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Microelectrode analysis of the response properties and loci of neurons in frog telencephalon.

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MICROELECTRODE ANALYSIS
OF THE RESPONSE PROPERTIES AND LOCI
OF NEURONS IN FROG TELEENCEPHALON

A Dissertation Presented

By

RUSSELL G. CAREY

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

DOCTOR OF PHILOSOPHY

August, 1977

Major Subject: Psychology

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MICROELECTRODE ANALYSIS
OF THE RESPONSE PROPERTIES AND LOCI
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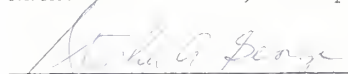
A Dissertation Presented

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ABSTRACT

Microelectrode Analysis of the Response Properties
and Loci of Neurons in Frog Telencephalon
(August, 1977)

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The present study, using extracellular recording techniques, examined the response properties of single-unit and multi-unit activity in the frog telencephalon. The results indicate that the vast majority of units that could be classified as responding to visual and/or tactile stimulation were localized in the ventral regions of the telencephalon. Visually responsive units were localized, not only in the ventral striatum, but also in the nucleus accumbens, lateral forebrain bundle, and the amygdala, pars lateralis. One set of visual, multisensory activity was encountered in the medial pallium. Multisensory (visual-tactile) units were primarily localized in the amygdala, pars lateralis, and to a lesser extent in the ventral striatum. Tactile responsive units were found primarily in the region of the dorsolateral pallium.

All units were highly complex, with very large receptive fields, some of which were binocular. Based on the degree and type of adaptation, the visual and visual-tactile units tentatively have been divided into three classes--"newness", "complex-field adaptors" and "newness-complex". "Newness" units were very responsive to movement and showed rapid adaptation to constant, unvarying movement. Some of the "newness" units also were responsive to tactile stimulation, with little observed adaptation. The "newness" cells were localized in the lateral forebrain bundle and the amygdala, pars lateralis, with all the multisensory "newness" cells localized in the latter.

"Complex-field adaptors" were units that adapted very rapidly to stimulus presentations, with prolonged periods of unresponsiveness. Furthermore, the adaptation appeared to affect large segments (or sectors) of the receptive field. These units were more responsive, or at least did not adapt as rapidly, to small moving targets as compared to complex stimuli. These "complex-field" units mainly were localized in the ventral striatum and lateral forebrain bundle.

The majority of the units ("newness-complex") appeared to have characteristics of both of the above classes, showing rapid adaptation to complex stimuli while remaining

responsive to moving targets for long periods of time. These units were localized in all of the nuclei that were responsive to visual stimuli.

Although the results indicate that both the amygdala, pars lateralis and the striatum receive a tectal input, the present study suggests that the amygdala is homologous to the tectal recipient region of the dorsal ventricular ridge in reptiles and birds. Finally, although the present results are suggestive of a visual projection to the medial pallium and a tactile projection to the dorsolateral pallium, it is unclear how these regions might be homologous to reptilian telencephalic nuclei.

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Traditional theory as expounded by Herrick (1929, 1948) and Diamond & Hall (1969) states that the ingrowth and establishment of the nonolfactory sensory systems in the diencephalon preceded the great expansion of the mammalian thalamus and cortex. Of particular importance in this classical view are the proposed evolution in mammals of a dual visual system arising from (1) a direct, retinothalamic, and (2) an indirect, retino-tecto-thalamo-cortical projection via the recently evolved dorsal lateral geniculate (LDNd) and the lateral posterior (LP) structures, respectively. Diamond & Hall (1969) speculate that the LDNd differentiated from an older mammalian thalamic area in response to the secondary acquisition of the direct retinal input and that the LP is a remnant of this older region. In other words, the tecto-thalamic projection predates that of the direct retino-geniculate projection in mammalian evolution.

According to this classical viewpoint, nonmammalian species were simply considered to be mainly (or exclusively) "tectal" animals. Retinal projections to the thalamic region were thought to be of minor importance and to project primarily to the ventral thalamus, without a concomitant telencephalic projection. Thus, the mammalian and nonmammalian species' visual systems were conceived to be totally different. Such assumptions gained much support from the

earlier physiological studies (Lettvin et al., 1961; Humphrey, 1970) that tentatively demonstrated a sequence of encephalization and complexity of retinal units and central neural structures (derived mainly from the sequence of frog, cat and monkey).

These differences between mammalian and nonmammalian species were derived mainly from inferential physiological and anatomical studies on a relatively limited number of convenient species. Such early investigations indicated that the tecti of the nonmammalian species are relatively large and that the great preponderance of the retinal fibers projected there (Ariens Kappers, 1929; Herrick, 1948). Conversely, in the mammalian species, the tectum (superior colliculus) is reduced in size and the dorsal thalamus (in particular, the lateral geniculate and lateral posterior-pulvinar) is greatly expanded. Further, early experimentation with the mammalian species indicated that removal of the cortical region receiving the lateral geniculate projections rendered the animal effectively blind, whereas tectal lesions produced a greater deficit in nonmammalian species (Kluver, 1941, 1942; Humphrey, 1970; Ingle, 1976).

In contrast to these results, more recent examinations of the vertebrate visual system have indicated that the major retinal projections that are observed in the mammalian species (e.g., dorsal and ventral thalamus, pretectum, tectum, and

hypothalamus) are also found in the nonmammalian species. It is possible, as stated by Ebbesson (1970), that these projections may be shared by all vertebrates. Furthermore, recent behavioral studies with both mammalian and nonmammalian species have indicated that a more complex relationship exists between the thalamus, tectum and telencephalon in mediating visual behavior than previous thought (Ingle, 1977; Snyder & Diamond, 1968; Schnider, 1969).

Much of the problem stems from the classic view of Herrick (1948) indicating olfactory dominance of the telencephalon and diencephalon in the nonmammalian species. Furthermore, according to Herrick, the evolution of these structures was characterized by an ingrowth of non-olfactory sensory systems, reaching its pinnacle in the mammalian species where the other sensory systems (vision, audition and somatosensory) have clearly displaced olfaction. However, recent investigations (as summarized by Ebbesson, et al., 1972) have indicated that in every nonmammalian species studied, visual input dominated the thalamus. When other modalities were investigated, they (with the exception of the tectal input) were found to be relatively unimpressive and mainly non-overlapping. Ebbesson et al., (1972) speculates:

Instead of being marked by the ingrowth of nonolfactory sensory systems, these modalities, especially vision, were probably represented much earlier than hitherto believed. If further experimental analysis of other species remain consistent with this hypothesis, then it would

appear that the system that was supplemented was vision
--not olfaction. (Ebbesson et al., 1972, p. 123, underline added)

Furthermore, recent investigations on species as divergent as birds, frogs, turtles, and even the "archaic" sharks have demonstrated that the olfactory system in no way dominates the telencephalon of these nonmammalian species. As Ebbesson points out, the olfactory representation in the telencephalon of the nonmammalian species is probably no more extensive than in the mammalian species. Ebbesson (1972) further indicated that comparative studies of the optic nuclei in the vast majority of vertebrate phyla examined are vastly similar and may have their origin clear back to the origin of the cartilaginous fish.

It is apparent that much more information will be necessary before any conclusive statements can be made on the possible homologies of the visual nuclei and pathways of birds, reptiles and mammals. The present results, however, are extremely suggestive of this possible homology.¹ In all three vertebrate classes, the following appear to be true:

1. The retina projects to two thalamic nuclei (or nuclear complexes), one dorsal (dorsal lateral geniculate) and one ventral (ventral lateral geniculate);

¹Homologies for central nervous structures are normally based on connective, histochemical and topographical similarities seen in the different species.

2. The ventral nucleus similarly receives direct tectal and telencephalic innervation;
3. The dorsal nucleus projects in a topographical manner to a distinct region of the telencephalon; and
4. A second dorsal thalamic nucleus (e.g., lateral-posterior in mammals, rotundus in birds and reptiles) receives direct tectal projections and projects to a different region of the telecephalon in the respective species.

The question that naturally arises is, are there similarities of these projection systems in the extant species of amphibia, the class of vertebrates that preceded the evolution of the reptiles, birds and mammals?

Amphibians. The great wealth of information regarding the amphibian visual system stems from investigations on urodeles, or tailed species, mainly from Herrick's classic works and more recent work by Jakway & Riss (1972) and Gruberg et al., (1972). An accurate assessment of the visual projections in terms of nuclei, however, is hampered by the relatively undifferentiated state of the neural structure of these species.

The information concerning the visual projection systems in anurans has stemmed from extensive studies on a limited number of species mainly in the family Ranadae and, in

particular, the species Rana pipiens. Caution should then be used when inferring that these results are representative either of the order Salientia or of amphibians as a whole. Keeping these limitations in mind, are there similarities between the projection systems of the ranid species and those seen in reptiles that may suggest possible existing homologies?

Retinal Projections

The retinal projections of Rana mainly have been studied in two species: Rana pipiens (Knapp, et al., 1965; Scalia, et al., 1968; Scalia & Gregory, 1970; Scalia & Fite, 1974) and Rana esculenta (Lazar & Szekely, 1969; Lazar, 1971). The results from the two species are complementary; therefore, only the results of the more extensively examined species (R. pipiens) will be discussed. The retina projects bilaterally to two distinct neuropil regions in the thalamus, the "nucleus" of Bellonci (henceforth referred to as neuropil of Bellonci) and the corpus geniculatum thalami (CPG)--see Figure 1. Although it is generally reported that the retinal projections are restricted to these two neuropil regions and do not extend to the medial cell groups (as is the case in the reptilian species), Scalia and co-workers indicate in their original paper that retinal fibers do end in and among the medial cell groups, most noticeably among the nucleus rotundus and the lateral geniculate nucleus of Frontera (1952).

These retinal afferents have also been verified in the toad Bufo americanus (Ehrlich, personal communication).

The neuropil of Bellonci is essentially composed of two parts: a peripheral myelinated fiber sheath and a central "fiber-free" area. Contralateral degeneration appears throughout the neuropil, whereas ipsilateral degeneration appears to be restricted to the periphery (Scalia & Gregory, 1970) or sheath plexus (Scalia, et al., 1968). Sparse ipsilateral degeneration is observed in the dorsal and ventral corners and along the medial edge of the neuropil CPG. As in Bellonci, the contralateral projection appears to be throughout the entire extent of the neuropil and overlaps that of the ipsilateral projection. Scalia & Fite (1974) have further shown that the retinal projections to these two neuropil regions, as well as to the posterior thalamic and pretectal neuropils, are retino-topographically organized.

It is indeed tempting, when viewing the dorsal and ventral neuropils of the frog anterior thalamus, to consider them as distinct entities and equate them to the dorsal and ventral divisions of the lateral geniculates of reptiles, birds and mammals. At a gross level, their appearance and positions is definitely similar to that seen in the reptilian species. It would simply seem to be a matter of locating the respective cell groups that innervate these neuropil regions for evaluating the possible relationships with other

species. However, the situation is more complex. The Golgi study of Scalia & Gregory (1970) indicates that the vast majority of cell groups (as presently defined) send dendrites into both neuropil regions. This is especially true of the nucleus rotundus and lateral geniculate nucleus of Frontera.

A ventral and dorsal component of the anuran lateral geniculate nucleus can be determined on a cytological basis. Dorsally, the cells are small and densely packed, while ventrally they are larger and scattered; but this subdivision does not appear to correspond to the dorsal-ventral dichotomy used by Frontera (1952). A further segment of this nucleus is enclosed in the sheath plexus of the neuropil of Bellonci.

The cells that send long dendrites and presumably synapse in the CPG, again appear to originate from various cell aggregates, particularly the LGN and nucleus rotundus with additional endings from the ventro-lateral nucleus and possibly the nucleus entopeduncularis. Dendrites from cells of the nucleus entopeduncularis were never observed by Scalia & Gregory to enter the CPG proper; but the nucleus has a lateral extension which invades the optic tract, and some degeneration was found within the nucleus by Scalia & Gregory (1970). Thus, it seems that either the present nuclei of the anterior thalamus should be redivided or that the division into dorsal and ventral neuropil regions is simply not related

to a dorsal-ventral thalamic division. Possibly, these two neuropil regions segregate two different aspects of retinal information which ultimately are received by all the cell groups, unlike that seen in the reptilian and "higher" species, where each cell group receives its independent retinal supply.

Tectothalamic and Thalamotectal Projections

Tectal efferents to the thalamus have been investigated in Rana pipiens (Rubinson, 1968) and Rana esculenta (Lazar, 1969) with relatively similar results that are significant for the understanding of the visual projection system in Rana. The projections are bilateral, with the ipsilateral component being considerably larger. The tectal efferents are almost exclusively restricted to the CPG, posterior thalamic nucleus (lateral neuropil) and the neuropil of Bellonci. Tectal efferents to the Bellonci region are apparently still unresolved and are not mentioned in the review of Fite & Scalia (1976). Electro-physiological recordings by Fite, Carey & Vicario (1977) strongly suggest (at least to the second author) that tectal efferents may project to the neuropil of Bellonci.

Trachtenberg & Ingle (1974) studied the projections from the rostral thalamus to the tectum and found that this projection appears to originate almost exclusively from the

region of the corpus geniculatum laterale (CPL & LGN). This projection is exclusively ipsilateral and projects to both the superficial and deep tectal layers and to the pretectal region. On the basis of these findings, they suggest that CPL is the possible homologue of the ventral lateral geniculate of both mammals and reptiles.

Thalamotelencephalic Projections

Recently, Scalia & Colman (1975) have investigated the thalamic cell populations that give rise to the telencephalic projection in the frog Rana pipiens using the retrograde transport of Horseradish peroxidase (HRP). Their preliminary data indicate that at least two separate cell areas give rise to two distinct afferent projections. One projection is to the medial telencephalic region (i.e., the dorsal pallium/primordial hippocampus) via the medial forebrain bundle--see Figure 2. The second projection via the lateral forebrain bundle ends in the lateral telencephalic regions (i.e., the striatum). The projection to the lateral telencephalic region appears to originate from the cells of the posterolateral nucleus. The posterolateral nucleus is a cellular mass that abuts the lateral neuropil region, the site of the tectal efferent projections. In fact, when the dendrites of the cells of the posterolateral nucleus are backfilled with HRP, the dendrites are observed to extend

into the lateral neuropil region. This system then (tectothalamo-telencephalic) is very reminiscent of the tecto-cortical projection system that has been observed in reptiles, birds and mammals. The projection to the medial telencephalic region seems to originate in the posterocentral thalamic region. It is believed by Scalia & Colman that this portion of the posterocentral nucleus sends dendrites into the dorsal neuropil region of Bellonci, thereby providing a likely candidate for a "LGNd" in the frog. However, adequate backfilling of the dendrites of these cells in posterocentral nucleus necessary to verify this scheme has not been achieved.

Anterograde degeneration studies by Kicliter & Northcutt (1975) have demonstrated that afferents from the dorsal thalamus also project to the dorsal and dorsal lateral pallium of the telencephalon via the medial forebrain bundle (MFB). They suggest that the dorsal lateral pallium and not the medial pallium is the possible homologue of the reptilian general cortex (the site of the LGNd projection in turtle). These results from Scalia & Colman (1975) and Kicliter & Northcutt (1975) indicate that a "dual" thalamo-telencephalic visual projection system may, indeed, exist in the amphibian frog. Recent electro-physiological studies have further suggested the existence of two distinct visually responsive regions in the frog telencephalon. Supin & Gusel'nikov (1964); Karamian et al., (1966) and Vesselkin

et al., (1971) indicate that the primordium hippocampus is the site of neurally evoked activity from electrical stimulation of the optic nerve and parts of the dorsal thalamus, as well as from photic stimulation of the eye. These authors further report that this region of the telencephalon is multi-sensory in that it also responded to electrical stimulation of the sciatic nerve. Liege & Galand (1971) and Gruberg & Ambros (1974), on the other hand, using microelectrode recording techniques, report multi-unit visual activity only in the ventral regions of the telencephalon. Gruberg & Ambros further report that these units were exclusively visual and were not poly-sensory. Of these studies, only that of Gruberg & Ambros marked the exact recording site, and their histological results indicate that the vast majority of the visually responsive units were localized in the region of the ventral lateral striatum.

The purpose of the present study was to further investigate the response properties and loci of neural units in the frog telencephalon, with special emphasis being placed on those units that exhibited responses to visual and/or other sensory stimulation. These results were analyzed in terms of their similarity to the reported sensory responses that occur elsewhere in the nervous system. Finally, the loci and response properties of the visual units were analyzed to determine if (1) a possible dual thalamic projection

exists in the frog as would appear to exist given the results of previous studies, and (2) whether distinct differences in response type are associated with particular telencephalic nuclei. These results should also prove valuable in determining if visual regions exist in frog that may be homologous with the telencephalic, visual-recipient regions of reptiles, birds and mammals.

Methods

Subjects and Surgical Procedure

Healthy Rana pipiens, obtained from a Vermont supplier and maintained and fed under controlled laboratory conditions, were used as subjects. Prior to surgery, the frog was anesthetized by immersion in an aqueous solution of Tricain Methane-Sulfonate, 1-2 gms/1000 cc water (Klicliter, 1973). The frog was placed on a moistened, wooden block and the head securely fastened between a nose clamp and two rods positioned directly behind the jaw bone on each side. Longitudinal and lateral skin incisions were made in order to expose the fronto-parietal bone. The dorsal skull cap overlying the telencephalon and thalamus was removed with the use of a dental burr and the protective dura and arachnoid membranes removed from the region from which recordings

were to be attempted. Extreme care was taken so as not to damage or impair either the pineal, thalamic or telencephalic vascular systems. If damage to these systems occurs, blood clotting and brain hydrocephalus generally occurs, rendering recording either difficult or impossible. The eyes were elevated by use of a small wad of moistened paper inserted in the mouth. The eyes and the exposed muscle tissue were kept moist with mineral oil, and pupillary dilation was achieved with the use of ten percent ophthalmic neosynephrine, topically applied. The surface of the body of the frog was kept moistened during the recording session, since anesthetized and/or curarized frogs can maintain respiration solely through the skin surface. The animal was immobilized for the duration of the experimental session either by (1) light, 0.05 cc, dosage of Tubocurarine (3 mg/cc) intramuscularly injected; (2) continuous soaking with Tricain; or (3) from pithing of the spinal cord.

Apparatus

Microelectrodes. Recording electrodes were conventional Woods-metal filled, glass micropipettes. Electrodes were pulled with a David Kopf vertical pipette puller (Model 700C) to a tip size of two to five microns. The electrodes were filled to the tip with Woods-metal and plated with platinum and gold, similar to the procedures of Dowben and

and Rose (1953) and Gesteland et al., (1959). Electrode impedences were measured at one Hertz with a Frederick Haer Impedence Checker and were normally in the range of 0.1 to 1.0 megohms.

Recording Apparatus. Recording and amplifying circuits were conventional but included a Frederick Haer spike-enhancer module to improve the signal-to-noise ratio. This module appears to be essential for the isolation of single units in neuropil regions of the frog thalamus and telen-cephalon. A Frederick Haer amplitude analyzer followed the spike-enhance, and was connected in parallel with a dual-channel oscilloscope and digital counter. Records of the neural activity were stored on electromagnetic tape for future analysis and for photographing with a oscilloscope-mounted Polaroid camera.

Stimulating Apparatus. An aluminum sphere (radius = 40 cm) mounted on a movable wooden stand was used for the determination of the receptive field of the visual units and for an assessment of the visual responsiveness of the units to moving targets and lights. The inner surface of the sphere was a flat white and the outside surface was marked off in radial coordinates. Circular black targets, ranging in size from 4 mm to 40 mm were moved across the inner surface of the sphere by means of small, hand-held magnets moved on the outer surface. In addition to these circular

targets, square, Munsell-paper targets similar to those used by Muntz (1962) were used to assess the visual responses to moving, colored targets. The entire sphere subtended approximately 120 degrees of visual angle at 40 cm from the animal and when aligned with the mid-point between the eyes, covered the major portion of the frontal, binocular field of view (Fite, 1973). By shifting the sphere away from the center of gaze, the perimeter could be positioned so as to cover most of either the frontal-contralateral or frontal-ipsilateral visual field. A movable tungsten light, in conjunction with the ambient houselights, served to illuminate the inner surface of the perimeter.

A second stimulator, consisting of a 19-volt, 80 watt, GE quartzline light source, shutter and lens assembly, and fiber optic bundle was used to present chromatic stimuli either as small targets projected upon the perimeter or as light projected directly upon the eye of the frog. At the termination of the optic fiber bundle was a second lens assembly which could focus light either as small spots in Maxwellian-view at the pupil (1-2 mm in diameter) or so as to stimulate the whole eye. The fiber optic bundle could also be mounted on a movable arm so as to stimulate anywhere within the frog's visual field. This stimulus system was also used to obtain latency data to visual stimuli. If the receptive-field of the neural activity was small, then the

stimulus light was presented in Maxwellian-view. If the field was large or undeterminable, then the whole eye was illuminated. Latency to the on-off of the stimulus was measured from the onset-offset of the stimulus as triggered electronically by the opening and closing of the shutter. The electronic shutter was connected in series with a F. R. Vetter FM recording adaptor which fed into one of the channels of the stereo tape recorder, while the neural activity fed into the other. All latency-data was recorded on tape for future analysis with an oscilloscope with a calibrated time base.

Stimulus spectral composition and intensity was controlled in front of the shutter assembly with Bausch and Lomb, second-order interference filters, and neutral-density filters, respectively. The spectral characteristics of the interference filters, neutral density filters and the light source itself was previously determined with an ISCO spectral radiometer (Fite, Carey & Vicario, 1977). The interference filters that were used were chosen at points in the spectrum that corresponded with the reported λ -maxima of the frog photoreceptor pigments and ganglion-cell spectral response properties (Reuter, 1969; Reuter & Virtanen, 1969; Backstrom & Reuter, 1975) as follows: 433 nm, 460 nm, 500 nm, 558 nm, 600 nm, and 650 nm. The latter two filters were always used with a short wavelength blocking filter (Wratten

No. 21). Other light stimuli consisted of an ordinary hand-held flashlight and a Welch Allyn ophthalmoscope which can also project assorted bar and circular patterns.

Procedure

Since the time period for recording from any particular unit was relatively short, there was a definite limitation on the amount of data that could be collected from any neural locus. Therefore, it seemed imperative to first assess the general response characteristics of the neural activity before attempting to determine the finer points of any particular response characteristic. Normally, the protocol that was followed was to first determine the general response characteristics of the activity occurring within a region, and then, if time permitted, examine more fully the general response characteristics. The characteristics first examined were:

1. Is there spontaneous activity; and, if so, does the spontaneity change with time?
2. Is there a neuronal response (on and/or off) to gross changes of the general illumination?
3. Is the unit or units contralateral, ipsilateral or binocular?

4. Does the unit or units respond to large moving targets, e.g., hand, body, flashlight, etc.?
5. Is there neuronal response to tactile and/or auditory stimuli?
6. Are there multi-sensory units and/or units that respond to different sensory modalities at a particular neural locus?
7. Is there a response to small moving lights and/or targets?
8. What is the nature of the receptive field of the unit(s), i.e., relatively small (less than ten visual degrees), medium (ten to thirty visual degrees), large (thirty to one-hundred or more visual degrees), or undeterminable?
9. Does the nature of the response change with continuous presentation of a stimulus, thus preventing, or at least hampering, additional assessment of the response characteristics?

The direction of subsequent questions was determined from the results of the above questions, and was greatly influenced by question Number 9. It consisted mainly of collecting additional data on the responsiveness of the unit(s) to direct light stimulation and moving targets, and a more complete examination of the nature and extent of the receptive field of the unit(s).

In general, a search pattern for units was begun at the anterior end of one of the exposed telencephalic lobes. Using penetrations to depths of 500 to 750 microns, the neuronal activity of the dorsal units was first assessed. If unit activity was either not found or was not quantifiable, then penetrations further posterior were made. Since it is also important to know the neural locus of non-visual regions, several of these regions were lesioned for histological verification (see below). This search pattern was used so that over the course of the study, all sectors of the exposed telencephalon would be examined.

After the dorsal search, deeper penetrations, in regions not previously marked with a lesion, were made in order to study the response properties of the more ventral units. A careful record of electrode depth and position along the lobe was maintained in the case of multiple lesions in the same telencephalic lobe. No more than one lesion was made in any particular brain locale (i.e., anterior-dorsal, posterior-ventral, etc.).

For histological localization of the recording sites, small electrolytic lesions (40 to 100 microns) were made by passing eight to ten micro-amps for eight to ten seconds (microelectrode negative). The animal was perfused with saline and formalin and the excised brain dehydrated and embedded in low viscosity nitrocellulose. Twenty-micron,

frontal serial sections were cut with a sliding microtome through the region of the telencephalon and anterior thalamus and stained with a Kluver stain, which clearly reveals both the fiber and cellular architecture of the brain.

Results

Nomenclature for the present study has been taken largely from Hoffman (1963) as adapted by Northcutt and his co-workers (Northcutt, 1974; Northcutt & Royce, 1975; Kicliter & Northcutt, 1975). On the basis of cytoarchitectural and histochemical observations, the frog telencephalon proper is normally divided into dorsal or pallial and ventral or subpallial regions (see Figure 2). The pallium is further subdivided into medial, dorsolateral, ventrolateral and medial regions. The dorsal pallium is considered to be a transitional area between the medial and dorsolateral pallia; and in Nissl-stained material, exact boundaries are difficult and often arbitrary. Northcutt (1974), on the basis of histochemical studies, concludes that the region defined as the dorsal pallium is actually a continuation of the dorsolateral pallium. Therefore, in accordance with Northcutt, the dorsal pallial nucleus will be considered as part of the dorsolateral pallium in the present study.

The ventral subpallial region is subdivided into three medial and five lateral cell nuclei. The medial nuclei are the amygdala, pars medialis, and the dorsal and ventral subdivisions of the septal nuclei. The lateral nuclei normally recognized are the dorsal and ventral subdivisions of the striatum, nucleus accumbens, amygdala, pars lateralis and the nucleus entopeduncularis. The latter nucleus is considered by Northcutt (1974) to be the caudal continuation of the ventral striatum as it merges with the lateral fore-brain bundle.

In general, the units encountered in this study appear (see Table 1) to indicate that the pallia region is considerably less responsive to sensory stimulation than would be expected from the results of evoked potential studies. In contrast, sensory responsive regions in the ventral subpallial areas appear to be more extensive than simply restricted to the region of the ventral striatum and also do not appear to be simply visual.

Dorsal Units

Unit activity in the pallial regions (dorsolateral, ventro-lateral, and medial pallium) of the telencephalon was examined in every animal, and normally five to ten isolated units were examined in each S. Since the majority of these units appeared non-responsive to any external stimulus

parameter used, only a representative sample was marked for histological verification. These dorsal units characteristically maintained a spontaneous rate and both spike amplitude and duration of the individual spikes were pronounced. These spontaneous units were encountered over the majority of the dorsal telencephalon, regardless of midline or lateral penetration and were found from the first 200 microns of the surface to depths of 750 to 1000 microns. More than 200 dorsal units were examined during the course of the study, but relatively few could be classified with any degree of certainty as responding to either visual or tactile stimulation. The majority of the units were either spontaneous with no obvious change in spontaneity when external visual or tactile stimulation was applied or were spontaneous with a pseudo-random rhythm. This latter property added to the problem of determining whether these units were responding to the stimuli being used.

The spontaneous units maintained a continuous rhythm with responses somewhat evenly spaced. This rhythm in certain units would be interrupted by a massive "shutdown" or cessation for the next few seconds, then return to a continuous rhythm. These units characteristically had high response amplitudes and spike duration. Units with smaller amplitudes and similar response frequencies were also observed at the same recording locus.

The "pseudo-random" group also maintained a spontaneous firing pattern, but without the strict regularity observed in the above group. The absence of a constant firing pattern greatly hampered accurate assessment of whether or not these units were responding to the stimulus manipulations. Often, a dramatic change in the response firing (both increases and decreases) would occur with a stimulus manipulation (e.g., change in the illumination level, movement or touch). However, the inability to reproduce this firing change with additional stimulus presentations limited the interpretation of these "pseudo-random" responses. In several of these units, after time lapses of from one to five minutes, response changes again would occur in the presence of the stimulus. Unit activity also varied without deliberate stimulus manipulation, e.g., standing still or with the lights off. Thus, it is not known if the lack of response reproducibility is simply due to rapid adaptation of these units to a repeated stimulus or if the changes observed were random events totally unrelated to the stimuli. It is probably best to simply classify the response of these units to stimulus changes as being very questionable; and if, in fact, they are stimulus-bound, then their response parameters are probably very complex and adapt rapidly.¹

¹It should be pointed out that this "pseudo-random" type of response has also been observed in the visual cortex of the bushbaby (personal observation), tree shrew (Dr. T. Norton,

A third group of dorsal units could definitely be classified as being visual (N = 1) or tactile (N = 4) by their responses. These units maintained either a low or no spontaneous rate, thereby making assessment of their response characteristics more certain. The one region of visual responses (Units of No. 31) was located in the anterior portion of the medial pallium. These units responded to both general changes in the illumination level and to moving targets. The visual responses were rapid to adapt and showed short, brisk responses to initial movements and then gradually became unresponsive to repeated movements. The responses to general changes in the illumination were mainly to the increases in illumination, with very few "off" responses being observed. It is not certain if the units that responded to the offset of illumination were the same units that responded to the onset or increases of illumination. For the most part, single firing of the units was observed from the onset with a latency of 175 to 200 msec for each stimulus presentation. Occasional double-firings of certain units were observed with an interspike latency of approximately fifty msec. Unit firings to chromatic stimuli were mainly

personal communication) and rhesus monkey (Dr. S. Zeki, personal communication) that appeared to be related to edema and possible trauma even when the observable edema was slight. Since the whole lobe was bared in this experiment, these responses may be due to the traumatic effects of such a surgical procedure.

confined to the first two or three presentations of the stimulus, and best responses were obtained at wave-lengths of 460 nm, 500 nm, and 558 nm with lesser responding to stimuli of the longer wave-lengths (600 nm and 650 nm).

Many other units, for example Number 29, in the dorsolateral pallium of the telencephalon at times appeared to be responding to various visual stimuli. However, given the nature of the responding and the pseudo-random spontaneous rate, it could not be determined whether these units were, in fact, visual but extremely complex adaptors, or if the responses were simply coincidental.

Dorsal Tactile Units. Neural responses to tactile stimulation were also recorded in the electrode position of the Units of Number 31. These units appeared as small, background fibers with very short spike-duration and may have represented fibers of passage (Dr. Stephen George, personal communication). Although best responses were obtained by touching/stroking on the contralateral forelimb, lesser responses were observed on the ipsilateral forelimb and snout region. As with the visual responses, these units showed rapid adaptation to repetitive stimulation.

Three sets of units (Numbers 44, 46 and 54) were localized in the telencephalic region of the anterior portion of the dorsolateral pallium. These three sets of units

all responded best to tactile stimulation of certain segregated body regions and fewer responses occurred to stimulation of other body regions. Units of Number 54, for example, gave maximal responses to tactile stimulation of the contralateral forelimb, and in particular the hand digits and pad. Fewer, rapidly adapting responses were also observed to touch of the other appendages. Units of Number 46 gave maximal responses to touch of the ipsilateral forelimb with reduced responding being observed from touch of contralateral forelimb (see Figure 3). This class of tactile-response was also characterized by a prolonged period of discharge at the cessation of the tactile stimulation (release discharge). One particular unit of Number 46 (see Figure 3b) fired only at the initiation and termination of the stimulation. These dorsal, tactile units were very difficult to hold for periods longer than five minutes; and, therefore, the amount of information that was obtained was limited.

Ventral Units--Visual

Unlike the majority of the dorsal units, those encountered in the ventral, subpallial regions could be classified as responding more easily to one or more stimulus dimensions. Many of these units encountered, like the dorsal units, maintained a type of spontaneity. However, the spontaneous activity of these units appeared to decrease during the session, which may reflect the effect of the anesthesia

on these neurons. Decreasing spontaneity over time was observed both in the curarized and Tricaine Methane-Sulfonate anesthetized preparations. Normally, if a region was found that appeared to be visual and showed a high degree of spontaneous activity, the preparation was left alone for an hour or so. If the spontaneous rate had diminished sufficiently at this time, investigations would begin anew on the response characteristics of the unit(s).

Visual units--light. The vast majority of the units that responded to visual stimuli responded to changes in the general illumination level. For the most part, these responses were both "on" and "off" and were rapidly adapting (see Figure 4a). Two units (Numbers 7 and 9) showed exclusive responses to the changing illumination level. These two units maintained spontaneous activity in both light and dark and showed a rapid, transient increase at the termination of illumination or to movement per se. These units greatly resemble the "dimming fibers" seen in the tectum (Lettvin et al., 1961), anterior thalamus (personal observation), and caudal thalamus (Dr. K. Fite, personal communication) except with more complex "behavior". Unit Number 7 located in the neuropil of the ventral striatum would respond only to the termination of all illumination (see Figure 4b) and did not respond to stepwise changes in the illumination level as did the "dimming fibers" (Lettvin et al., 1961). Furthermore,

this particular unit would not respond at the termination of small light sources, but only to large illuminating sources (e.g., the house lights, floor lamp) and thus responded like a "global dimming fiber." The second unit, Number 9 (histology lost), responded not only to the termination of all illumination, but also to stepwise decreases. This unit appeared to be totally ipsilateral with no obvious response on the contralateral side. For the duration held, neither of these units showed any marked adaptation to continuous light terminations.

Many other units with somewhat similar characteristics were seen in the ventral telencephalic regions. During the session, however, these units showed rapid adaptation to repetitive presentations and a decreased spontaneity. Other units maintained no spontaneous rate but showed "off" responses to decreases in the illumination level. It is not clear to what extent the presence of spontaneity should be used in classifying these units, since as stated above the degree of spontaneity generally decreased during a session. Furthermore, the major responses of these "off" units were not to general changes in illumination, but appeared to be to movements within the visual field. It is not presently known if these other "off" type units simply represent variations of the "dimming fiber," convergence with other response classes, or different response classes altogether.

Only one set of "on" units (Number 18) located in nucleus accumbens was encountered during the study. These units were held for only a short period of time, were very movement sensitive throughout the contralateral field, and fired briskly to the first onset of light. To subsequent onsets of light, the latency to respond increased dramatically, and after a few presentations had increased beyond ten seconds and were then unresponsive to further illumination changes (see Figure 5), although still very responsive to movement.

All visual units, with the exception of the two complex "dimming fibers," showed responses to moving stimuli with varying degrees of adaptation to continuous and/or repeated movements. Most, but not all of these units, also displayed sensitivity to illumination changes. For purposes of description, these units will be divided into two main categories--visual-movement and multisensory-movement-tactile--with each being subdivided according to type of observed adaptation.

Visual units--movement. The degree of adaptation that these units underwent varied remarkably between the different units. Three rough classes were observed which may, in fact, represent a continuum rather than distinct classes similar to the continuum for the different classes of tectal cells as suggested by Fite (1969).

"Newness" Cells. At one extreme were units that responded vigorously to any and all movement within the visual field and would adapt only if the movement remained constant (i.e., in a single plane or continuous circular movement); but firing was quickly re-established by simply shifting to a different form of movement. Units with these firing characteristics were localized in the amygdala, pars lateralis (Number 11) and in the lateral forebrain bundle (Numbers 37 and 38). These units are very similar to "newness" cells reported in the tectum by Lettvin et al. (1961), except with much larger receptive fields. Units Numbers 11 and 38 were binocular and responded well throughout the whole field. Unit Number 37 was a large field, contralateral unit and had the best responses to moving targets and lights of any of the units encountered during the study. These units gave a continuous response to target movement which was very brisk with firings of up to twenty to thirty impulses/sec and higher being observed. During this brisk firing, the amplitude of the spikes was often noticed to diminish rapidly to spike heights reduced by fifty percent or more from that of non-rapid firing sequences. The majority of these units responded well to the general changes of the illumination with both "on" and "off" responses, although the "off" response was more prevalent. Latency data was obtained from the units of Numbers 11 and 38. The latency data obtained from the units of

Number 38 were unique in that the ipsilateral response ("off") was considerably faster than the contralateral response (150 to 200 msec vs. 250 to 300 msec) for the same stimulus energy levels.

"Complex-Field Adaptors." Other units showed varying degrees of rapid adaptation to moving stimuli and appeared to fall along a rough continuum. Some of these units showed considerable responsiveness to small moving targets for short periods of time, while more complex stimuli (i.e., a person, a hand, etc.) entering the visual field would produce a single, brisk response, with no responses occurring to successive presentations. These units demonstrated a type of segregation of the various parts of the visual field. That is, introducing the stimulus into a different segment of the visual field (e.g., the superior field) would produce a response from the unit, even though the other segments of the visual field had already been rendered unresponsive. These units had very large receptive fields responding over the entire contralateral field, with either reduced or no firing on the ipsilateral side to small moving targets. Introduction of a complex stimulus into the ipsilateral field, however, would normally produce the rapidly adapting, brisk response. These units, for the most part, exhibited limited responses to general changes in illumination, normally responding with single spikes only to the first and/or second onset-offset of the

lights. It is difficult to determine if those units that did not respond to general illumination changes were, in fact, not responsive or if the responses to such stimuli had already been previously adapted. It is more probable that all of these units were light-sensitive and units that showed no responses had been previously adapted.

Other units (Numbers 2, 52 and 53) only responded to the initial introduction of a stimulus into a part of its receptive field. As with the other complex units, the receptive field appeared to be composed of subsets, each of which apparently underwent its own independent adaptation to a stimulus. The responsiveness to moving targets in these units was greatly reduced, firing best to short jerky movements (from one to three separate bursts). The initiation of the response was not dependent on the stimulus being in any particular part of the field, but rather the unit(s) would fire at different times at different locations within the visual field, in a manner similar to the type response of the so-called "Sameness cells" of Lettvin et al. (1961). The adaptation of these units was prolonged and certain parts of the field appeared to initiate responses only once, making accurate assessment of the total field, especially on the ipsilateral side, undeterminable. One of the units, Number 53, unlike other units, would respond to a resting target for a short duration and then would not respond to the target again when

moved. Although some of these units would respond to moving light targets, the response was very brief and the adaptation very prolonged.

"Newness-Complex" Units. Inbetween these two extremes of "newness" and "complex-field" units were the vast majority of the units encountered in the lateral forebrain bundle (LFB), striatum and nucleus accumbens. These units showed several characteristics of both sets. Complex stimuli would produce single, brisk responses that appeared to adapt out whole sectors of the visual field. On the other hand, small moving targets on the perimeter would produce continuous, although greatly reduced, firing as long as the movement continued to vary. Gradually, the responsiveness of the unit diminished, and for some of the units of this class, the adaptation appeared to be to sectors of the visual field (i.e., a different target would not produce additional firing). For other units, the adaptation appeared to be only to a specific target, and a new target would re-establish firing, although greatly reduced. These units appeared to respond better to short, jerky movements than to long, continuous movements. Responses to the latter were generally an initial firing that decreased rapidly during the movement.

Some of these units (Numbers 13, 19 and 34) responded not during the actual movement but to the cessation of the

movement. These units underwent similar adaptation to repeated stimuli as the above intermediate units.

Multi-Sensory Units

As with the visual units, these multi-sensory units demonstrated varying degrees of adaptation to continuous movement and/or touch and a limited response to changes in the general illumination level. These multi-sensory units appeared to fall into two classes--one showing similarities to the "newness" cells in its responses to movement and little to no adaptation to tactile stimulation. The other class showed similarities to the rapidly adapting "complex-field" units.

Movement-Tactile -- "Newness". This class showed brisk continuous firing to movement that would not adapt unless the movement continued in the same plane or pattern. The response to movement in all these units was more prominent within the contralateral rather than within the ipsilateral visual field. It further appeared that the response to movement solely in the ipsilateral sector was of a different nature than that of the contralateral side. One such unit, Number 31, gave very limited responses to actual movement within the ipsilateral sector but responded briskly to the termination of the movement, or the removal of the moving stimulus from the ipsilateral side.

As with the majority of the other classes, it is difficult to assess the actual responsiveness of these units to simple changes in the illumination level due to the rapid and prolonged adaptation that occurs. At one extreme of responsiveness were units Numbers 25 and 26. These two units showed a spontaneous rate in light and "suppressed" firing in the dark. At the termination of the lights, the units gave a very rapid firing prior to the suppression (see Figure 7). Note the decrease in spike amplitude during this rapid firing sequence. At "on" the units gave a similar rapid response with decreasing amplitude, but not as dynamic as the response to the "off", and then reverted to the spontaneous rate. The prolonged firing to the onset of the lights would diminish with time, and the rapid response to the onset-offset of the illumination would also quickly adapt with continuous presentations. Other units (Numbers 28 and 30) showed no response to either the onset or offset of the illumination level. Unit Number 28 did have a spontaneous rate, but showed no obvious change in firing to illumination changes.

The response to touch of these units is illustrated in Figure 8. The figure shows the neural response to a moving stimulus in a constant plane, the adaptation to the movement, the response to touching of the skin, then movement without touching, and finally with touching again. Note that the neural response is not as dramatic with the second tactile stimulation. Complete adaptation to touching/stroking

was not observed in any of the units. Discharge rates to both touch and movement were in the order of twenty to thirty impulses/second, and one of these units (Number 28) gave a prolonged after-discharged response at the termination of the tactile stimulation.

"Complex". Two sets of units, both of which were located within the ventral striatum, gave responses to both visual and tactile stimulation but in a manner similar to that described above for the complex visual adaptors. These units would give an initial response to the touch or stroking of the skin and then would not respond again for extended periods of time (normally twenty to thirty seconds, but occasionally longer). The response to tactile stimulation was bilateral over the appendages as well as short brisk responses to touch around the snout region. It is difficult with these two sets of units to accurately determine whether the units that responded in one modality also responded in the other mainly due to the complex responses and the fact that the recording was of multi-unit activity. However, it appeared that at least certain units responded to both modalities. Whether these units were multi-sensory or not, the units that responded to the tactile stimulation responded in a totally different way than those classified as multi-sensory, "newness" cells.

Ventral Tactile Units

Only one set of exclusively tactile fibers was encountered in the ventral telencephalon. This set of multi-unit activity (Number 34) was localized in the fibers ventral to the ventral striatum nucleus. These units occurred at a recording locus that was also visually (and possibly auditorily) responsive. The units responded only to the gentle twisting of the contralateral hind digits and did not appear to adapt with continuous and/or repeated twistings. These units were characterized as being small background fibers with very fast spike duration and may, in fact, have been fibers of passage rather than synaptic or soma potentials (Stephen George, personal communication). Although these units may have been responding more to the noxious quality of the twisting, no responses were obtained from gently pricking the skin in the same region that produced the response.

Auditory response. Of all the units studied, only one (Number 36) gave responses that could be related to auditory stimuli and the certainty of auditory response is limited even for this unit. This unit appeared to fire to auditory stimuli such as clanks and metallic banging and responded well to a magnet scraping across the perimeter without a target while in the dark. The responses of this unit adapted rapidly, which further hampered accurate assessment of its possible auditory response.

Neural Loci of Response Groups

Although the amount of data is relatively limited in terms of the number of recordings in each of the nuclear groups, certain classes of responses were observed more frequently at one location than at others. Whether this simply represents sampling biases or a true segregation of response types cannot be determined at this time. With these limitations in mind, the following classifications were observed at the various neural loci.

Amygdala, pars lateralis (APL). The most obvious distinction of the neural response in this region as compared with the other regions is that this locus was the sole site of the multi-sensory (movement-tactile) "newness" type class as well as movement-"newness". These units, as previously mentioned, did not show "field adaptation" but rather adaptation similar to the "newness cells" in the optic tectum as reported by Lettvin et al. These units were characteristically large field, and responded at least over the major part of the visual contralateral field as well as seeming to respond to tactile stimulation over the entire body. The majority of the APL units responded to illumination changes but were rapidly adapting. Most importantly, this region was the site of very sensitive visual movement and visual movement/tactile neurons encountered in the study.

Striatum. The most notable characteristic of the units encountered within and around the ventral lateral fibers of the ventral striatum was the rapid rate of adaptation that the units underwent during either continuous or repeated stimulation. In the majority of these units, the major response was to moving targets; although the responses to movement were not as dynamic as those of APL units. It appeared with most of these units that the rate of adaptation was somehow related to the type of stimuli being used. That is, rapid adaptation (one or two responses) would occur to "complex" stimuli such as the experimenter or parts of his body; and this adaptation appeared to be field dependent. The various units further showed different rates of adaptation to moving targets, with some units maintaining responsiveness for considerable periods of time, while others showed rapid adaptation. Some of these striatal units responded not to the movement of the target but to the termination of the movement. Some units within the striatum also responded to tactile stimulation and again with the same rapid adaptation, appearing to effect large sectors of the body and not just the site of stimulation. With the exception of the "global off" unit, the striatal units that responded to changes in illumination showed rapid and prolonged adaptation lasting for considerable periods of time.

The most characteristic response of these striatal units was to the introduction of a novel stimulus into its

visual field, especially large novel stimuli. This would normally produce a single, brisk response, and then no response to any aspect of movement of that stimulus. One unit (Number 2), also located on the ventral fringe of the striatal cells, maintained a spontaneous rate. At the introduction of a large novel stimulus (i.e., the experimenter entering the room), the unit would first exhibit very brisk responses and then "inhibition" of the spontaneous rate would occur for a few seconds before going back to a spontaneous rate. This response underwent rapid and long-lasting adaptation to repeated stimuli. At one point in the testing of this unit, a co-worker (Dr. K. Fite) was present in the room while the experimenter left and subsequently returned. During the experimenter's absence, the unit continued its spontaneous rate and did not respond to the presence or movements of the co-worker. On the experimenter's entrance into the room, the unit gave its characteristic above response.

Lateral forebrain bundle. As should be expected, the response characteristics of the units encountered within the lateral forebrain bundle (LFB) bore resemblances to the responses in neural regions that are recipients of the LFB fiber, with one notable exception. No unit activity of any sort related to tactile stimulation was observed while recording within the LFB. During the recording, it was often determined since the unit activity was confined to a region

of 100 to 500 microns, that recording was from the LFB. Throughout this region of responsiveness, tactile as well as visual stimulation was given, but no units responsive to tactile stimulation were ever observed. Units responding to visual stimulation, according to lesion sites, were confined to the dorsal aspect of the LFB, which is in accord with the results of anterograde degeneration studies (Kicliter & Northcutt, 1975).

Nucleus Accumbens. Three sets of units (Numbers 18, 19 and 20) were examined in the region of the nucleus accumbens. For the most part, the neural responses in this region were similar to those observed in other regions; and the units could tentatively be classified among the intermediate group of the "newness-complex" cells. However, unlike other neural loci, this nucleus was the site of units showing exclusively "on" responses. The response to continuous presentations of the onset of the lights was also different in that the latency to respond increased with the continuous presentations (see Figure 6).

Miscellaneous units. Three sets of units were examined in the region of the amygdala, pars medialis (APM). These units were very similar to the majority of the dorsal units, maintaining a pseudo-random, spontaneous rate and at times appearing to be responding to the various stimuli, although more likely the responses were simply coincidental.

Two spontaneous units were localized in the region of the anterior lateral septum which were unresponsive to all stimuli. Although attempts were made to examine unit activity in the region of the medial forebrain bundle, ventro-lateral pallium and the dorsal striatum, none of the units in the study were recorded in these regions.

Discussion

The main questions addressed in this investigation were:

1. To what extent are the visual and/or other sensory modalities represented in the dorsal and ventral subdivisions of the telencephalon?
2. What, if any, are the differences in the response characteristics seen in the various loci?
3. To what extent do these response characteristics resemble those reported in the tectum and thalamus?
4. To what extent do these results suggest the existence of possible nuclei homologous with those of other vertebrate classes?

The results, similar to those of Gruberg & Ambros (1974) clearly indicate that the ventral regions of the telencephalon

are the sites of sensory activity, whereas the dorsal regions of the pallium are relatively unresponsive. The present study did, however, localize visual and tactile responsive regions in the dorsal, pallial regions. Further, differing from the study of Gruberg & Ambros, is the finding of visual and/or multi-sensory (visual-tactile) units in cell nuclei other than the striatum; namely, the amygdala, pars lateralis and the nucleus accumbens. The results further indicate that the visual activity resembles the reported visual activity of the frog optic tectum and clearly suggest the possibility of a tecto-thalamo-telencephalic pathway. The present study, however, suggests that the amygdala, pars lateralis and not the striatum, is the site of the cells homologous with the tectal recipient region of the dorsal ventricular ridge in reptiles and birds.

Response Classes

The overwhelming characteristic shared by all of these visual and multi-sensory, visual and tactile, units was the size of the receptive field. Similar to the results of Gruberg & Ambros (1974), no small field units were encountered in the telencephalon. These units responded over the majority of the frontal field-of-view, with many seemingly responsive over the entire contralateral field. Many of the units were binocular, and again the ipsilateral field was in excess

of ninety degrees. Similarly, in those units that were tactile or visual-tactile, responses were elicited from large sectors of the body to tactile stimulation.

Ventral units. Although the visual units in the study have tentatively been placed in categories based on the type and degree of observed adaptation, these categories ("newness", "complex-field", "newness-complex") most likely represent a continuum possibly reflecting the continuum of the tectal cells proposed by Fite (1969). At one extreme are the units classified as "newness-movement" and "newness-movement plus tactile." These units, the majority of which were located in APL, were very responsive to movement over, at least, the entire contralateral field-of-view and showed rapid adaptation to a constant, unvarying movement. The adaptation, however, was only to that particular movement; and firing could be re-established by simply changing the type of movement. In those units that also responded to tactile stimulation, brisk responses could be elicited from the entire body region, with little observed adaptation.

The visual response of these cells is very reminiscent of the tectal cells classified as "newness" by Lettvin et al. (1961) and Fite (1969), except with much larger receptive fields. The tectal "newness" cells of Lettvin et al. had receptive fields of approximately thirty visual degrees and showed transient, adapting responses to illumination

changes. In response to movement, these cells maintained a constant discharge, but would rapidly adapt if the movement was maintained in any constant plane. Lettvin et al. further reports that these tectal cells had optimal preferred directions for movement, however no obvious difference in firing was noticed in the telencephalic units in relation to direction of the movement.

At the other extreme in these telencephalic units are units classified as "complex-field" adaptors. The most prominent feature of these cells was not simply their rapid adaptation to visual stimuli, but that complex stimuli appeared to adapt out whole large segments of the receptive field with as few as one or two presentations, while other segments still remained responsive. The adaptation of a particular sector was profound and often lasting beyond five minutes. Certain features of these units are similar to the tectal cells classified as "Sameness" by Lettvin et al. (1961) and as "extreme adaptors" by Fite (1969). These "complex-field" adaptors appeared to respond to novel stimuli independent of being in any particular part of the visual field and would respond at different times at different locations within the receptive field, similar to the "sameness" cells of the optic tectum. The extremely complex response of these telencephalic cells and the vague description of the characteristics of "sameness" cells by Lettvin et al., make

it difficult to determine how similar these two types of responses are. The tectal cells of Lettvin et al. are not described as undergoing any degree of adaptation; however, Fite (1969) mentions "rapid adaptors" with prolonged periods of non-responsiveness after just one presentation. Unlike the majority of these tectal units described by Fite, the majority of the present cells were not multimodal. In those "complex-field" adaptors that were multimodal, single tactile stimulation would often render whole segments of the animal's body unresponsive to additional stimulation. Again, this adaptation was prolonged.

The majority of the cells encountered, however, had response characteristics with varying degrees of "newness" and "complex-field" responses and are tentatively classified as "Newness-Complex". It was at times very difficult to determine if a cell belonged in the "newness-complex" or "complex-field" categories. This probably reflects the lack of distinct cell classes and the existence of a continuum of responsiveness. Even the "newness" cell of the telencephalon, which were very unique in their response characteristics, often had complex responses associated with stimuli in the ipsilateral field.

It seems probable that these visual responses originate from the optic tectum. Since visual unit activity recorded in the lateral forebrain bundle (LFB) was basically

similar to that localized in the various nuclei, it is probable that this projection from the optic tectum traverses via the LFB. Further, the convergence necessary to form the majority of these large field, complex, units probably occurs prior to the telencephalon, most likely in the lateral neuropil of the anterior thalamus or in the posterolateral nuclei which is believed to receive synaptic input from this neuropil (Scalia & Colman, 1974). No information is presently available on the response properties of either of these thalamic regions.

A problem arises, however, in assessing the route via which the tactile responses reach the telencephalic nuclei. Multisensory cells were described by Fite (1969) in the deep layers of the optic tectum, but it is uncertain if these cells project to the telencephalon. More importantly, no tactile responsive units were encountered in the LFB in either the present study or that of Gruberg & Ambros (1974). It is possible that the tactile fibers traverse in a different segment of the LFB and/or, given the biases of the microelectrode technique, may traverse via fibers that are not readily encountered. Likewise, in the case of the complex, adapting tactile units, it is conceivable that these units may have already previously adapted. Another possibility, however, is that the tactile fibers may not traverse via the lateral forebrain bundle, but in the medial forebrain bundle (MFB).

Tactile unit activity was localized in the region of the dorsolateral pallium, which is a recipient only of MFB fibers. The MFB also projects bilaterally to the APL (Kicliter & Northcutt, 1975). It is possible, then that the tactile innervation of APL is via the MFB and the multi-sensory response is formed at the telencephalic level, rather than elsewhere in the thalamus or optic tectum. As will be discussed later, the APL is also the major recipient of a direct accessory bulb projection. Thus, this nucleus may represent an important region for the combination and integration of sensory information from these major senses.

Dorsal Units

The results of the evoked potential studies of Supin & Guselnikov (1964), Karamian et al. (1966) and Vesselkin et al. (1971) would appear to indicate the dorsal regions of the telencephalon is a multisensory responsive region. In particular, their results indicate that the region of the medial pallium is responsive to electrical stimulation of the optic and sciatic nerves, and to photic stimulation of the eye. These authors indicated widespread evoked responses over the majority of the medial and posterior aspects of the frontal lobe.

Visual units. Scalia & Colman (1974), in their retrograde transport study using the enzyme horseradish

peroxidase (HRP), indicate that injections in the region of the medial pallium selectively stains cells in the anterodorsal subdivision of the posterocentral nucleus of the anterior thalamus. This subdivision of the posterocentral nucleus is believed by Scalia & Colman to be postsynaptic to the neuropil of Bellonci, a major recipient of direct retinal fibers in the thalamus. Their results, in conjunction with those from the evoked potential studies, would seem to indicate that the region of the medial pallium is a highly responsive visual region and may represent a homologue of a "geniculo-cortical" pathway in the frog (Scalia, 1976).

Gruberg & Ambros, on the other hand, report the inability to localize any activity in the pallial regions responsive to visual stimulation. The present study did localize one region of visually responsive units in the medial pallium, but in a region more anterior and lateral than indicated by the evoked potential studies. Visually responsive units from approximately the same anterior region are mentioned by Grusser & Grusser-Cornehls (1976). No information is given in their report on the response properties of these units.

The response properties of the present set of pallial visual units did not appear to be qualitatively different from the majority of visual units recorded elsewhere in the telencephalon. These units responded to illumination changes (predominately "on" responses, but a few "off") and to move-

ment. The response would quickly adapt to any single type of stimulus. Since only one set of units was encountered, however, no statement can be made as to whether all visual units in this region respond similarly.

This medial pallial region, from which the visually responsive units were recorded, was very difficult to reach with the microelectrode, mainly because it is surrounded, dorsally and laterally, by the lateral ventricle. This may explain why unit activity was not readily recorded in this dorsal region. However, even if this limited region does exist, it is uncertain to what extent the visual responses arise solely from the direct retinal projection of the dorsal thalamus. Retinal fibers to the neuropil of Bellonci are reportedly strictly "on" fibers (Muntz, 1962). Activity recorded in this pallial region, while mainly composed of "on" responses also contained "on-off" activity. A recent electrophysiological study (Fite, Carey & Vicario, 1977) has indicated that other than simply "on" fibers can be recorded in the region of the neuropil of Bellonci. It is not known if these "off" fibers are retinal or tectal in origin. Tectal innervation of the dorsal lateral geniculate has been described for other vertebrate species (Ebbesson, 1972). More crucially, however, no data is available concerning the response properties of the cell nuclei postsynaptic to the neuropil of Bellonci. Preliminary investigations of this

region (personal observation) indicate that, unlike the response activity within the neuropil region, the activity among the cell bodies shows considerable adaptation and complex responses.

Tactile units. As with the visual units, very few of the dorsal units could be classified as responding to tactile stimulation. Three sets of multi-unit tactile activity was localized in the dorsal telencephalon. However, these units were localized in the anterior segment of the dorsolateral pallium and not in the medial pallial region. The activity of these units did appear to be different from the tactile responses associated with the region of the amygdala, pars lateralis and striatum in that these units appeared to have maximal responses associated with particular segments of the body. Whether these tactile responses are truly qualitatively different or simply reflect a sampling bias is impossible to determine at present. Since only the MFB is believed to innervate the dorsolateral pallium (Kicliter & Northcutt, 1975), this tactile activity most likely reaches this pallial region via the MFB. It is, however, totally unknown from what thalamic nucleus this projection originates.

The results, then, clearly indicate that the number of sensory-responsive units were neither as widespread nor as massive as the results from the evoked potential studies would seem to indicate. It is, therefore, quizzical why the

evoked potential studies recorded best potentials in these dorsal regions, especially with the use of photic light stimuli. The results of the present study would indicate, if anything, that continuous photic stimulation would render the cells unresponsive. Further, the evoked potentials derived from such stimulation are subject to interpretation problems, or as Gruberg and Ambros restate: ". . . but they were extremely inconsistent, their amplitude was variable and considerable fatigue was displayed in rhythmical stimulation." Finally, the recording of such evoked potentials does not necessitate that they either represent synaptic activity in response to the stimulus or passing fibers relaying such information but may conceivably be non-specific responses (Burns & Smith, 1962; Dr. Stephen George, personal communication).

Dual Visual System

What conclusions can be drawn from the results of the present investigation in relation to the possible existence in Rana of a dual-visual-telencephalic projection similar to that in reptiles, birds and mammals? As summarized by Ebbesson (1972), these species each appear to have two distinct visual projections arising from: (1) a direct retinal-thalamic, and (2) an indirect retinal-tectal-thalamic cortical system via the dorsal lateral geniculate and rotundus/lateral posterior structures, respectively.

Tectofugal system. The present study indicates that visual activity similar to that observed in the tectum occurs in the ventral telencephalon. This is consistent with the suggestion of others (Liege & Garland, 1972; Gruberg & Ambros, 1974; Scalia & Colman, 1974; Scalia, 1976) that the tectum projects to the ventral striatum via the lateral forebrain bundle in Rana. Thus, these results appear to confirm the possible existence of a cell aggregate that is homologous with the cells of the dorsal ventricular ridge (DVR) in reptiles and birds. Karten (1969) and Northcutt & Royce (1975) speculate that the DVR may have developed in response to a migration of the striatal cells into the pallial field and that the tectal projections associated with these striatal cells maintained their visual connectivity.

The results of the present study indicate the existence of a second telencephalic nucleus that also is a recipient of a tectofugal projection; namely, the amygdala, pars lateralis. It should be mentioned that although this nucleus has been classified as a ventral subpallial structure, recent studies suggest that it is, in fact, derived from the lateral pallium and is, therefore, a pallial structure (Northcutt, 1974; Northcutt & Royce, 1975).

Thus, there appears to be two likely candidates for the possible region of the cells from which the DVR could be evolved, each of which appears to receive different visual

information via the LFB. Kicliter & Northcutt (1975) speculate that the ventral striatum of the frog, given its similar topographical relation and connectivity, as well as histochemical similarities (Northcutt, 1974) is homologous with the corpus striatum of reptiles and birds. Northcutt & Royce (1975) further speculate that the "anuran lateral pallium and the pars lateralis of the amygdala are field homologies of the reptilian dorsal ventricular ridge and lateral cortex" (p. 266). The present finding of visual and tactile polymodal cells in the APL will certainly strengthen these suggestions.

Furthermore, it has been shown that in reptiles and mammals (Hall & Ebner, 1970; Pritz, 1975) and possibly birds (Karten, 1970), the nucleus rotundus (lateral posterior in mammals) projects not only to the DVR (peristriate cortex in mammals), but also to the basal telencephalic nuclei of the corpus striatum (basal ganglia in mammals). Hence, it appears that the separate tectal projections to the APL and striatum do not represent two possible structures homologous with the DVR, but a tectal projection scheme similar to that observed in the other vertebrate classes. In agreement with Northcutt (1974), the present study suggests that the basal striatal region and amygdala, pars lateralis are possibly homologous with the reptilian and avian corpus striatum and dorsal ventricular ridge, respectively. Further strengthening

this suggestion are the findings of Halpern (1972) that the main efferent projection to the thalamic nuclei of the posterocentral and posterolateral nuclei arises from the APL and not the striatum. The striatum projects primarily to the midbrain tegmentum which is similar to that described in birds and reptiles (Karten, 1969; Halpern, 1972).

Thalamofugal system. It is more difficult to determine if a "geniculo-telencephalic" projection occurs in Rana that is homologous with that of the other vertebrate classes. The results of the evoked potential studies of (Supin & Guselnikov, 1964; Karamian et al., 1966; Vesselkin et al., 1971) would appear to indicate that the medial pallial region of the frog receives a prominent and extensive visual projection. Their results, in conjunction with those of Halpern et al. (1968), and Scalia & Colman (1974), have prompted certain investigators to suggest that the medial pallium is possibly homologous with the visual recipient region of the general cortex of reptiles (Halpern, 1972; Scalia, 1976). The results of the present study, although suggestive of a visual region in the medial pallium, indicates that it is neither as extensive nor as prominent as previously thought.

The recent histochemical study of Northcutt (1974) indicates that the frog medial pallium is more similar to the medial limbic corticies, and not the general cortical

region of reptiles. Northcutt speculates, on the basis of histochemical and connective similarities, that the region of the dorsolateral pallium is homologous with the general cortical regions of the reptiles. However, although limited tactile activity was localized in the dorsolateral pallium, no activity could be classified as being visual. Thus, the case of a dorsal thalamic visual projection to the dorsal parts of the telencephalon is problematic. The results indicate the possibility of a visual area in the region of the medial pallium, which is presently not thought to give rise to the reptilian general cortex, and no visual activity in the dorsolateral pallium, which is thought to give rise to this region.

Of course, the possibility exists that the frog lacks a retino-thalamic-telencephalic system comparable to that of the other species. The embryological studies of Senn (1974) on the development of the thalamic structure in amphibians and reptiles indicated that the reptilian dorsal thalamus is formed from a part of the "pretectal" region. That is, the pretectal region splits into a caudal part--the pretectum; and a rostral part--the dorsal thalamus. Senn speculates that the dorsal thalamus of the amphibian species is qualitatively different from that of the reptilian species, and the amphibian equivalent of the reptilian dorsal thalamus is still a part of the rostral pretectum. His views are highly

plausible. However, the qualitative difference that this speculation is based upon is that the amphibian species lack a well-differentiated dorsal thalamus (i.e., a clearly distinguishable nucleus rotundus and nucleus dorsolateral anterior, of which the LGNd is a part). Results of the present study indicate that a "rotundus" region may actually exist in the frog. Whether the projection to the medial pallium indicates that a "geniculate" type region also exists is difficult to determine given the present results.

Conrad & Stempf (1975) indicate that in the mammalian tree shrew, Tupia glis, a direct retinal projection exists to the anterodorsal nucleus. This retinal projection with the known anterior thalamic-retrosplenial projection provided a pathway for a direct retinal input to the limbic system. It is possible that the visual projection to the medial pallium of Rana is similar to this third visual projection. It is further possible, given the extreme difficulty encountered in recording from the dorsolateral pallium, that a small, localized visual region does exist in this area. Either of these suggestions may be possible. However, before the "straws are grasped" to account for the data, it may be more prudent to determine, first, how representative the conditions found in Rana are of Amphibia in general. Very possible another species from a different family, such as Bufo, would indicate a different projection scheme for the retino-thalamic system. Recent results (Dr. Glenn Northcutt,

personal communication) indicates that a third, more dorsal neuropil region exists in Bufo that receives a direct retinal projection. The projections of this region may be very enlightening in solving the present dilemma of the locus in amphibians of a region homologous with that of the general cortex of reptiles.

Summary

The present study, using extracellular microelectrode recording technique, examined the response properties of single-unit and multi-unit activity in the frog telencephalon. The results indicate that the vast majority of units that could be classified as responding to visual and/or tactile stimulation were localized in the ventral regions of the telencephalon. Visually responsive units were localized, not only in the region of the ventral striatum, but also in the nucleus accumbens, lateral forebrain bundle, and the amygdala, pars lateralis. One set of visual multi-unit activity was encountered in the medial pallium. Multisensory (visual-tactile) units were primarily localized in the amygdala, pars lateralis and to a lesser extent in the ventral striatum. Tactile responsive units were found primarily in the region of the dorsolateral pallium.

All units were very complex, with large receptive fields, some of which were binocular. The visual and visual-tactile units tentatively have been divided into three classes --"newness", "complex-field adaptors" and "newness-complex"-- based on the degree and type of adaptation. "Newness" units were very responsive to movement over the entire contralateral field and showed rapid adaptation to constant, unvarying movement. Some of the "newness" cells also responded to tactile stimulation essentially over the entire body, with little observed adaptation. The "newness" cells were localized in the lateral forebrain bundle and the amygdala, pars lateralis with all of the multisensory "newness" cells localized in the latter.

"Complex-field adaptors" also appeared to have very large receptive fields responding over the entire contralateral as well as ipsilateral fields of view. These units adapted very rapidly to stimulus presentations with prolonged periods of unresponsiveness. Furthermore, the adaptation appeared to affect large segments (or sectors) of the receptive field. These units were more responsive, or at least did not adapt as rapidly, to small moving targets as compared to complex stimuli. The majority of these "complex-field" units were localized in the ventral striatum and lateral forebrain bundle.

The majority of the units ("newness-complex") appeared to have characteristics of both of the above classes, showing

rapid adaptation to complex stimuli while remaining responsive to moving targets for long periods of time. These units were localized in all of the nuclei that were responsive to visual stimuli. Although the results indicate that both the amygdala, pars lateralis and the striatum receive a tectal input, the present study suggests that the amygdala is homologous with the tectal recipient region of the dorsal ventricular ridge in reptiles. Finally, although the present results are suggestive of a visual projection to the medial pallium and a tactile projection to the dorsolateral pallium, it is unclear how these regions might be homologous to reptilian telencephalic nuclei.

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Table 1. A listing of units encountered in the various cell nuclei.

(a) Ventral units

(b) Dorsal units

Dorsal units reflect only the more "interesting" of the over 200 units examined.

SU--Single unit; MU--Multi-unit; MU(d)--Multi-unit activity with a single unit being determinable.

TABLE 1A

RECORDING SITE	UNIT NUMBER	RESPONSE PROPERTIES
Striatum	2--SU	Complex-field, good response to movement, inhibition to initial introduction of novel stimulus.
	4--MU	Complex-field.
	7--SU	Global off unit.
	10--MU(d)	Newness-complex, complex response on ipsilateral side, otherwise only contralateral, rapid adaptation to targets.
	14--SU	Newness-complex, very movement sensitive, latency data.
	15--SU	Newness-complex, movement sensitive.
	21--MU	Newness-complex, responds to moving light.
	34--MU	Tactile to twisting of paw, possibly fibers of passage.
	35--MU	Complex-field, fires to cessation of movement.
	36--MU(?)	Possible auditory response.
	42--MU	Newness-complex.
	52--MU (3-5)	Very complex-field to visual and tactile.
	53--MU (3-5)	Very complex-field to visual and tactile, fires to resting target.
Amygdala, pars lateralis	5--MU	Newness-complex, complex response on ipsilateral side to novel stimuli.
	11--MU	Newness, binocular unit, latency data mostly off responses, very responsive movement even in the dark.
	25--SU	Newness-tactile and visual, suppressed firing in the dark.

Table 1A (Continued)

RECORDING SITE	UNIT NUMBER	RESPONSE PROPERTIES
	26--SU	Newness-movement and tactile, tactile response is not as brisk as others.
	28--SU	Newness-movement and tactile, spontaneous, no response to light.
	29--SU	Newness to movement, spontaneous in light brisk off response.
	31--SU	Newness--visual and tactile.
Accumbens	18--SU	Quickly adapting "on" unit, spontaneous in light, reduced responsiveness to movement.
	19--SU	Newness-complex, binocular with better response on ipsilateral side.
	20--SU	Movement sensitive, no response to light.
Lateral fore-brain bundle	6--MU(d)	Newness, responds to moving targets and lights, units responded as long as target moved, no adaptation to the movement as with other newness units.
	12--SU	Newness-complex, contralateral.
	13--MU	Newness-complex, good firing to movement that adapts, some units fire at cessation of movement, fires to first on-off of light only.
	23--MU	Complex-field, limited responses to movement.
	24--MU	Newness-complex.
	37--SU	Newness to movement, best responses to movement of all units in study.

Table 1A (Continued)

RECORDING SITE	UNIT NUMBER	RESPONSE PROPERTIES
	38--MU(3)	Newness, binocular units, very movement sensitive, latency data with faster ipsilateral response.
Septum	3--SU	Spontaneous
	56--SU	Spontaneous
Amygdala, pars medialis	49--SU	Spontaneous
	50--MU	Questionable tactile
	51--SU	Questionable responses
No histology	9--SU	Ipsilateral dimming fiber
	39--SU	Very movement sensitive, even to moving lights, very good "on-off" responses to light changes.

TABLE 1B

DORSAL PALLIAL UNITS

RECORDING SITE	UNIT NUMBER	RESPONSE PROPERTIES
Dorso-lateral pallium	1--SU	Spontaneous
	17--SU	Triphasic unit, large amplitude
	27--SU	Possible tactile
	30--SU	Possible visual
	40--MU(d)	Questionable responses
	43--SU	Spontaneous
	44--MU	Tactile response, better in certain body parts than in others.
	45--MU	Questionable visual and tactile responses.
	46--MU	Tactile with prolong release discharge.
	54--MU	Tactile to fore digits, but some response to other body regions.
	55--MU	Tactile to ipsilateral and contralateral forelimbs.
	57--SU	Possible tactile response, appears to inhibit spontaneous rate to tactile stimulation.
Medial Pallium	16--SU	Spontaneous, questionable
	32--MU	Visual to lights and movement
	33--MU	Tactile fibers of passage
	41--SU	Questionable responses
	47--MU	Questionable visual responses
Histology lost	48--MU	Questionable visual and tactile responses.

Figure 1. Drawing of three coronal sections through the frog anterior thalamus illustrating the topographical relation of the neuropil regions and the cell nuclei (from Fite, Carey & Vicario, 1977).

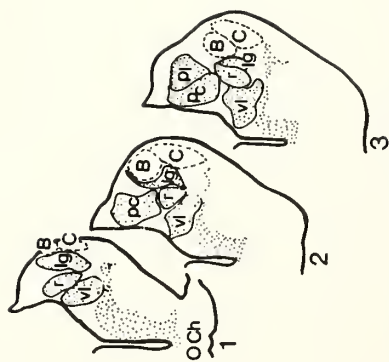


Fig. 1. Drawings of 3 coronal sections through the anterior thalamus showing the neuropil of Bellonci (B), and corpus geniculatum neuropil (C) in relation to thalamic cell groups, lateral geniculate (lg), nucleus rotundus (r), ventrolateral nucleus (vl), posterocentral nucleus (pc), posterolateral nucleus (pl) and optic chiasm (OCh).

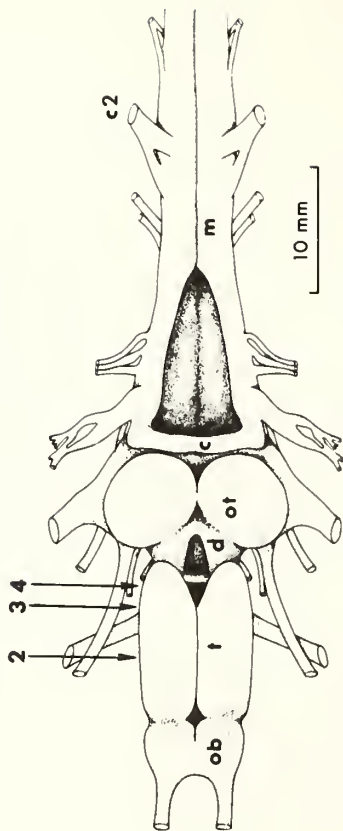
Figure 2. Dorsal view of the brain of frog and three transverse sections illustrating the topographical position of the cell nuclei of the telencephalon. Arrows indicate the level of the three transverse sections (from Northcutt, 1974).

HISTOCHEMISTRY OF THE BULLFROG. TELECEPHALON

Abbreviations

ab, accessory olfactory bulb
 a.pl, amygdala, pars lateralis
 a.pm, amygdala, pars medialis
 bn, bed nucleus of pallial commissure
 c, cerebellum
 c2, second cervical spinal nerve
 d, diencephalon
 dip, dorsal pallium
 en, entopeduncular nucleus
 ifb, lateral forebrain bundle
 lot, lateral olfactory tract
 lp.pd, lateral pallium, pars dorsalis
 lp.py, lateral pallium, pars ventralis
 lb, lateral septal nucleus

m, medulla oblongata
 mp, medial pallium
 ms, medial septal nucleus
 na, nucleus accumbens
 npg, neuropile of the preoptic periventricular gray
 ob, olfactory bulb
 on, optic nerve
 ot, optic tectum
 pg, preoptic periventricular gray
 st.pd, striatum, pars dorsalis
 st.py, striatum, pars ventralis
 t, telencephalon
 v, lateral ventricle



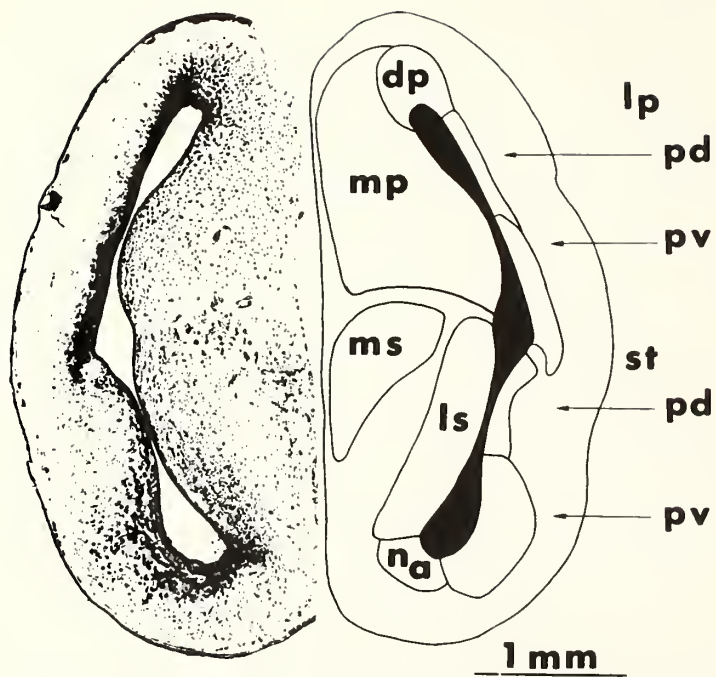


Fig. 2 Transverse section through the rostral telencephalon of the bullfrog. Preparation stained with cresyl violet. At this level the dorsal and ventral divisions of the lateral pallium and the striatum are clearly evident. The dorsal region traditionally designated as dorsal pallium is also seen at this level. This region should probably be included as part of the pars dorsalis of the lateral pallium.

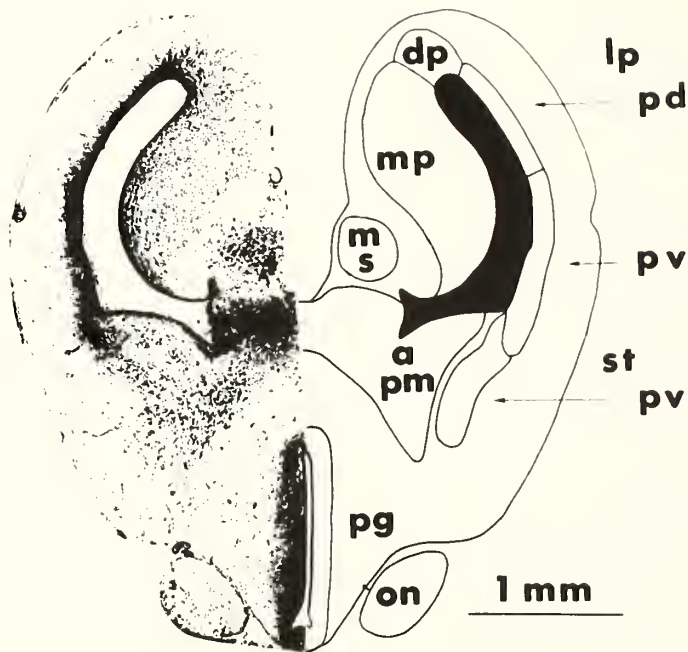


Fig. 3 Transverse section through the telencephalon just rostral to the level of the interven-tricular foramen. The pars medialis of the amygdala reaches its maximal extent at this level. However the pars lateralis of the amygdala will not replace the pars ventralis of the striatum until a more caudal level is reached.

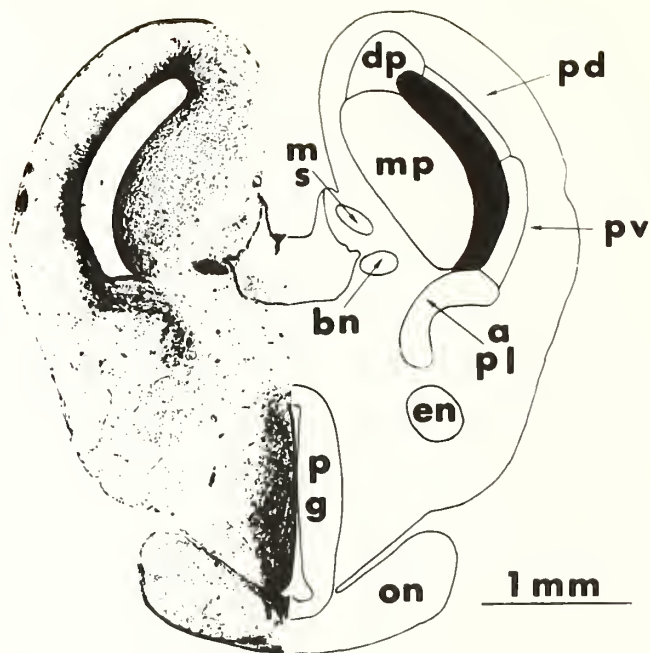


Fig. 4 Transverse section through the telencephalon caudal to the interventricular foramen. The pars medialis of the amygdala has been replaced by the bed nucleus of the anterior commissure. The caudal continuation of the pars ventralis of the striatum is represented by the entopeduncular nucleus. A new cellular mass, the pars lateralis of the amygdala dominates the ventrolateral hemispheric wall at this level.

Figure 3. Photographic records of the multi-unit activity that illustrate the responses to (a) tactile stimulation, and (b) release discharges following termination of stimulation. Top photo shows response to touch of ipsilateral leg of units of Number 46 (scope speed = 2 sec/cm.). Bottom photo shows response to touch of contralateral leg of units of Number 55 (scope speed = 0.5 sec/cm.). Both sets of units were localized in the dorsolateral pallium (see Figure 8). Arrows indicating the onset and termination of stimulation (in this and following records) are approximate times as derived from voice cue on tape and should not be considered as exact.

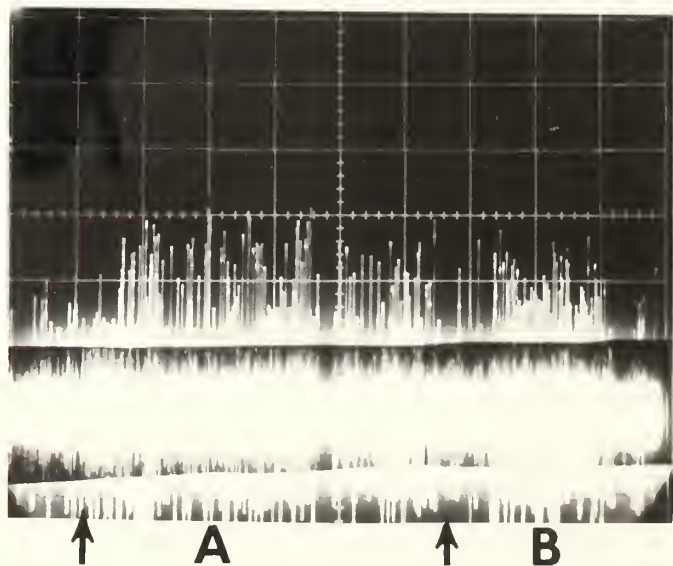
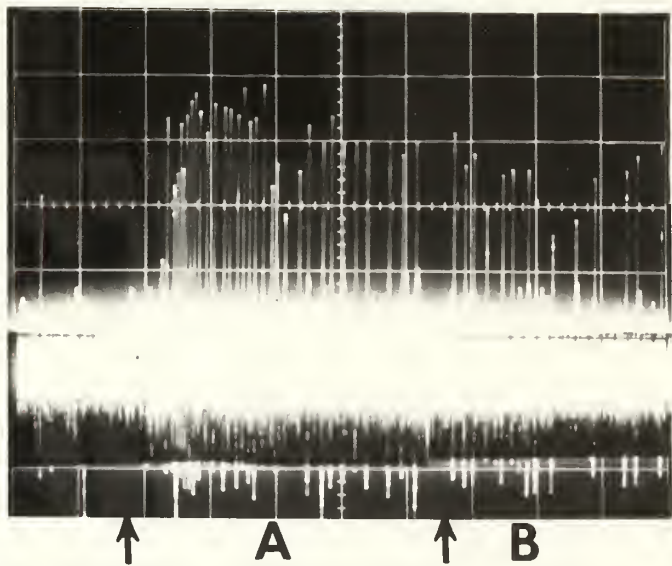


Figure 4. Photographic records of two units illustrating responses to general illumination changes. Top record show the adaptation of Unit Number 12, to continuous onsets and offsets of lights. This unit was localized in the lateral fore-brain bundle (scope speed = 2 sec/cm.). Bottom record shows the response of Unit Number 7 ("global dimming fiber") to termination of all lights (scope speed = 0.5 sec/cm.). Arrows indicate approximate time of on and/or off of lights.

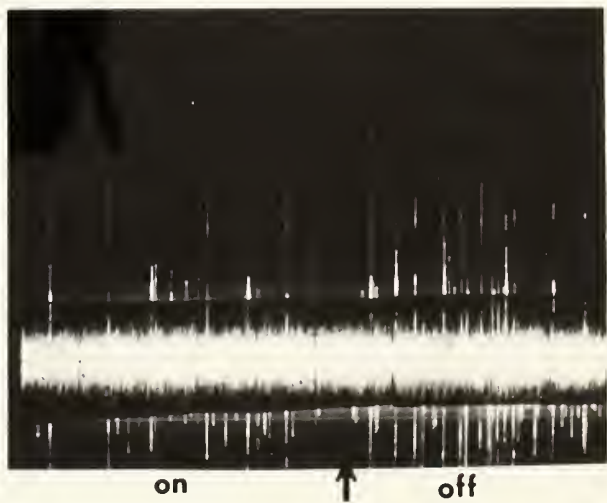
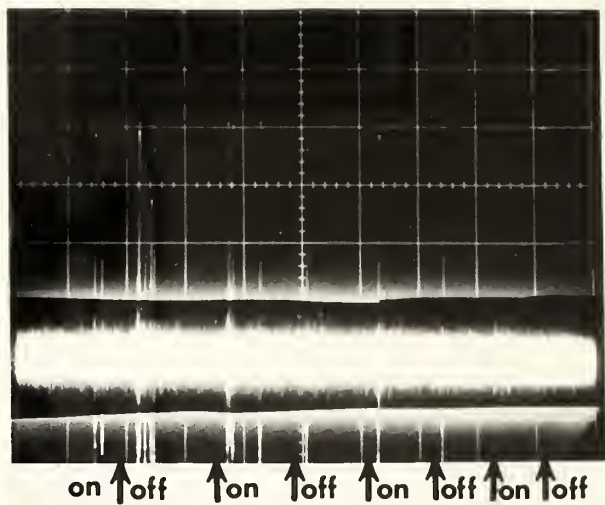
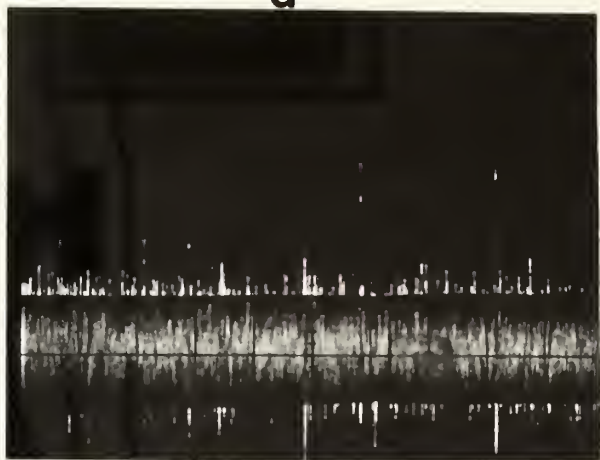


Figure 5. Photographic record of the "on" Unit Number 18. These two photos illustrate the increasing latency to respond of this unit to successive onsets of light.

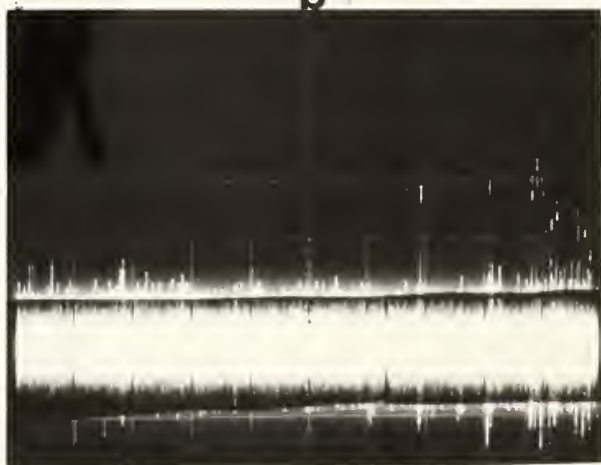
- (a) Latency to respond for first onset of light (scope speed = 0.1 sec/cm.).

- (b) Latency to respond to fourth onset of light, "m" indicates the response to movement (scope speed = 1.0 sec/cm.).

a



b



m

Figure 6. Photographic record of the response of Unit Number 25 to "on" and "off" of lights. Top-left photo shows the response to "off" (A and C) and "on" (B). Note the decreasing spike size during the rapid firing of this unit to the off of the lights (scope speed = 1.0 sec/cm.). Photos A through C are faster speed (0.1 sec/cm.) views of the neural activity at A, B and C of top-left photo. Unit was localized in the amygdala, pars lateralis.

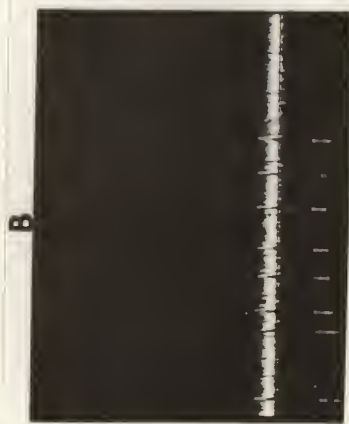
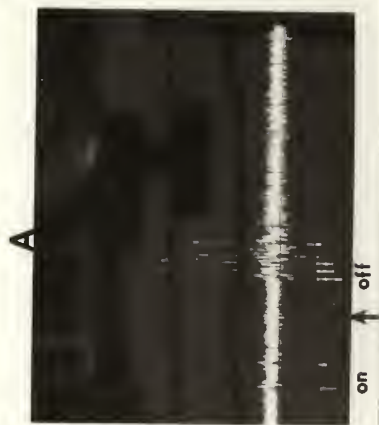
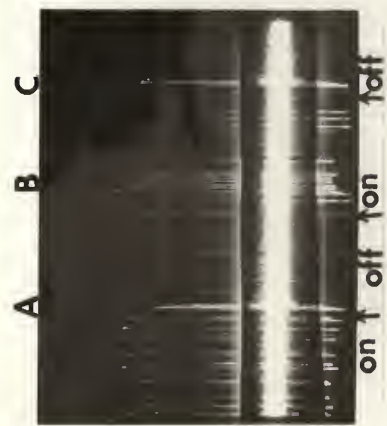


Figure 7. Photographic record of multisensory Unit Number 31 illustrating responses to movement and touch.

- (a) Response to movement without touching;
- (b) Adaptation to the movement;
- (c) Touching of the contralateral leg;
- (d) Moving over leg without touching; and
- (e) Touching again (scope speed = 2 sec/cm.).

Unit was localized in the amygdala, pars lateralis (see Figure 10).

a b c d e

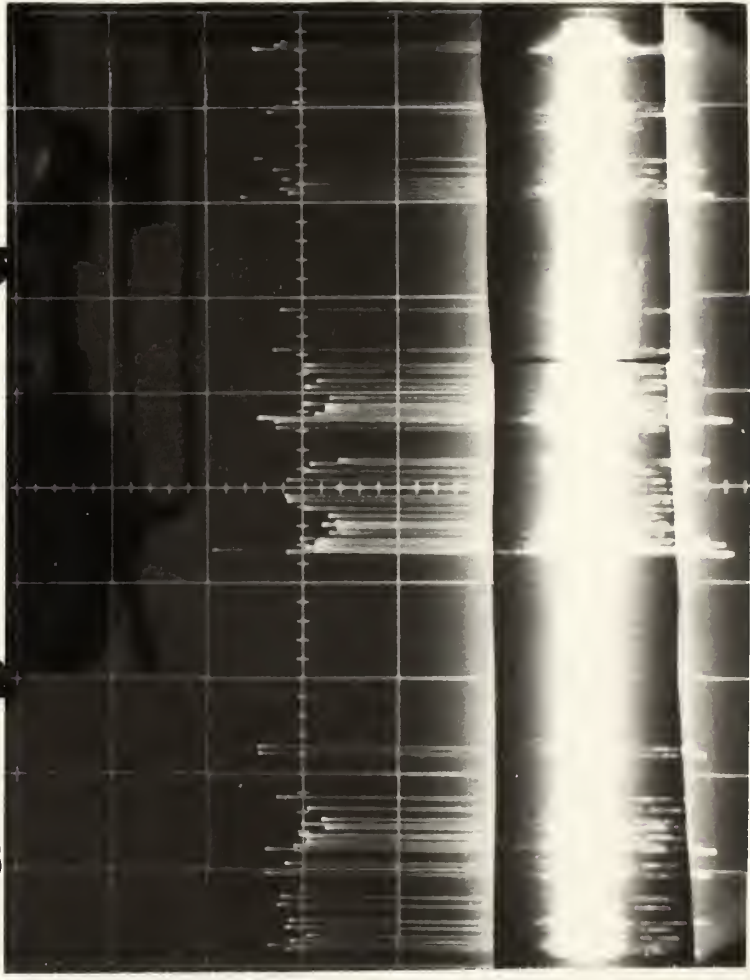


Figure 8. The following figures (8 through 13) are photomicrographs showing examples of the histological localization of the lesion sites associated with neural activity encountered in the frog telencephalon. Arrow indicates the lesion site, scale equals 200 microns. Figure 8 shows the locus of the tactile responsive units of Number 54 localized in the dorsolateral pallium.

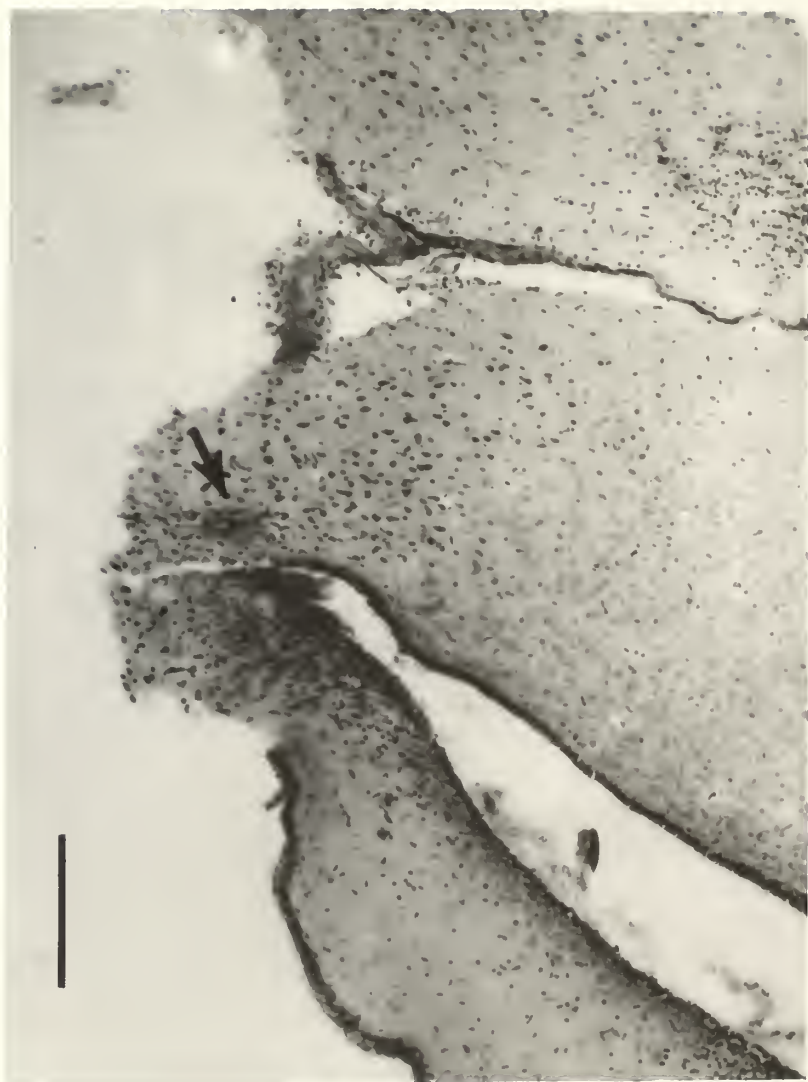


Figure 9. Lesion site of the visually responsive units
(Number 32) localized in the medial pallium.



Figure 10. Example of lesion localized in the amygdala, pars lateralis. This recording site was the locus of the "newness" multisensory Unit Number 31.

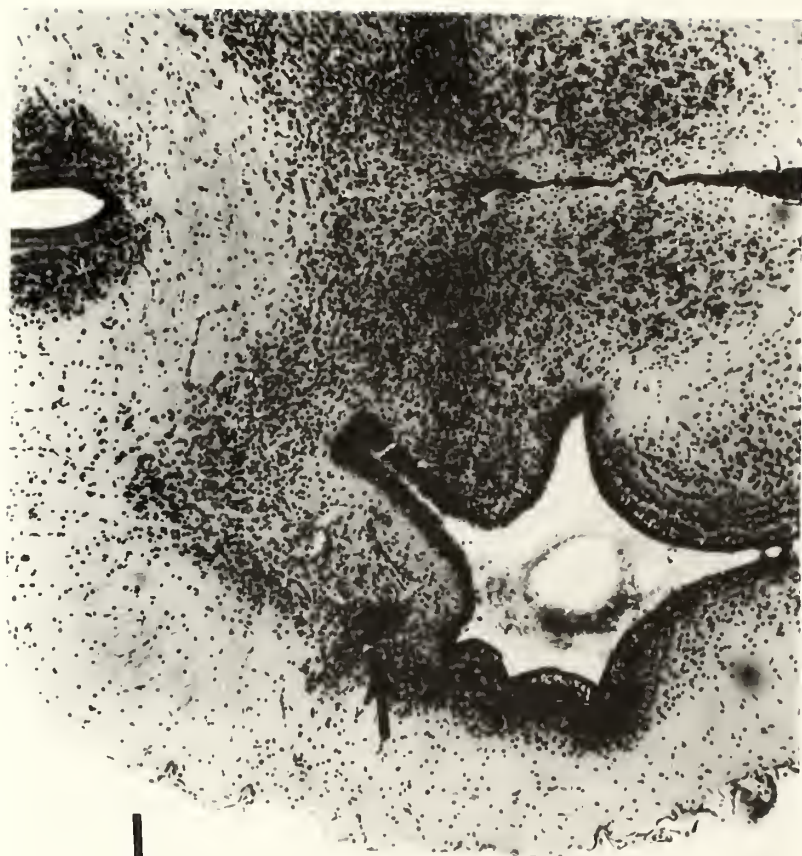


Figure 11. Example of lesion site localized in the ventral striatum. This recording site was the locus of the "complex-adaptor" units of Number 52.

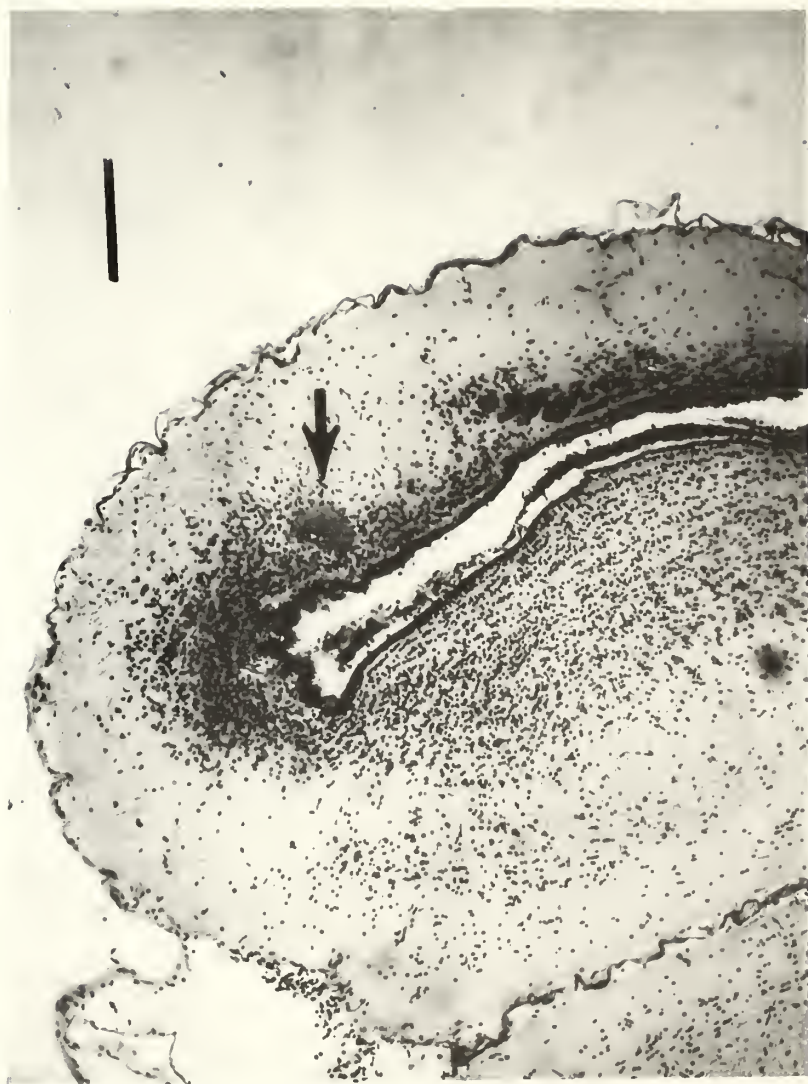


Figure 12. Example of lesion localized in the lateral forebrain bundle. This recording site was the locus of the unit activity of Number 12. All lesions localized in the lateral forebrain bundle were restricted to the dorsal part of the fiber bundle.

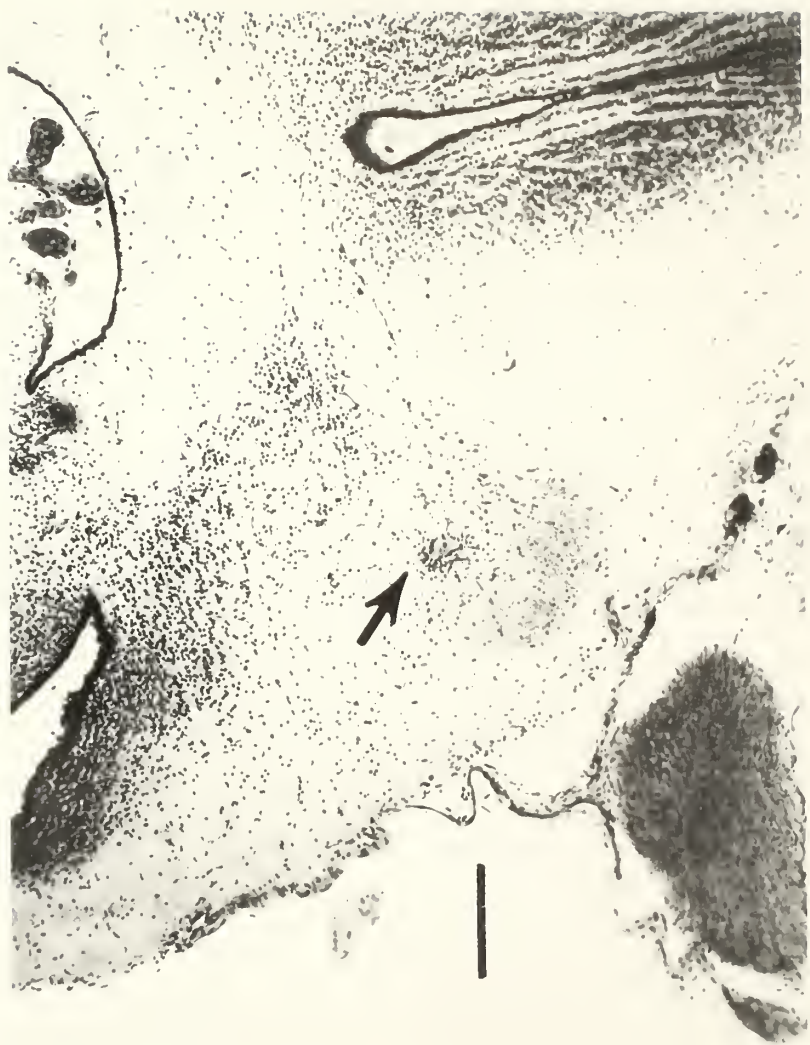


Figure 13. Example of lesion localized in the nucleus accumbens. This recording site was the locus of the exclusive "on" activity of Unit Number 18.



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