO
P
HP
HP
P.PYR
V
V

fibrous endings of the apical dendrites, that originate from the somata in the lower granular layer (Servit and Strejckova, 1970).

In comparison to other pallial structures in the frog's forebrain, the hippocampus primordium is the most advanced in regards to cortical differentiation (Herrick, 1933). The high degree of differentiation is demonstrated by the absence of direct olfactory input to the dorso-medial forebrain, the large influx of sensory information (i.e. non-olfactory) from the diencephalon via the medial forebrain bundle, innervation from the dorsal association fibers, and also from the septal cortical tracts of the forebrain (Herrick, 1933a).

In concert with the neuroanatomical evidence of retinal innervation of the thalamo-cortical structures, Karamian et al. (1966), Voronin, Gusselnikov (1959), Voronin, Gusselnikova, Gusselnikov, and Supin (1968), and Servit and Strejckova (1970) have shown that the visual system (to a limited degree) is represented in the rostral region of the frog's brain. In all the experiments, the investigators found that from the hippocampus primordium, the evoked responses could be elicited by retinal stimulation (i.e. electrical and visual). Karamian et al. reported that the mean response latency in the contralateral hippocampus primordium to visual and electrical stimuli was 110 msec. and 65 msec. longer, respectively, than the response latencies recorded in the contralateral tectum. Also, it was reported (Karamian et al., 1966) that electrical stimu-

lation to the contralateral dorso-thalamic area produced evoked responses (with a latency of less than 65 msec.) in the hippocampus primordium. In addition, evoked responses to retinal stimulation continued to be recorded from the contralateral hippocampus primordium following a contralateral tectalectomy.

Thus, it appears, on the basis of the histological and electrophysiological evidence presented, that the visual system in the frog involves a more elaborate network of afferent fibers and brain structures than was originally conceived by Cajal (1911) (figure 3).

In the higher mammalian vertebrates (eg. cats, monkeys), the two visual systems (retino-tectal and retino-thalamo-cortical) have been shown (Held, 1970) to be important, functionally, in two separate but integrated modes of visual behavior: stimulus localization (i.e. in the visual field) and stimulus identification (i.e. discrimination). Schneider (1969) reported that ablations made only in the colliculus of the hamster resulted in the animal's inability to orient (spatially) to visual stimuli, but it could identify (i.e. discriminate) the shapes of the stimuli if it were guided to them. However, the reverse behavior was observed when an ablation was made only in the visual cortex of the animal. That is, the hamster was able to localize the stimulus object, but it was unable to distinguish it from the surrounding objects. (i.e. The animal was pattern blind.)

The actual role of the hippocampus primordium in the frog, in processing visual information is not known. It has been hypothe-

sized (Ingle, 1970) that this primitive cortical structure represents an early stage in the development of the more elaborate visual cortex of the higher vertebrates. In comparison to the visual systems of higher vertebrates (eg. primates), the anatomical (Dowling and Boycott, 1963) and electrophysiological (Lettvin et al., 1959; Maturana et al., 1960; Grusser-Cornhels et al., 1963) complexity found in the frog's retina, together with the lack of cortical representation in the frog, suggests that the degree to which the cerebral hemispheres of the anuran participate in the processing of visual information is minimal. Moreover, the non-specific nature (i.e. the recruitment of responses) of evoked hippocampal responses, to light stimulation, that were recorded by Karamian et al. (1966) is further evidence of the rudimentary role that the primordium hippocampus plays in the processing of visual information in the frog.

The following study is an attempt using an electrophysiological recording technique, to determine the extent to which primary retinal fibers are represented in the retino-tectal and retino-thalamocortical systems of the frog (Rana pipiens). Response latencies to photic and optic nerve stimulation were used to identify the types of fiber components (i.e. fast and slow, direct and indirect) subserving the two visual systems.

METHOD

The twenty two large and medium sized leapord frogs, (Rana pipiens), ranging in weight from 21 to 36.6 grams, used in this study were kept in a terrarium at room temperature ($68^{o} \pm 4^{o}F$). The animals were anesthetized with Diabutal (50 mg per kilogram) administered interperitoneally or in the lymphatic sacs. During the experiment, the animal was pinned to a surgical board covered with a moist cotton gauze with another cotton gauze draped over the back of the animal. Pond water was applied periodically to the gauze to keep the skin moist and to the eyes during the visual stimulation experiment.

To expose the tectal lobes and dorso-medial region of the forebrain, a dental burr was used to thin the fronto-parietal bone, which was removed by cutting it with a scalpel blade. Care was necessary to avoid damaging the underlying neural tissue and blood vessels which were attached to the bone by means of connective tissue. Following the removal of the bone, the tough outer membrane (meninges) was cut away leaving the underlying pia matter and cortical structure intact. The extreme caudal and lateral parts of the tecta were not exposed because of major blood vessels that were present in those areas.

The physical dimensions of the average sized tectal lobe (taken from the tectum of a medium sized frog) were 2.4 mm across the medial-lateral surface, 1.7mm across the medial antero-postero surface, and 2.2 mm across the lateral antero-postero surface (figure 8). The

depth of the tectal lobe was not measured directly, but according to Kemali and Braitenberg (1969), the tectum was approximately 2.5 - 3.0 mm thick.

The two modes of stimulation used in this study were electrical and light stimulation. The circuitry for recording was the same in both stimulus conditions (figure 9).

In the light stimulation condition, the animal's eyes were dark adapted for approximately twenty five minutes. A disc of light (approximately 1mm in diameter) was focussed in the center of the frog's pupil (nictitating membrane removed) subtending a circular field of approximately 40°. A flash of light (3×10^{-4} lumens) was presented automatically by means of an electromagnetic shutter arrangement, at sixty second intervals, for .5 - .7 seconds. When the flash of light was presented manually, the inter-stimulus interval ranged from 45-90 seconds. By means of two relay timers (Hunter Manufacturing Co.), the sweep on the oscilloscope (Tektroninx Number RM 585) and opening of the camera shutter preceded the onset of the light flash by 100 - 500 msec.

The manual presentation of visual stimuli was done by operating (setting and resetting) the second Hunter timer which controlled the opening and closing of the shutter in the optical system. During the manual presentation of light flashes, the sweep on the oscilloscope was triggered by the stimulus artifact produced by the opening of the shutter via an electromagnetic arrangement in the optical system. Photographic records during this particular procedure were taken manually.

Extracellular recordings were made with 3M KCl glass micropipettes

FIGURE 8. PHYSICAL DIMENSIONS OF OPTIC TECTUM

Dimensions of a medium-sized frog:

2.4 mm across medial-lateral surface

1.7 mm across medial-antero-postero surface

2.2 mm across lateral-antero-postero surface

Scale of magnification is 10 times.

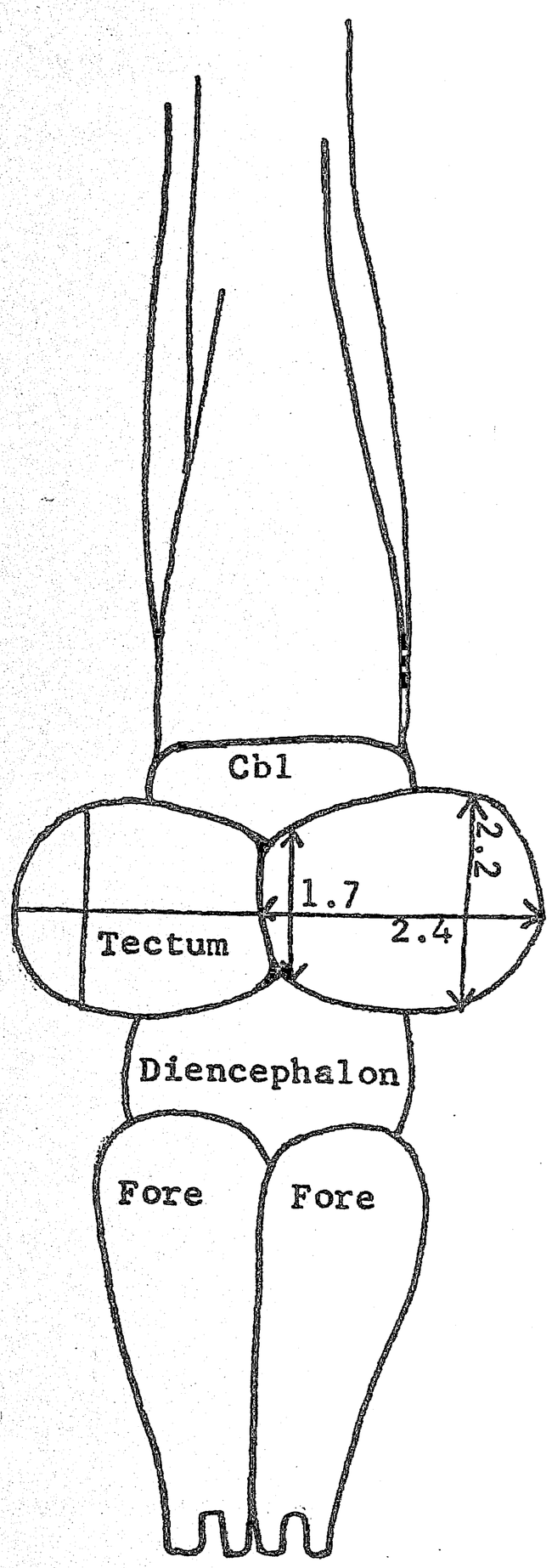
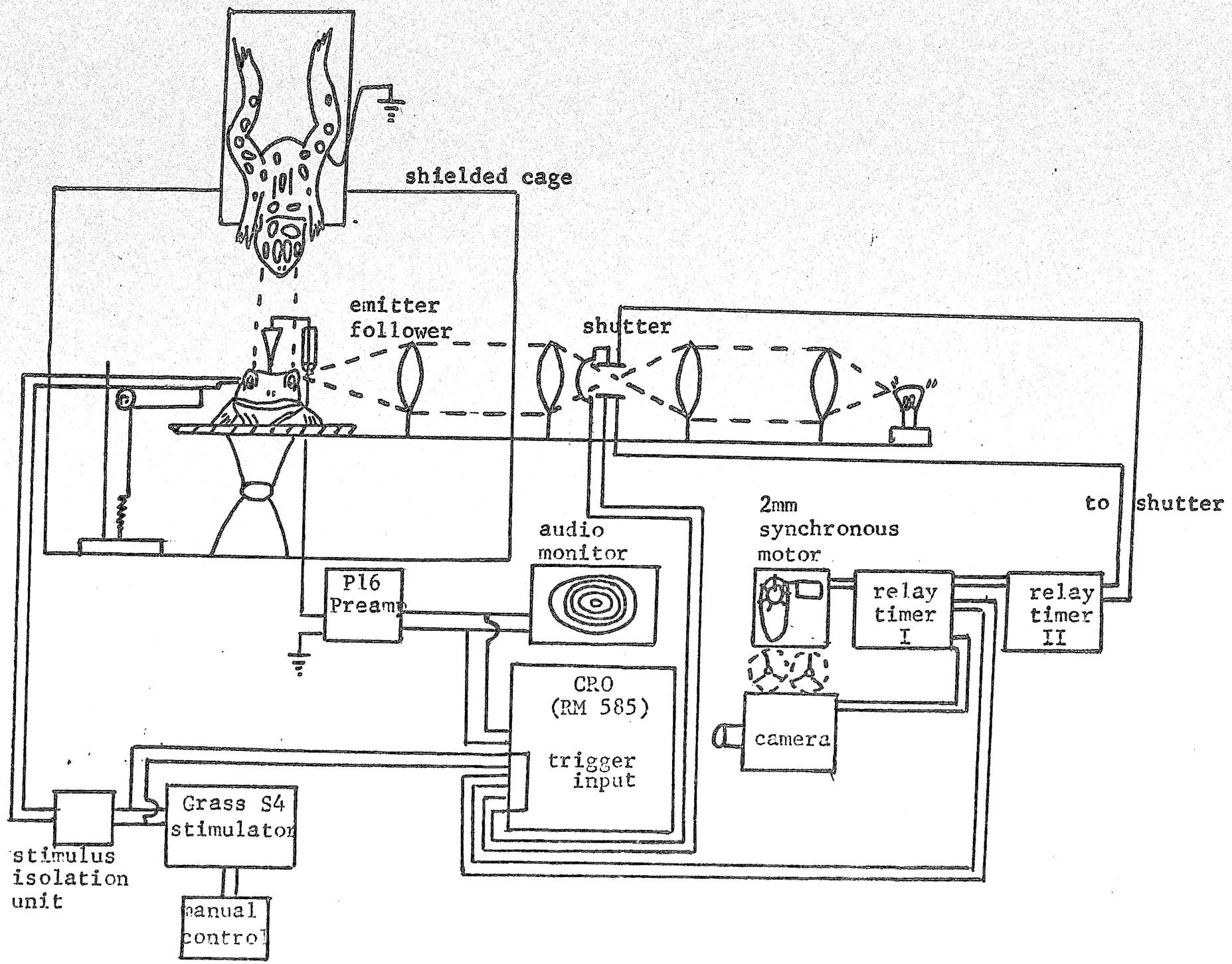

Cbl
2.2
1.7
2.4
Tectum
Diencephalon
Fore
Fore

FIGURE 9. SCHEMATA OF THE EXPERIMENTAL APPARATUS USED IN THE RECORDING OF SPIKE ACTION POTENTIALS TO PHOTIC AND OPTIC NERVE STIMULATION.


shielded cage
emitter
follower
shutter
audio
monitor
2mm
synchronous
motor
to shutter
P16
Preamp
relay
timer
I
relay
timer
II
CRO
(RM 585)
trigger
input
camera
Grass S4
stimulator
stimulus
isolation
unit
manual
control

with tip impedences ranging from 5meg - 50 meg ohms (median impedence = 10 meg ohms). The recording circiut was completed with an emmitter follower and either a capacitance coupled or direct coupled preamplifier (Grass P16) which was connected to a second preamplifier in the oscilloscope. The indifferent electrode was a silver wire placed under the hind leg of the preparation. All outputs from the P16 preamplifier were monitored by an audio speaker (Grass Am 5A), and all records of the oscilloscope (CRO) displays were photographed automatically with a Grass Kymograph Camera on 35mm high contrast Kodak film.

In the electrical stimulation experiments, the nictitating membrane, cornea, iris, and lens of the eye were removed, leaving the retina intact. A square wave pulse (.03 msec. duration and 15v - 110v DC amplitude) was delivered by a bipolar electrode (two stainless steel needles with the distance between tips = 350u) across the optic disc of the exposed retina. The electrode was insulated to within .5mm of the tips. Large scale amplification and polarity changes of the electrical stimulus was produced with a stimulus isolation unit in series with the stimulating electrode and voltage source. Oscilloscope displays were triggered by the stimulus artifact of the voltage source and the photographic records of these displays were taken manually.

In the control experiments for electrical stimulation, a 24 guage needle was used to inject .025cc. Novocain (2%) into the optic disc. Accuracy of the injection was facilitated by inserting

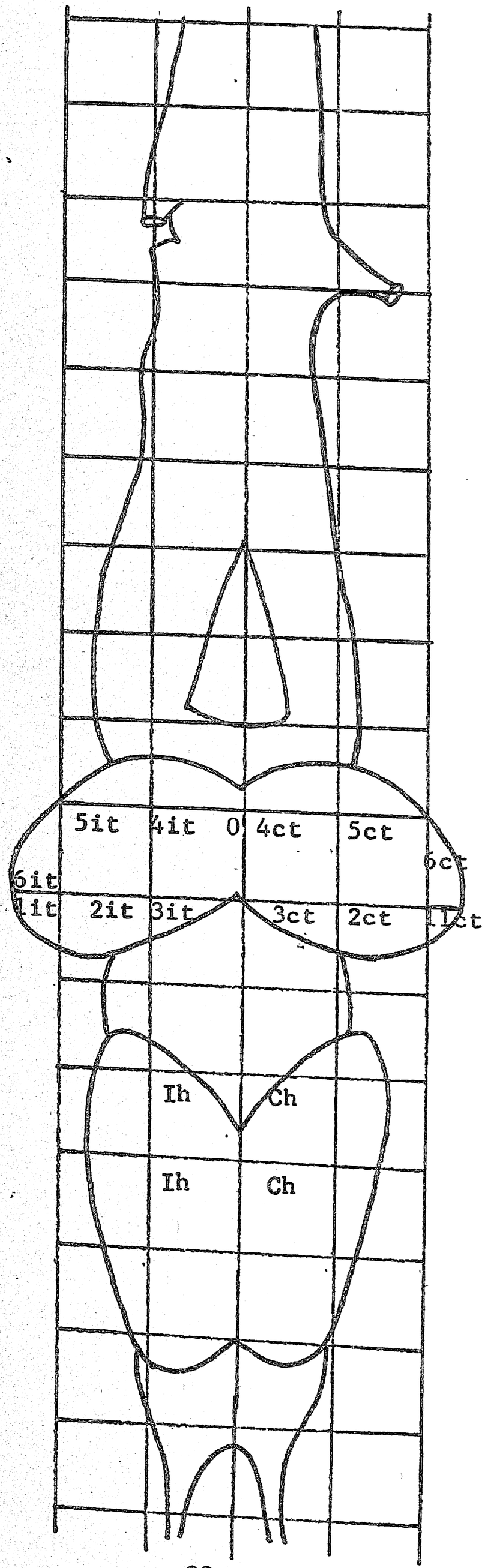
the needle's tip between the two electrode tracts that were made by the stimulating electrode. Immediately after the injection, the needle was withdrawn and the stimulating electrode was returned to its original position in the eye.

In order to minimize the error in the placement of the recording electrode, schematic copies (figure 10) of the dorsal view of the frog's excised brain (Kemali and Braitenberg, 1969), superimposed by a two dimensional coordinate grid, were used as a reference during each preparation, to identify and mark the approximate points in which electrode penetrations were made, in the different areas of the brain. Numbers with lettered subscripts (to denote anatomical position, eg. Ct - contralateral tectum) were assigned to sections of the grid covering each tectum and hippocampus, to differentiate between the various parts of structures being studied. (See Table I.)

Accuracy in obtaining a vertical insertion of the recording electrode was dependent upon visual approximation.

FIGURE 10. A SCHEMATA OF THE FROG'S BRAIN

A schematic copy of the frog's brain, with a coordinate scale, that was used in making an accurate penetration with the recording electrode. Ct - contralateral tectum, It - ipsilateral tectum, Hc - contralateral hippocampus, Hi - ipsilateral hippocampus.


5it
4it
0
4ct
5ct
6ct
6it
1it
2it
3it
3ct
2ct
1ct
Ih
Ch
Ih
Ch

RESULTS

All of the responses to electrical stimulation, with the exception of two preparations, were recorded from the contralateral tectum (figure 11). In these two preparations (6/18, 7/13) spike responses were obtained from area $^{4}_{It}$ of the ipsilateral tectum. There were no responses to electrical stimulation recorded from the primordium hippocampi in any of the preparations. Recording from the extreme caudal and lateral regions of both tecta was not attempted because of the inaccessability of these areas surgically.

The typical responses that were recorded from the tectal layers were triphasic (i.e. negative, positive, negative) in configuration. For example, in figures 12a and 12b, the clusters of triphasic spikes (indicating various sized fiber bundles) were recorded from the surface layers of areas $^{2}_{Ct}$, $^{5}_{Ct}$ respectively. In the deeper layers of the tectum, some biphasic spike potentials (i.e. positive, negative) were also recorded (figure 12c). Because the amplitude and latency (31.6 msec.) of these responses were constant, they were thought to be the result of monosynaptic activation. However, in most cases, it was difficult to distinguish between tectal cell and retino-tectal fiber responses.

The photographic records taken from the surface layers in areas $^{1}_{Ct}$, $^{2}_{Ct}$, $^{5}_{Ct}$, and $^{6}_{Ct}$ were characterized by massed responses of fast (response latencies $<$ 5 msec.), slow (5 msec. $\leq$ latencies $<$ 20 msec.) and very slow (20 msec. $\leq$ latencies $<$ 72 msec.) spike components (figure 12a, b). In contrast areas $^{3}_{Ct}$ and $^{4}_{Ct}$

FIGURE 11. TECTAL AREAS FROM WHICH RESPONSES TO OPTIC NERVE STIMULATION WERE RECORDED

The diagram illustrates the areas in the tecta and hippocampi in which recordings to optic nerve stimulation were attempted. The empty circles represent responses obtained; solid circles indicate areas in which no responses were recorded.

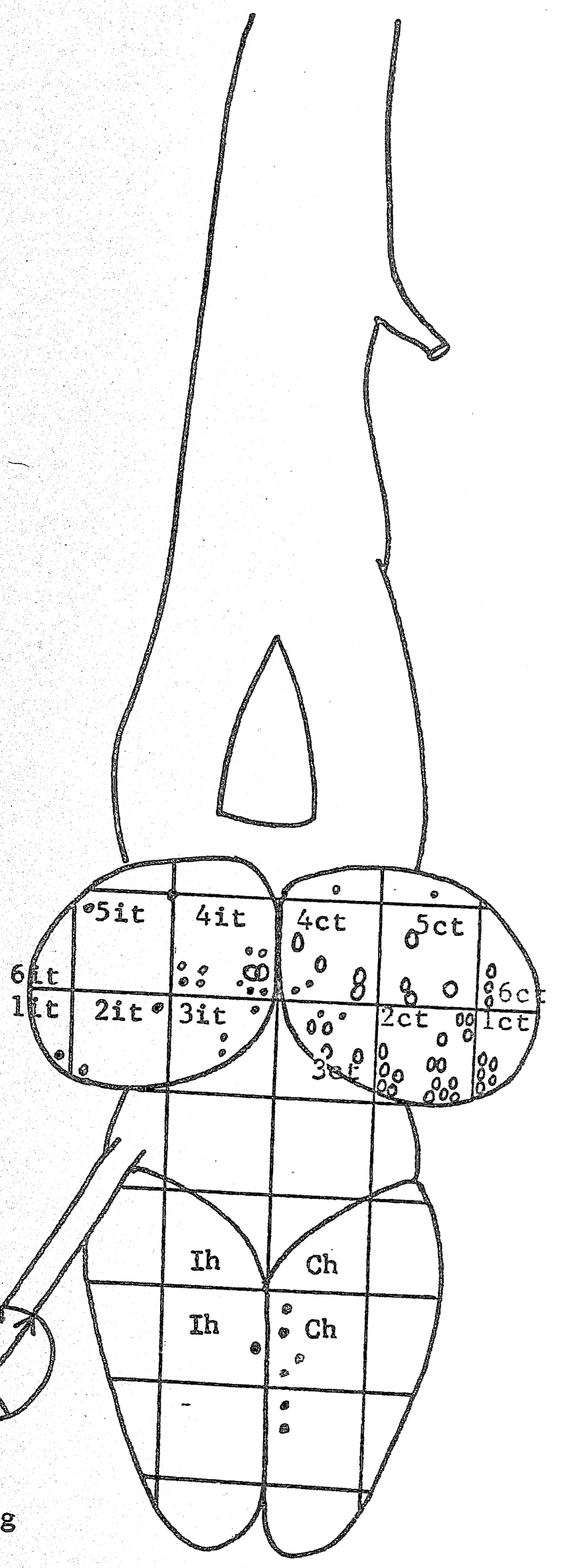
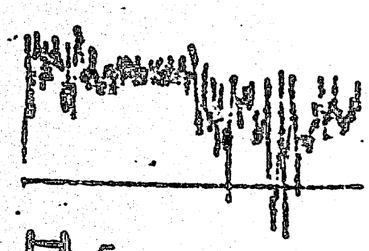

5it
4it
4ct
5ct
6it
6ct
1it
2it
3it
2ct
1ct
3ct
Ih
Ch
Ih
Ch
stimulating
electrode

FIGURE 12. BIPHASIC AND TRIPHASIC RESPONSES IN THE CONTRALATERAL TECTUM

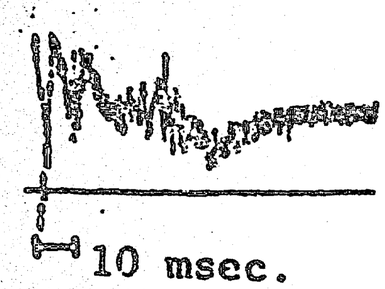
a. Examples of massed slow (latencies - 21-43 msec.) and fast (latencies - .8-8 msec.) triphasic components recorded from the surface layer of area 2_{Ct}, f 7/21.

b. Fast and slow triphasic components recorded from surface of area 5_{Ct}, f 7/21, latency 1.6 38.3 msec.

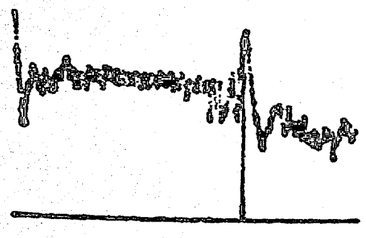
c. Isolated biphasic spike responses recorded 715μ below the surface in area 2_{Ct}, f 7/3, latency 30 msec.



a



b



c

(figure 13a, b) were found to elicit fewer fast and slow responses, with the majority of responses in the latter category. The apparent short latencies of the responses in figure 13b were the result of a change in sweep speed from 5 msec. per cm. to 10 msec. per cm. for the photographic records.

Representation of retinal fibers in a given area and at a given depth of the tectum was determined by the differential response thresholds of the fiber components. Some examples of the shift in response distribution (as a result of differences in excitation of fast and slow fibers), is shown in figure 14. It can be seen that the fibers that responded earliest (i.e. fastest) had a significantly lower response threshold than the slower fibers.

However, in figure 15a, the slower fiber components had a lower response threshold than the faster fibers. Similar differences in response thresholds for late and early fiber components were found in three other preparations (6/19, 6/27, 7/13, figure 15b). There was no indication that these peculiar results were specific to a particular depth of the tectum, but there was evidence of it occurring in a specific area (l_{Ct}). In preparation 7/3 (figure 15a), the difference in response thresholds between the early-occurring and late-occurring responses (latencies = 1.6-27.5 msec., respectively) were found at a depth of approximately 400μ below the tectal surface. In the other three preparations, the differences in response thresholds were recorded in the initial layer of the anterior

FIGURE 13. RESPONSE DISTRIBUTION FOUND IN THE MEDIAL TECTUM. Sample of the response distribution recorded from (a) ^{3}Ct, f 7/13 and (b) ^{4}Ct, f 7/21, were found to have few fast and slow spike reponses, with the majority of responses being solw (16-40 msec. in a; 23-73 msec. in b). The early spikes in b had latencies of 1.6-8.3 msec.

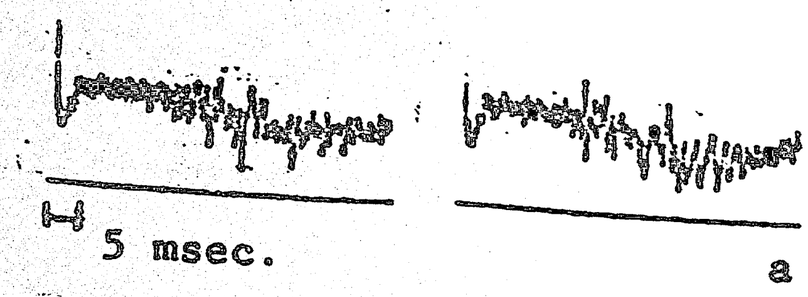
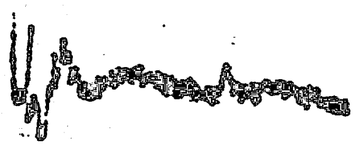

5 msec.
a
10 msec.
b

FIGURE 14. DIFFERENTIAL RESPONSE THRESHOLDS OF THE FAST AND SLOW FIBER COMPONENTS.

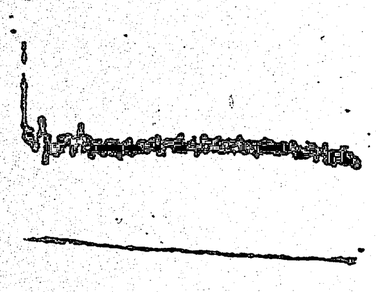
A sample of the differential response thresholds of the fibers in the surface layers of area 2_{Ct}, f 7/14, range of intensity - 15-100 volts. Threshold of early responses (1.6 msec.) was between 30 and 40v. The threshold for late spikes (21.6 msec.) was between 70 and 80v.

5 msec.

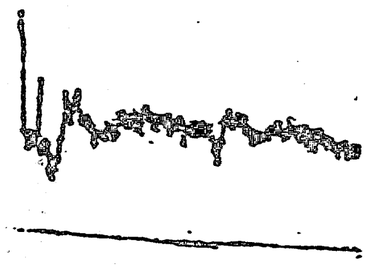
15v



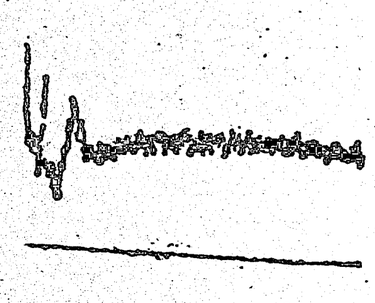
70v



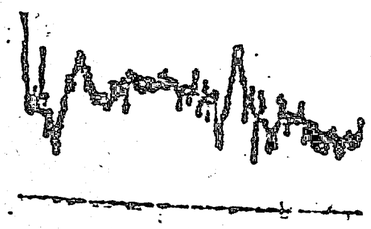
30v



80v



40v



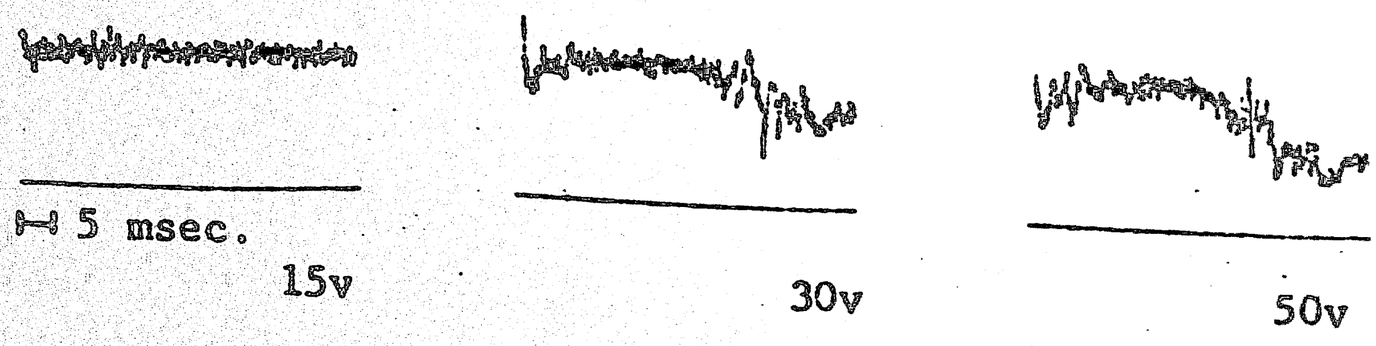
100v

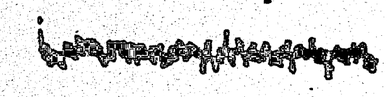
55v

FIGURE 15. REVERSE THRESHOLDS OF FAST AND SLOW COMPONENTS RECORDED IN AREA l_{Ct}.

a. An intensity series in the deep layers of area l_{Ct}, f 7/3, showed the late spike components (latency 27.5 msec.) to have a lower threshold (0-15v) than early spike components (latency 1.6 msec.), threshold between 25-30 volts.

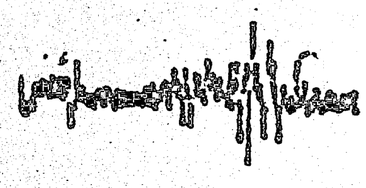
b. This was another example of the differential response thresholds that were recorded in the surface layers of area l_{Ct}, f 7/27, The threshold for late components (latency 21.6 msec.) was 20-30volts and the threshold for early spike components (latency 1.8-5.0 msec.) was between 40 and 50 volts.


5 msec.
15v
30v
50v
19v
36v
60v
25v
40v
70v

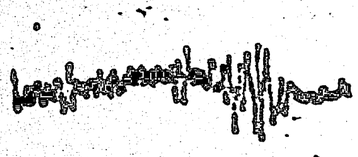


5 msec.

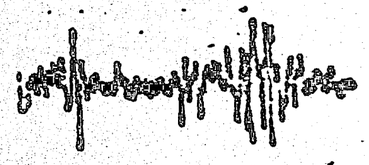
20v



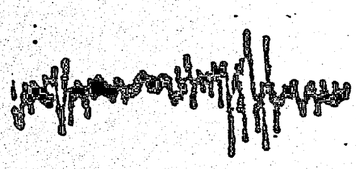
30v



40v



50v



60v

areas of the contralateral tectum.

To summarize the distribution of responses (to electrical stimulation) that were recorded, a series of frequency distributions was constructed for each of the seven areas in which responses were found in both tecta. The data used in the analysis were taken at four hundred (± 50μ) micron intervals to a depth of 2000 microns (figure 16). The 400μ interval was selected arbitrarily, as a distance between recording levels, to minimize sampling error and at the same time to maximize the number of preparations that could be used to make it a representative sample.

Typically, the distributions of spike latencies were found to change as a result of the fiber layers from which responses were recorded. For example, in figure 16, the proportion of fast and slow fibers decreased in number with an electrode penetration of 400μ from the tectal surface of area 5_{Ct}. This shift in response distribution of fast and slow responses occurred over a shorter distance than was found in penetrations of the anterior tectum. For example, in area 2_{Ct}, changes in distribution of fast and slow fibers were found at a depth greater than 1200μ below the tectal surface (figure 16). At that depth, the shape of the response distribution flattened out.

However, not all penetrations in the more densely populated fiber areas were found to yeild a massed distribution of responses. For example, from an electrode penetration in 2_{Ct}, (figure 17) it

FIGURE 16. FREQUENCY DISTRIBUTION OF RESPONSES DURING INWARD PENETRATION OF RECORDING ELECTRODE

A series of frequency distributions of the seven areas from which responses to electrical stimulation were recorded during penetration of recording electrode. In general, responses were trimodally distributed, with the greatest number of responses found in area 2_{Ct} and 1_{Ct}. Except for areas 2_{Ct} and 1_{Ct}, no responses were recorded below 800u.

The greek letter, μ refers to the measurement in microns of depths in which retinotectal responses were sampled.

The n refers to the number of animals represented in a given area and at a given depth.

The ordinate is the frequency of occurence and the abscissa is latent time in msec.

The range in which responses were distributed was restricted in this figure for sake of illustration. The numbers that generated the above frequency distribution can be found in the table of raw data in the appendix.

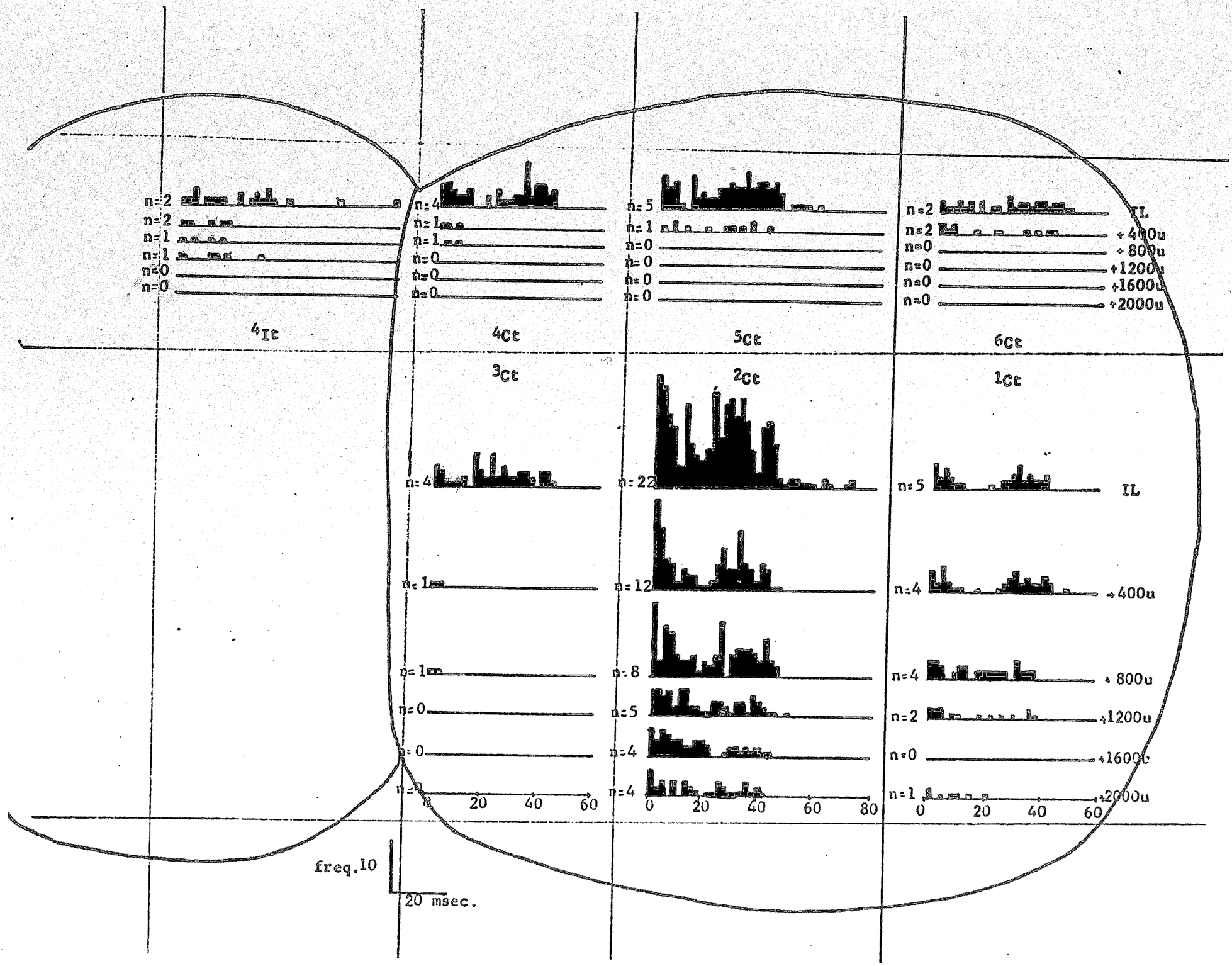
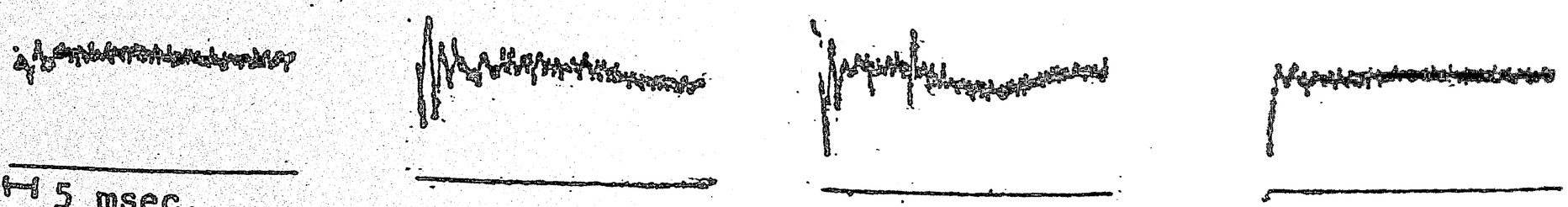
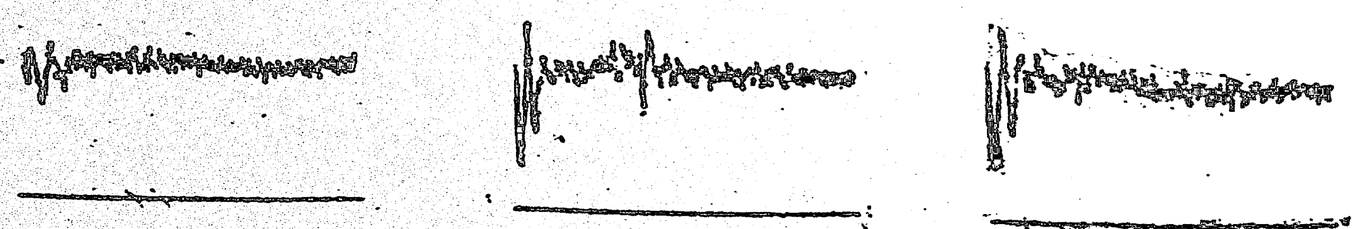

n=2
n=2
n=1
n=1
n=0
n=0
4It
n=4
n=1
n=1
n=0
n=0
n=0
4Ct
n=5
n=1
n=0
n=0
n=0
n=0
5Ct
n=2
n=2
n=0
n=0
n=0
n=0
IL
+400u
+800u
+1200u
+1600u
+2000u
6Ct
3Ct
n=4
n=1
n=1
n=0
n=0
0
20
40
60
2Ct
n=22
n=12
n=8
n=5
n=4
n=4
0
20
40
60
80
1Ct
n=5
IL
n=4
+400u
n=4
+800u
n=2
+1200u
n=0
+1600u
n=1
+2000u
0
20
40
60
freq.10
20 msec.

FIGURE 17. EARLY SPIKE COMPONENTS

An early group of spike components that were recorded over a distance of 2130μ from the tectal surface of area ^{2}Ct, f 6/23. The fixed latency (.8 msec.) and change in amplitude as a function of tectal depth indicated that these early spike components were the same throughout the penetration.



80u 1330u 1730u -120u



430u 1730u 1355u

830u 2130u 280u

can be seen that the fast components (latency≅ .8 msec.) were the predominant response group. This compound action potential peaked in amplitude at a depth of approximately 830μ from the tectal surface and then declined with the advancement of the recording electrode.

In comparing the response distribution among the different areas of the tectum, it was noted that most responses to optic disc stimulation (electrical) were in areas $^{2}_{Ct}$ and $^{1}_{Ct}$ and to a lesser extent in $^{6}_{Ct}$, $^{5}_{Ct}$, $^{4}_{Ct}$, and $^{3}_{Ct}$, respectively (figure 16).

In figure 16, the distribution of total responses recorded in the tectal areas were characterized as trimodal in shape. In relation to the different number of preparations that were represented in each area, approximately equal numbers of fast (i.e. latency ≤ 5 msec.), slow (5 msec. ≤ latency ≤ 20 msec.) and very slow (20 msec. ≤ latency ≤ 70 msec.) fibers were present, particularly in the surface layers. However, the population of fast and slow fibers was greatest in area $^{2}_{Ct}$. Also, the trimodal distribution of fast and slow responses was most prominent in area $^{2}_{Ct}$. The various fiber components identified in area $^{2}_{Ct}$ had conduction velocity speeds ranging from twenty meters per second (20m/sec.) to eight hundredths meters per second (.08m/sec.). The range of response latencies of the fiber distribution (.3 msec to 70 msec.) in $^{2}_{Ct}$ was the greatest among the six areas.

Area $^{1}_{Ct}$ was found to be innervated with many fibers which resembled the fibers in area $^{2}_{Ct}$ in distribution. However, the

trimodal distribution of fibers in 1_{Ct} was less pronounced than in 2_{Ct}. This triple peaked characteristic persisted into the deeper layers (1200u) of the tectum.

Areas 2_{Ct} and 1_{Ct} were the only two areas in which responses were recorded at the maximum depth of 2000u. Also, it was noted that there was a significant decrease in the number of responses found below 400u in the medial and posterior half of the tectum. In fact, in none of the areas except 2_{Ct} and 1_{Ct} were there responses recorded below the depth of 800u.

In regards to the total distribution of responses in the contralateral tectum, the shift in the number of fast and slow fibers from the surface to the deeper layers of the tectum, (particularly in 2_{Ct} and 6_{Ct}) was consistent with the shift in response distributions found in individual penetrations. That is, the relative number of fast and slow (i.e. slow and very slow) fibers remained relatively constant, but the total number of responses decreased progressively from the higher to the lower areas of the tectum.

Area 4_{It} was the only area of the ipsilateral tectum which responded to electrical stimulation (see figure 11). The distribution of responses in the surface layers was found to include very few fast fibers (6m/sec.) and a small number of slow (.16-3m/sec.) fibers. Also, the fast fiber components were found to have high response thresholds (45v) (figure 18). In one preparation, (frog 6/18), responses were obtained as deep as 2800u from the tectal sur-

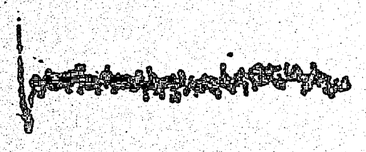
FIGURE 18. THRESHOLDS OF RESPONSES IN THE IPSILATERAL TECTUM.

The records of the differential response thresholds recorded from surface fiber layers of area 4_{It}, f 7/13. Response threshold for early components (latency .8 msec.) was between 45 and 50 volts; latency of late spikes was 34.1 msec.

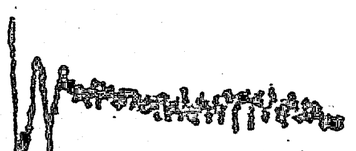
4.5 msec.

15v

85v

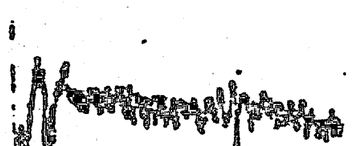


45v



100v

50v



120v

65v

face. The shift in response distribution found in the deeper layers of the contralateral tectum was not clearly demonstrated in this area.

In figure 19, the results of the control procedure used in the electrical stimulation experiments are shown. Figures 19a and b illustrate fiber responses that were recorded from area 2_{Ct} before the injection of Novocain into the optic disc; in figures 19c and d, the loss of spike responses that followed the Novocain injection is shown.

To determine the accuracy of the responses recorded from the different tectal depths, during the initial downard penetration of the recording electrode, a second set of histograms was generated from the responses recorded (at various depths) when the electrode was withdrawn from the tectum. The intervals analyzed were 400μ ($\pm$ 100μ) deep to 2000μ from the initial level of penetration. Because of the lack of systematic recording when coming out of the tectum, less data were obtained for this set of frequency distributions (figure 20).

As a result, the histograms constructed represented a smaller sample of responses than was collected in the downward penetration, but they did indicate an overall trend which was consistent with the first set of histograms of the tectal areas. The unfilled blocks in areas 4_{Ct} and 5_{Ct} represent responses that were recorded above the initial level of penetration. These responses were thought to be due to residual tissue that adhered to the recording electrode as it was withdrawn. Also, there was the possibility that these responses may have been recorded from the surface layers of fiber terminals that may have been bypassed in the original downward penetration of the recording elec-

FIGURE 19. EFFECTS OF NOVOCAIN INJECTION

Records a and b show the spike potentials recorded from the surface layers of area 2_{Ct}, f 7/22, to optic nerve stimulation. Record a was taken from one tectum and record b from the other tectum. In both cases, stimulation was to the contralateral eye. Records c and d show the loss of spike potential in the surface layers of 2_{Ct} immediately following a .025cc. injection of Novocain into the optic disc.

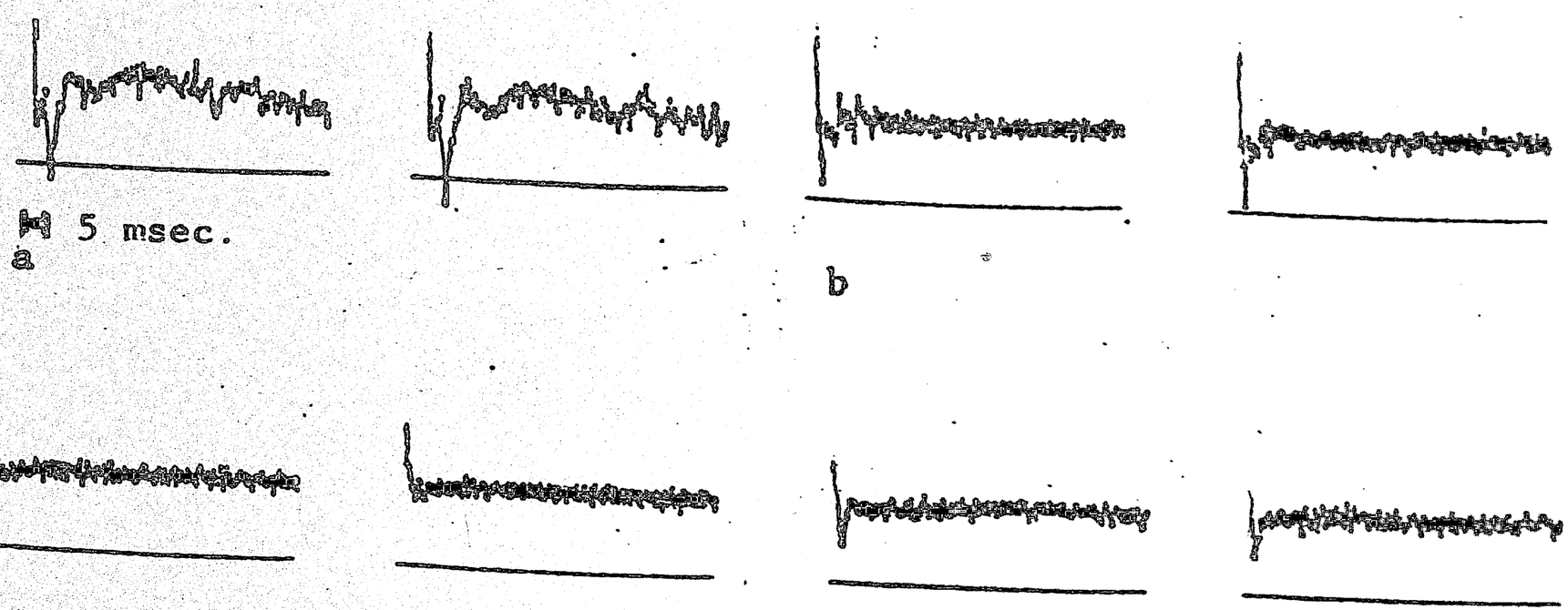
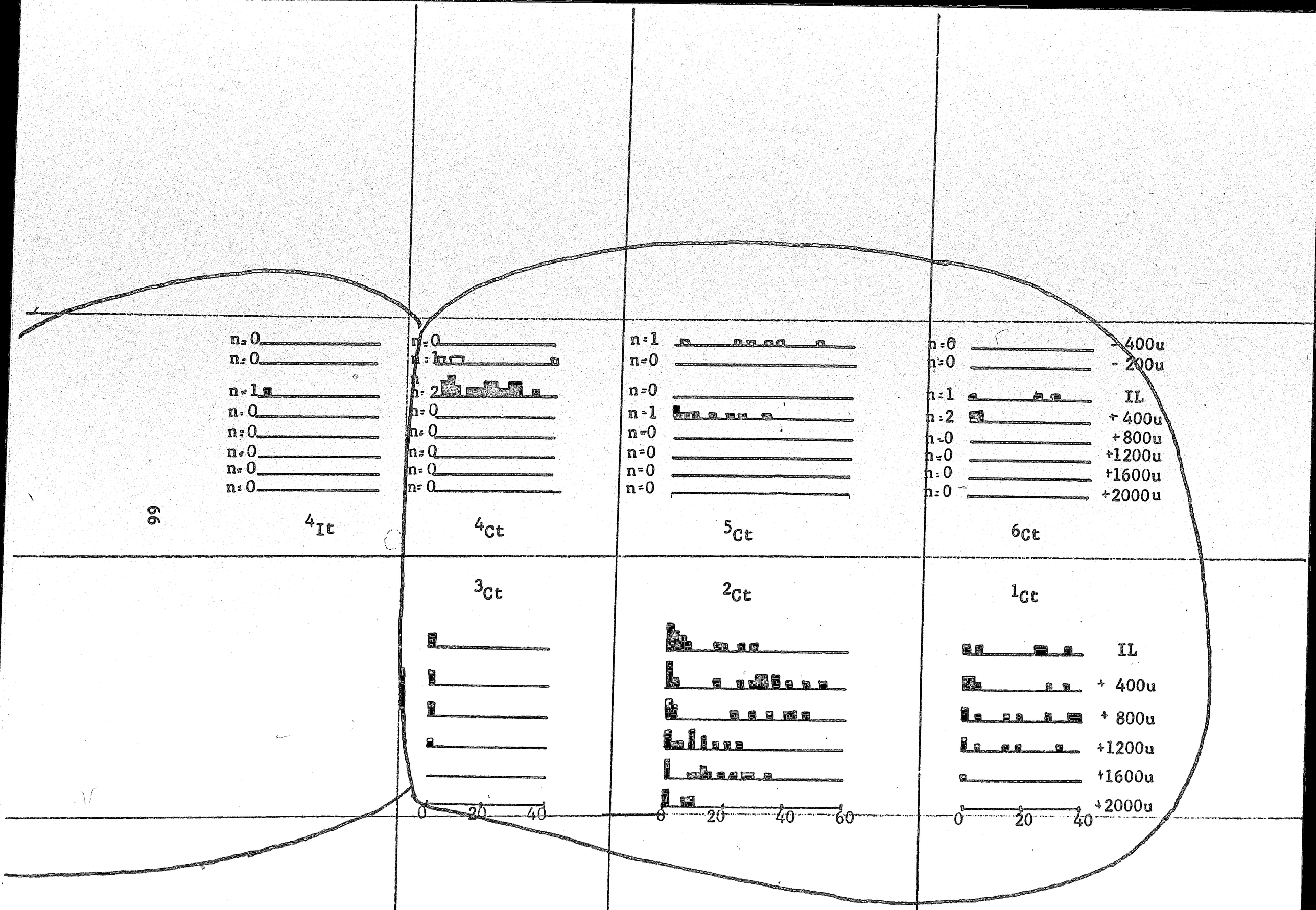

5 msec.
a
b
c
d

FIGURE 20. FREQUENCY DISTRIBUTION OF RESPONSES BY ELECTRODE WITHDRAWAL.

Set of frequency distributions of the responses in the seven tectal areas during the withdrawal of the recording electrode. The lack of systematic sampling resulted in the small distribution of response.

The n refers to the number of animals that were represented in each area and the depth for the data coming out of the tectum.

Negative numbers above the IL represent the level above the actual starting point in which responses were recorded during the withdrawal of the electrode. These responses were thought to be from residual tissue attached to the electrode.


n=0
n=0
n=1
n=0
n=0
n=0
n=0
n=0
4It
n=0
n=1
n=2
n=0
n=0
n=0
n=0
n=0
4Ct
n=1
n=0
n=0
n=1
n=0
n=0
n=0
n=0
5Ct
n=0
n=0
n=0
n=0
n=0
n=0
6Ct
- 400u
- 200u
IL
+ 400u
+ 800u
+1200u
+1600u
+2000u
3Ct
0
20
40
2Ct
0
20
40
60
1Ct
IL
+ 400u
+ 800u
+1200u
+1600u
+2000u
0
20
40

trode.

The recording of visual responses was made in both tecta and primordium hippocampi (figure 21). In general, responses to visual stimulation were not readily obtained from these areas. However, in one successful preparation (frog 4/26), evoked responses (response latency 35 msec.) were recorded from area 2Ct. At the same depth in the corresponding area of the ipsilateral tectum (2It), a feeble evoked response was recorded with a latency of 71 msec. (figure 22). In the same preparation, visual responses were elicited in both the contralateral and ipsilateral hippocampi primordium (figure 23). In the contralateral hippocampus, a small graded positive response (latency 107 msec.) was found to appear following the onset of a light flash (.5 msec. duration), which was presented asynchronously with the animal's heart beat. The evoked responses recorded from the corresponding area of the ipsilateral tectum had a latency of 89 msec.

In figure 23 , there is shown a series of responses recorded from the various levels of the ipsilateral hippocampus to a flash of light. Included in this series of responses are control trials (i.e. the eye was shielded from the flash of light) which were intermittently introduced between experimental trials. There were no other experimental controls (i.e. surgical or other) used in conjunction with these results.

FIGURE 21. RECORDING FROM THE CONTRALATERAL AND IPSILATERAL HIPPOCAMPI AND TECTA TO VISUAL STIMULATION.

Circled (X) show the corresponding points in the contralateral and ipsilateral tecta and hippocampi in which evoked responses to photic stimulation were recorded in f 4/26.

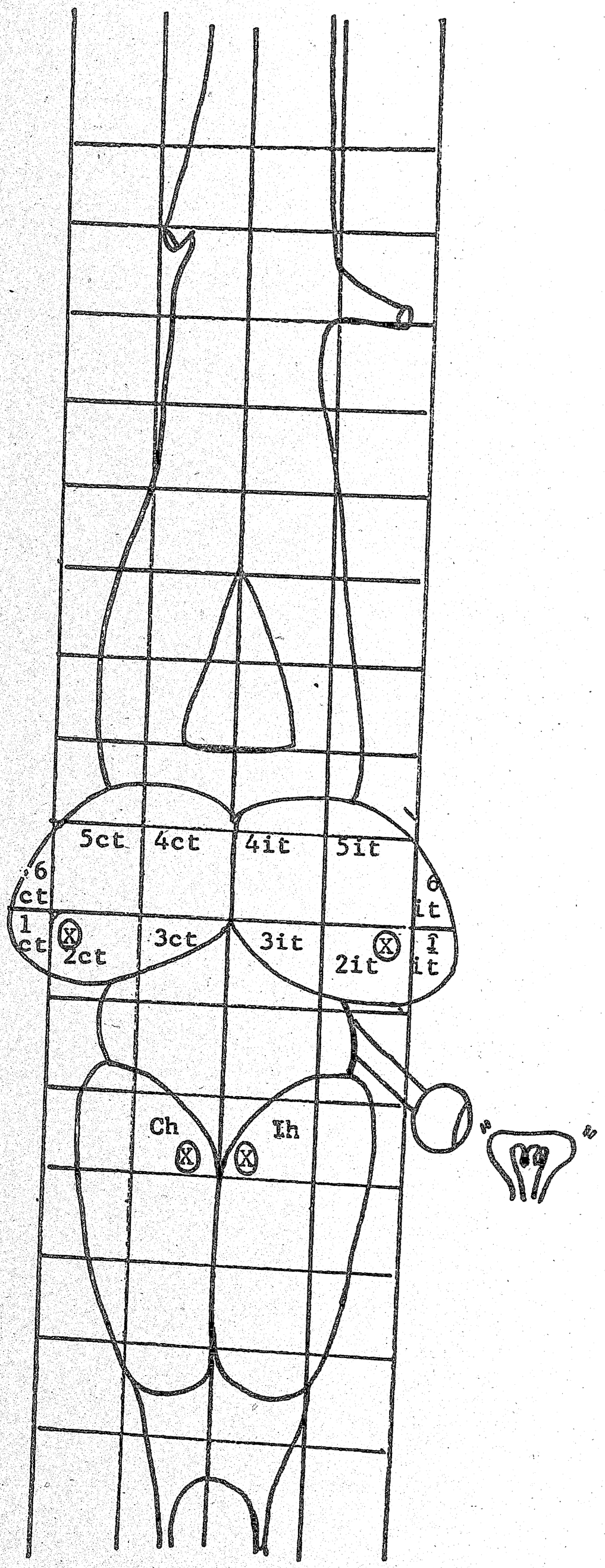
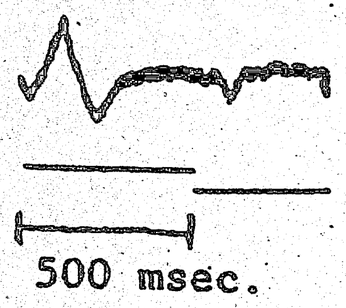

5ct
4ct
4it
5it
6 ct
6 it
1 ct
2ct
3ct
3it
2it
1 it
Ch
Ih

FIGURE 22. EVOKED RESPONSES TO VISUAL STIMULATION IN OPTIC TECTA

a. An evoked response with a latency of 35 msec. was recorded at a depth of 400μ below the tectal surface of area 2_{Ct}, f 4/26, following the onset of a light flash, the duration of which is indicated by the break in the trace of the lower beam.

b. An evoked response with latency of 71 msec. was recorded from the corresponding area 2_{It} and 400μ in depth, following the onset of a flash of light.



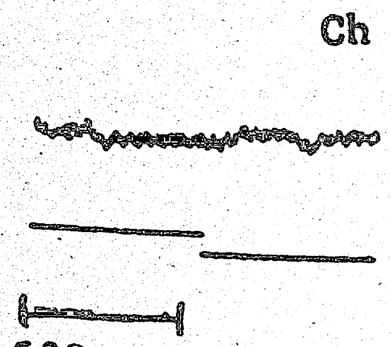
a

b

FIGURE 23. EVOKED RESPONSES TO VISUAL STIMULATION IN THE PRIMORDIUM HIPPOCAMPI

a. Records of the graded responses (latency 107 msec.) that were recorded from the various depths of the contralateral hippocampus to photic stimulation, f 4/26. It can be seen that the amplitude of evoked responses were higher in the deeper layers.

b. The evoked responses (latency 89 msec.) that were recorded from the various depths in the corresponding area of the ipsilateral hippocampus. Control records (CR) show the absence of response when the animal's eye was shielded.


Ch
500 msec.
0
Ch
400u
Ch
800u
a
Ih
0
b
Ih
CR
400u
Ih
Cr
800u

DISCUSSION

In this study, the distribution of response latencies recorded from the layers of the contralateral tectum was of the same trimodal character as that found by Bishop, in the optic nerve of the bull-frog (Rana catesbeiana) and by Maturana et al. in the optic nerve of the frog (Rana pipiens).

TABLE II

	Group I Very Slow	Group II Slow	Group III Fast
Bishop	0m/sec<v ≤.05m/sec.	1.5m/sec<v ≤4m/sec	4m/sec<v 17m/sec
Maturana et al.	.5m/sec or less	1m/sec<v ≤8m/sec	8m/sec≤v
Present study	.08m/sec<v ≤.3m/sec	.3m/sec<v ≤1.2m/sec	1.2m/sec<v ≤20m/sec

However, the extent to which the trimodal identity extended in the deeper tectal layers varied with the area and depth of the tectum from which the responses were recorded. In the deeper layers of the tectum, the number of spike potentials recorded was significantly less than in the surface layers. And, at a depth lower than 800u, spike potentials were recorded only in the anteroventral and lateral side of the tectum.

The decrease in the number of responses recorded in the lower layers of the posterior tectum was consistent with the fact that the tectal ventricle is located in the middle region of the tectum beneath the tectal layers. Also, the large number of fiber responses that were recorded in the layers of the anterior tectum, suggested that the principal site of entry for retinofugal fibers was

along the broad anteroventral rim of the tectum, as hypothesized by Potter (1969). Moreover, the density of responses found in the mid-tectal region ($^{2}_{Ct}$, $^{5}_{Ct}$) indicated that the incoming retinal fibers projected in a longitudinal direction across the surface of the tectum, as proposed by other investigators (Herrick, 1925; Lazar and Szekely, 1967; Potter, 1969). These electrophysiological findings did not appear to be consistent with Scalia et al's negative report of retinal fibers in the most superficial layer of the anterior and ventral tectum.

It is possible that the apparent inconsistency in these histological reports was the result of differences in the definition of the same neuroanatomical structures. That is, it is not clear whether the fiber free band, stratum zonale, described by Scalia et al. (1968) is the same as the superficial pial layer (also fiber free) reported by Potter (1969).

However, it is possible that the difference in reports may have been due to the staining techniques that were used. That is, the evidence of optic fibers across the surface of the tectum, reported by Herrick (1925), Lazar and Szekely (1967) and Potter (1969) was based primarily on the Golgi method of staining preserved nerve fibers. The negative results reported by Scalia et al. (1968) in the surface layers of the tectum, were based on the Nauta-Laidlaw and the modified Nauta-Gyax method of staining degenerated nerve fibers. Moreover, there may have been differences in the histological

findings as a result of the species of frogs that was studied.

In addition, it may have been possible that the fiber-free stratum zonale described by Scalia et al. was the result of an artifactual separation of fiber layers, produced by an inherent chemical property of the stain (as has been found with some stains, eg. thionin, Potter, 1969).

With regards to electrophysiological data, the responses recorded from the surface layer of the dorsal tectum by Maturana et al. were probably recorded from the stratum opticum (according to Scalia et al.) because of the extreme thinness of the stratum zonale in this area of the tectum.

In this study, most of the electrophysiological fiber responses that were recorded in the surface layer of the anterior tectum, were obtained from area 2_{Ct}. It is possible that the responses recorded from the surface layer may have been produced by volume conduction from the optic fiber terminals in the lower stratum opticum. Verification of the layers from which these responses were recorded, could only be made by further histological investigation.

Furthermore, the distribution of responses in the smaller tectal regions (3_{Ct} and 4_{Ct}) that bordered the mid-region of the tectum, represented the retinal fibers from the medial optic tract, while responses from tectal regions 1_{Ct} and 6_{Ct} represented the fibers from the lateral optic tract that pass along around the tectal perimeter (Potter, 1969).

In four preparations a discrepancy in response thresholds, between fast and slow fiber components, was found. In two preparations (f 6/19, f 7/13), the discrepancy may have been the result of stimulating the muscle surrounding the back of the eye. The basis for this interpretation was that the shape of the compound action potentials recorded, closely resembled a typical electro-myogram (emg). Also, these graded responses increased in amplitude with an increase of the emg threshold. In addition, the response thresholds of these early components were very close to the pre-determined emg threshold.

The findings in preparations 6/27 and 7/3, however, could not be explained as easily. Some possibilities for the unusual differences in response thresholds between early and late components were considered.

It was thought that the differences in the response thresholds for the early and late spike components were due to the distance of the recording electrode from the source of the early responses. In one preparation (frog 6/27), the early spike responses increased in amplitude with the advancement of the recording electrode. This change in response amplitude suggested that an orthodromic field existed in the lower tectal layers, but was not apparent until the stimulating voltage was increased. However, in preparation f 7/3, the early responses were lost when the recording electrode was advanced into the deeper tectal layers. The possibility that the early responses in frog 7/3 originated in the fiber endings of the higher layers above the electrode, was discounted because there were

no early components found during withdrawal of the recording electrode.

Direct retinal stimulation was another possibility considered. That is, the stimulating electrode may have straddled the optic disc in such a way that as the voltage intensity was increased, the current spread into the bipolar layers of the retina, producing an activation of some large optic fibers, and therefore, the appearance of the early responses.

Moreover, the possibility that the early components were an artifact produced directly by a muscle twitch (at the eye), or indirectly by a muscle twitch that stimulated some optic fibers near the eye, was thought unlikely, in view of the fact, that the response threshold of these early components was at least 10 volts below the emg threshold.

Finally, the late occurring fast responses may have been the result of volume conduction produced by the stimulated motor nerve fiber innervating the eye at the optic disc.

But, even though the characteristics of these early and late components were found in the same area of the tectum and were found to be similar in appearance, there is the possibility that these fast and slow responses were produced by two different and separate physiological mechanisms.

With respect to individual fiber components, fast fibers were recorded from cell layers of all the tectal areas, from which responses were recorded. This was not consistent with the notion

that there is a specific relationship between fiber size (i.e. velocity speed) and fiber depth, as hypothesized by Maturana et al. (1960). Also, it was thought that the responses recorded were either from the terminal endings of retinal fibers or possibly from tectal cells (that had response characteristics similar to retinal fibers), which have been found to terminate in the fiber layers of the tectum (Lazar and Szekely, 1967). In figure 17, the early spike responses recorded from the surface layers (i.e. stratum opticum) of area 2_{Ct}, were found to increase to a maximum amplitude at a depth of 830μ below the tectal surface. The response amplitude declined with the advancement of the recording electrode. It was thought that these early spike responses, found in the deeper layers of area 2_{Ct}, originated from tectal cells or possibly from the synaptic terminals of large optic fibers.

The possibility that these responses were recorded from the same fiber terminals, because fibers were pushed down ahead of the advancing electrode, was judged unlikely (in this example), because of the changes in response amplitude that were recorded during the advancement of the electrode. However, it was possible that other early responses recorded in the deeper layers were due to pushing down on large fiber bundles by the recording electrode. Also, the early spike components found in the deeper tectal layers, could have been attributed to the transmission of spikes by volume conduction down to the recording electrode tip, from large fiber endings in the superficial layers.

With respect to the late spike components (latency $\geq$20 msec.) that were recorded from the deeper tectal layers (400μ-2000μ, figure 16), it was thought that these responses may have originated from the terminal endings of very small unmyelinated fibers or from the tectal cells responding monosynaptically to the input from these small unmyelinated fibers, or possibly from the terminals or passing fibers of tectal efferents.

It has been found in other histological (Potter, 1969) and electrophysiological (Gaze and Jacobson, 1962) studies that the majority of tectal cells are located in the deepest layers of the rostral tectum. In this study, it was difficult to distinguish between spikes from tectal neurons and optic tract fibers. But according to the findings of other investigators (Maturana et al., 1960; Lazar and Szekely, 1967; Scalia et al., 1968; Potter, 1969), there was a high probability that most of the responses found in the deeper layers (i.e. below 220μ) originated from tectal cells. If this was the case, the trimodal distribution of responses in the deeper layers of $^{2}C_{t}$ and $^{1}C_{t}$ reflected the latency of responses produced by the synaptic delays of small and large size fibers on tectal cells. For example, the shortest response latency recorded from the deep layers (2000μ) in $^{2}C_{t}$ was .8 msec. This short latent period of responses was interpreted to be the result of large myelinated fiber components (conduction speed of 20m/sec.) with a response delay of .3 msec. and a monosynaptic delay of .5 msec.

Responses to optic nerve stimulation in the ipsilateral tectum were recorded only in the midline area (4_{It}). The range of response latencies (.8 msec to 36 msec.) recorded in this tectal region was similar to that found in the corresponding area (4_{Ct}) in the contralateral tectum. Also, fast responding fibers were found to have a relatively high threshold (45 - 50 volts), which suggested that these responses originated from the terminals of very small fibers that projected directly from the ipsilateral optic nerve. This finding was consistent with the observation of small direct retinal projections to the ipsilateral tectum made by Goldberg and Kotani (1970). However, none of the necessary control procedures (i.e. transection between tecta and inactivation of t' the contralateral optic tract) were used in conjunction with these results.

The fact that no responses were recorded in any other part of the ipsilateral tectum and hippocampi, was thought to be due (in part) to the inactivation of the polysynaptic pathways to these areas. That is, the anesthetic, Diabutal, has been found (Karamian et al., 1966) to suppress evoked responses in the frog's central nervous system. Moreover, it has been hypothesized (Bishop, 1933) that electrical stimulation does not provide the necessary temporal code to propagate multisnyaptic transmission to orthodromic stimula-

tion.

The evoked responses recorded from both tecta and hippocampi to photic stimulation favored this hypothesis. However, the low percentage of success in obtaining results in the visual experiments was also thought to be due to the nature of the anesthetic that was used.

The difference in response latencies recorded in the corresponding areas of both tecta, showed the ipsilateral response to be 36 msec. longer than in the contralateral area. This demonstration of an intertectal delay was consistent with the findings of other investigators (Andrew, 1955; Gaze and Jacobson, 1962a: Fite, 1969). In contrast, the evoked responses recorded from the ipsilateral hippocampus were found to have a latency 18 msec. shorter than the responses recorded in the corresponding area of the contralateral hippocampus. The shape (i.e.low, positive amplitude) of the responses recorded in both hippocampi were not consistent with those reported by Servit and Strejckova (1970). Moreover, these investigators and others (Karamian et al., 1966) did not report any responses in the ipsilateral hippocampus. But, the latent period of responses in the contralateral hippocampus (107 msec.) was consistent with Karamian et al.'s findings.

However, it is necessary that these results from photic stimulation, particularly in the forebrain area, be qualified. There were no controls used in the visual stimulation experiments to determine whether the responses found in the forebrain area were due to passive

conduction from the proximal (diencephalon) or distal (tecta) structures. Also, evoked responses in the forebrain may have been the result of the spread of ERG (electroretinogram) from the stimulated eye. Finally, there was the possibility that the responses evoked in the forebrain areas were produced from the excitation (of the photo sensitive) pineal eye located between the animal's eyes. (Dodt and Heerd, 1962).

In conclusion, the primary retinal fibers were trimodally distributed in all areas of the contralateral tectum, with the greatest representation of fast and slow fiber components located in the antero-lateral-tectal region. Furthermore, the dense population of fibers in the mid-anterior-posterior tectum, indicated that the broad anteroventral rim of the contralateral tectum was the principal site of entry of the fibers from the ascending optic tract, and that the afferent fibers projected longitudinally across the surface of the tectum.

With respect to the individual response components, the early spike components were present at all depths of the tectum from which responses were recorded. It was possible that not all of the early components sampled, were mutually exclusive.

In addition, the differential response threshold between fast and slow components in area l_{Ct} raised some interesting questions, none of which could be answered completely. A full explanation for these peculiar findings can not be made without further experimentation.

Also, it was thought that the spike potentials recorded from the cells in the deeper tectal layers, maintained the integrity of their specific presynaptic fiber components in the higher fiber layers.

Finally, with respect to photic stimulation, nothing more conclusive could be said about the results without additional data from both optic tecta and hippocampi, and the employment of the experimental controls described earlier in this paper.

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APPENDIX A. RAW DATA

The following table represents the frequency count of the responses that were used in the generation of the histograms, shown in figure 16, page 55. The extreme left hand column contains the latent time intervals in milliseconds, of the various spike responses that were recorded. Along the top of each column is labeled the tectal areas and the depths (measured in microns) from which the different spike components were recorded.

Time Intervals (msec.)	1Ct						2Ct						3Ct						4Ct						5Ct						6Ct						4It					
	I.L.	+400u	+800u	+1200u	+1600u	+2000u	I.L.	+400u	+800u	+1200u	+1600u	+2000u	I.L.	+400u	+800u	+1200u	+1600u	+2000u	I.L.	+400u	+800u	+1200u	+1600u	+2000u	I.L.	+400u	+800u	+1200u	+1600u	+2000u	I.L.	+400u	+800u	+1200u	+1600u	+2000u	I.L.	+400u	+800u	+1200u	+1600u	+2000u
0.0- 0.9	2	1	1	1	0	1	11	9	8	3	6	3	2	0	1	0	0	0	3	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0
1.0- 1.9	3	3	2	1	0	1	9	7	5	2	0	2	1	0	0	0	0	0	1	0	0	0	0	0	4	1	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0
2.0- 2.9	1	1	2	1	0	0	9	4	1	3	2	2	1	1	1	0	0	0	2	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
3.0- 3.9	1	1	1	1	0	0	9	7	2	2	1	0	2	0	0	0	0	0	2	0	1	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
4.0- 4.9	1	1	0	0	0	0	4	2	2	3	2	2	0	0	0	0	0	0	1	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
5.0- 5.9	3	4	2	2	0	1	11	4	7	1	3	1	1	0	0	0	0	0	2	0	0	0	0	0	2	1	0	0	0	0	1	1	0	0	0	0	2	0	1	0	0	0
6.0- 6.9	1	2	0	0	0	0	7	2	4	3	3	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
7.0- 7.9	1	0	0	0	0	0	4	3	4	2	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
8.0- 8.9	0	0	1	1	0	0	3	1	1	1	2	0	1	0	0	0	0	0	2	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
9.0- 9.9	0	1	0	0	0	1	1	1	3	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10.0-10.9	1	0	1	1	0	1	11	3	3	4	2	0	1	0	0	0	0	0	2	0	0	0	0	0	5	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0
11.0-11.9	0	1	1	0	0	0	4	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
12.0-12.9	0	0	0	0	0	0	1	1	2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13.0-13.9	0	0	2	0	0	0	7	2	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
14.0-14.9	0	0	0	0	0	0	1	2	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
15.0-15.9	0	0	0	0	0	1	5	1	3	2	1	2	3	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0
16.0-16.9	0	1	0	0	0	0	1	1	0	0	2	1	3	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
17.0-17.9	0	0	1	0	0	0	4	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
18.0-18.9	0	0	1	1	0	0	3	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
19.0-19.9	0	0	0	0	0	0	4	0	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20.0-20.9	1	0	0	0	0	0	7	0	2	2	1	0	4	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
21.0-21.9	0	0	1	0	0	1	10	2	0	1	1	1	2	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
22.0-22.9	0	0	1	0	0	0	3	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
23.0-23.9	0	0	0	1	0	0	6	4	2	2	0	1	2	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24.0-24.9	0	0	0	0	0	0	5	2	3	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Time Intervals (msec.)	1Ct					2Ct					3Ct					4Ct					5Ct					6Ct					4Tr				
	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u
25.0-25.9	2	1	1	0	0	0	10	5	6	0	0	3	3	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0
26.0-26.9	2	1	0	1	0	0	10	3	0	1	0	1	1	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
27.0-27.9	0	1	1	0	0	0	6	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
28.0-28.9	3	1	0	0	0	0	7	3	1	1	0	1	2	0	0	0	0	0	2	0	0	0	0	0	4	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0
29.0-29.9	0	2	0	0	0	0	6	1	3	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
30.0-30.9	2	3	2	1	0	0	12	6	2	2	2	1	2	0	0	0	0	0	4	0	0	0	0	0	4	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0
31.0-31.9	3	1	1	0	0	0	4	5	3	1	0	0	1	0	0	0	0	0	4	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0
32.0-32.9	0	1	0	0	0	0	5	3	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33.0-33.9	2	1	1	0	0	0	7	2	3	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	3	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
34.0-34.9	0	1	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35.0-35.9	3	2	1	0	0	0	7	2	4	3	2	2	1	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
36.0-36.9	1	1	0	2	0	0	3	2	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37.0-37.9	1	1	1	0	0	0	0	0	3	1	1	1	0	0	0	0	0	0	3	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
38.0-38.9	1	2	1	1	0	0	7	1	2	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
39.0-39.9	1	0	1	0	0	0	4	4	1	1	1	1	1	0	0	0	0	0	2	0	0	0	0	0	3	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
40.0-40.9	1	2	1	1	0	0	7	2	5	1	1	1	1	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
41.0-41.9	2	1	0	1	0	0	5	2	2	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
42.0-42.9	0	0	0	0	0	0	1	0	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43.0-43.9	0	2	0	0	0	0	7	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
44.0-44.9	0	0	1	0	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45.0-45.9	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
46.0-46.9	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47.0-47.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
48.0-48.9	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
49.0-49.9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Time Intervals (msec.)	1_{Ct}					2_{Ct}					3_{Ct}					4_{Ct}					5_{Ct}					6_{Ct}					4_{It}				
	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u	I.L.	400u	800u	1200u	1600u	2000u
50.0-50.9	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51.0-51.9	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
52.0-52.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53.0-53.9	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
54.0-54.9	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55.0-55.9	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56.0-56.9	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
57.0-57.9	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58.0-58.9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59.0-59.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60.0-60.9	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61.0-61.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62.0-62.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63.0-63.9	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64.0-64.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65.0-65.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66.0-66.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67.0-67.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68.0-68.9	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69.0-69.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70.0-70.9	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

VITA

Anthony R. Tagliaferro, son of Emma and Victor Tagliaferro, was born on June 13, 1946, in Somerville, Massachusetts.

The author attended Boston College from September 1964 until June 1968 where he obtained a Bachelor of Arts Degree in Psychology. Following graduation, he enlisted in the Army Reserves, and spent the following year on active duty at Fort Polk, Louisiana, and Fort Sam Houston, Texas.

In August 1969, he married Virginia J. Sliney in Everett, Massachusetts and for the next two years, September 1969 until July 1971, attended Lehigh University as a Graduate Research Trainee in the Department of Psychology. The author is presently an instructor in the Department of Psychology at Ithaca College, Ithaca, New York.

Mr. and Mrs. Tagliaferro are the proud parents of their one year old son, Jeffrey Paul.