

# Some Histochemical Observations on the Telencephalon of the Bullfrog, *Rana catesbeiana* Shaw

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**ABSTRACT** The histochemically determined distribution of acetylcholinesterase, monoamine oxidase and succinate dehydrogenase in the telencephalon of the bullfrog supports the classically recognized divisions of the pallium and subpallium. Analysis also corroborates the following generally recognized anuran-amniotic homologies: anuran medial pallium to amniotic medial cortex, anuran septal nuclei to amniotic septal nuclei, anuran striatum to amniotic corpus striatum. On topographical and histochemical criteria the ventro-caudal and basomedial portions of the anuran telencephalon are considered possible homologues to the mammalian amygdala. It is suggested that two divisions can be recognized: a pars lateralis which may be homologous to the mammalian cortico-medial group, and a pars medialis which may be homologous to the mammalian baso-lateral group. Further analysis suggests, particularly when viewed in the light of recent experimental anatomical studies, that the anuran lateral pallium consists of a pars dorsalis and a pars ventralis. The pars dorsalis may be the reptilian homologue of the dorsal cortex and the pars ventralis may be the field homologue of both the reptilian piriform cortex and the dorsal ventricular ridge.

Recent advances in neurohistochemistry have significantly increased the armamentarium with which neuroanatomists search for clues to central nervous system homologies and have thus provided a better understanding of vertebrate brain evolution. The availability of a new investigative method is particularly useful for application to the complexities of telencephalic organization. The variation of this structure among vertebrates is extensive, and as homologies are pragmatically based on similarities between structures, the recognition of telencephalic homologies has, at best, been extremely difficult. The past 100 years have demonstrated that no single method has yet been the answer to unravelling homologies in this brain region, nor is histochemistry likely by itself to be a neural Rosetta Stone. It is, however, a welcome tool that can yield data greatly facilitating the identification of telencephalic homologies.

Perhaps the most striking difference in the telencephalic organization of most an-amniotic and amniotic vertebrates is the elaboration in amnioties of a dorsal ventricular ridge. In reptiles and birds the

dorsal ventricular ridge appears to form by a proliferation of the lateral pallial wall (Johnston, '16; Kuhlenbeck, '38; Källén, '62). This proliferation of cells almost obliterates the lateral ventricle and results in a mass of neural tissue with a variable number of recognizable cytological fields in different taxa (Karten and Hodos, '67; Northcutt, '67, '70a). Despite this cytological variability, all amniotic taxa that have been examined experimentally possess a dorsal ventricular ridge which receives discrete thalamic projections related to vision and audition (Karten, '68, '70; Hall and Ebner, '70; Pritz, '72, '73). Comparisons between sauropsid vertebrates and mammals based on a wide variety of techniques suggest that the sauropsid dorsal ventricular ridge is homologous to part of mammalian isocortex (Källén, '62; Karten, '69; Northcutt, '69a,b; Nauta and Karten, '70; Parent and Olivier, '70).

Does the telencephalon of living amphibians possess a field of neurons homologous to the sauropsid dorsal ventricular ridge? If so, what is its topographical position and what are its connections with other forebrain structures? In an attempt

to partially answer the first of these questions the following histochemical studies were undertaken in the bullfrog, *Rana catesbeiana* Shaw. This species was chosen as it possesses a well differentiated brain which maximizes the ease of these studies.

#### MATERIALS AND METHODS

##### *Normal anatomy*

For study of the normal anatomy of the telencephalon, paraffin serial sections in the three standard anatomical planes were available and were stained with cresyl violet and the Bodian silver method. Comparisons with cytoarchitectonic relationships in other anurans were made from comparative material available in the collection of the Department of Zoology at The University of Michigan. Taxa examined include: *Ascaphus truei*, *Bufo americanus*, *Bufo marinus*, *Ceratophrys varia*, *Hyla cinerea*, *Rana pipiens*, *Rana temporaria*, *Scaphiopus hammondi*, and *Xenopus laevis*.

##### *Histochemistry*

Animals were killed by decapitation without anesthesia. Following decapitation, the brains were placed in plastic embedding molds containing a commercially prepared, water-soluble resin. Quick-freeze was achieved by immersing the brains in 2-methyl-butane cooled to  $-70^{\circ}\text{C}$ . Twenty-five micron transverse sections were then cut on a Harris cryostat at  $-20^{\circ}\text{C}$ . The sections were immediately attached to slides and dried for 10 minutes in a vacuum-desiccator at room temperature. The methods for demonstrating various enzymatic activities were as follows: the method of Koelle (Gomori, '52) for acetylcholinesterase (AChE), the method of Glenner et al. ('57) for monoamine oxidase (MAO), and the method of Pearse ('60) for succinate dehydrogenase (SDH). Incubation periods ranged from 30 minutes to 2 hours at  $30-42^{\circ}\text{C}$ . An incubation period of one hour at  $42^{\circ}\text{C}$  was finally selected as optimal for all three histochemical methods. As a control for the specificity of the cholinesterases demonstrated, additional sections were incubated in the reaction mixture with butyrylthiocholine rather than acetylthiocholine as the substrate. No nonspecific cholinesterases were demonstrated by this method. These results

are in agreement with the results of Shen et al. ('55) who were also unable to demonstrate nonspecific cholinesterases either manometrically or histochemically in anuran brains. As a control for the specificity of monoamine oxidase, sections were incubated in the reaction mixture from which tryptamine hydrochloride had been omitted. In these cases no staining reaction was obtained. No specific chemical inhibitors of AChE or MAO were employed as further controls.

The regional distribution of enzymatic reactions and their relative activities were analyzed by projecting individual sections and tracing the outline of the sections and the boundaries of the reactive zones. The optical density or absorbance (O.D.) of these zones was then measured using a Photovolt photometer (Model 502M) coupled to a Leitz Ortholux II microscope. The relative O.D. of different zones restricted to a single brain section was determined by setting the photometer to read infinite density when no light fell on the photocell and to read zero density when light was transmitted to the photocell through an area of the brain section judged to be most free of an enzymatic reaction. All measurements were made with a white light source (12v 50W tungsten halogen lamp). O.D. values less than 0.15 were not reported since these values fall within the range of background absorbance of the unstained tissue sections. The range of intensities of the histochemical reactions is reported in terms of O.D. values to avoid the more subjective terms of light, intermediate or heavy staining reaction which have usually been reported in studies of this nature.

#### RESULTS

##### *Normal anatomy*

Nomenclature in this study was taken largely from Hoffman ('63) with several exceptions. The terms dorsal, lateral and medial pallia (figs. 2-4) are used in place of Hoffman's terms primordium general pallium, primordium piriform area and primordium hippocampi in order to avoid the homologies implied by these terms. The recognition of a distinct dorsal pallium is rather arbitrary. An examination of the cytoarchitectonics of the dorsal roof

## 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  
 dp, dorsal pallium  
 en, entopeduncular nucleus  
 lfb, lateral forebrain bundle  
 lot, lateral olfactory tract  
 lp,pd, lateral pallium, pars dorsalis  
 lp,pv, lateral pallium, pars ventralis  
 ls, 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,pv, striatum, pars ventralis  
 t, telencephalon  
 v, lateral ventricle

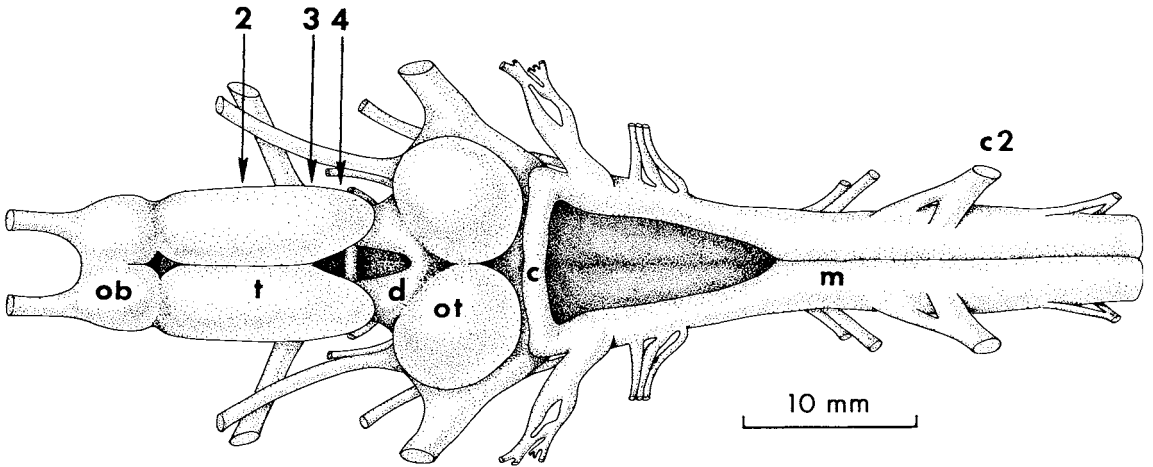


Fig. 1 Dorsal view of the brain of the bullfrog, *Rana catesbeiana*. Arrows indicate the level of transverse sections illustrated in figures 2 through 4.

(figs. 2–4) clearly reveals a change in the packing of the cell somata. This region of transition from the medial pallium to the lateral pallium, 0.38 millimeters in cross-sectional diameter, has traditionally been considered homologous to the dorsal cortex of reptiles. The lateral pallium in *R. catesbeiana* can clearly be divided into at least two distinct cytological fields; a pars dorsalis and a pars ventralis. The pars ventralis of the lateral pallium is one of the cytological targets of the lateral olfactory tract (Scalia et al., '68; Royce and Northcutt, '69). The lateral olfactory tract only projects to the ventral half of the pars dorsalis of the lateral pallium. Further experimental studies may require a new interpretation of pallial boundaries in which the presently recognized dorsal pallium is only considered as a cytological

transition between the medial pallium and the pars dorsalis of the lateral pallium. The pars dorsalis of the lateral pallium might then be redefined as the homologue of the reptilian dorsal cortex.

Rostrally the ventrolateral hemispheric wall consists of a tier of nuclei: a lateral pars dorsalis and pars ventralis of the striatum proper and a medial nucleus accumbens adjacent to the septal nuclei (figs. 2–4). This region of the hemispheric wall is composed of a series of cellular laminae whose spacing and packing density varies almost continuously in both a rostro-caudal and a dorso-ventral direction. There are no cell free areas to aid in the recognition of subdivisions. For this reason no general agreement exists in the literature on the basic number of recognizable cytological units or their homologous rela-

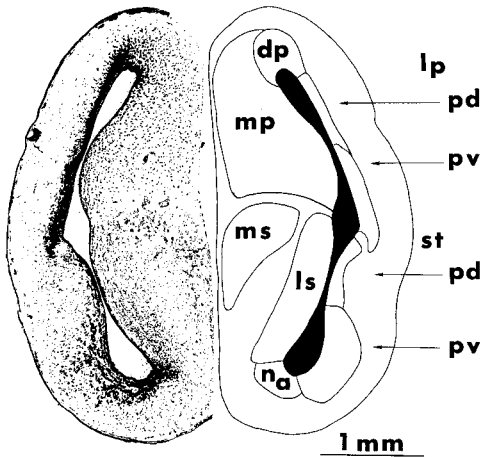


Fig. 2 Transverse section through the rostral telencephalon of the bullfrog. Preparation stained with cresyl violet. At this level the dorsal and ventral divisions of the lateral pallium and the striatum are clearly evident. The dorsal region traditionally designated as dorsal pallium is also seen at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

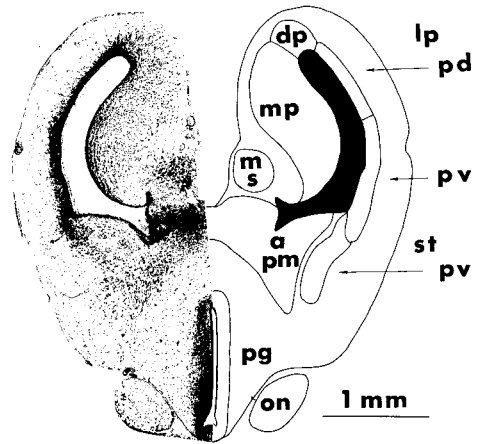


Fig. 3 Transverse section through the telencephalon just rostral to the level of the interventricular foramen. The pars medialis of the amygdala reaches its maximal extent at this level. However the pars lateralis of the amygdala will not replace the pars ventralis of the striatum until a more caudal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

tionships with amniotic taxa. The nucleus accumbens of the present account is defined as a population of cells arising just caudal to the accessory olfactory bulb and occupying a subependymal position in the floor of the lateral ventricle. These cell somata are closely packed and stain more darkly with cresyl violet than the more laterally placed cell populations. At rostral levels this population corresponds to the population similarly labeled by Hoffman ('63). The cell population labeled in the present study as nucleus accumbens could not be traced beyond the rostral lamina terminalis and does not include the caudal cellular population labeled as accumbens by Hoffman ('63) in his figures 11, 14, 27 and 28. Hoffman's caudal cellular population is interpreted as the pars medialis of the amygdaloid complex in the present study.

Two distinct cellular populations are interpreted as parts of the amygdaloid complex in the present study. One population, pars medialis (fig. 3), is thought to be of basal origin as it lies ventral to the septal nuclei while the second population, pars lateralis (fig. 4), is thought to be of pallial origin as its cells are con-

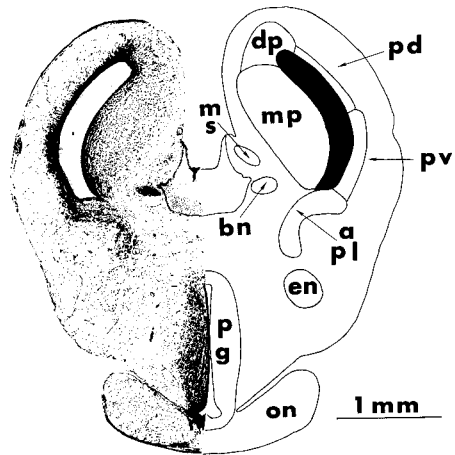


Fig. 4 Transverse section through the telencephalon caudal to the interventricular foramen. The pars medialis of the amygdala has been replaced by the bed nucleus of the anterior commissure. The caudal continuation of the pars ventralis of the striatum is represented by the entopeduncular nucleus. A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

tinuous with the ventral part of the lateral pallium. The pars medialis of the amygdala begins just rostral to the lamina terminalis as a cellular population immediately ventral to the lateral septal nucleus. The cellular nuclei of the pars

medialis are smaller than those of the nucleus accumbens and are far more densely packed than those of the lateral septal nucleus. The pars medialis continues to enlarge as it is traced caudally where laterally it forms a distinct ridge in the floor of the lateral ventricle, and medially it fuses with the contralateral pars medialis across the lamina terminalis (fig. 3). The pars medialis can not be traced caudal to the rostral edge of the anterior commissure. The topographical position of pars medialis ventral to the septal nuclei and continuing into the lamina terminalis suggests that this cellular population is of basal origin.

Caudally the ventrolateral hemispheric wall is formed by the second amygdaloid population, the pars lateralis (fig. 4). At

the level of the lamina terminalis, the pars dorsalis of the striatum can no longer be followed as a distinct population. The pars ventralis of the striatum continues caudally but becomes restricted both laterally and medially. As the pars ventralis tapers it also moves ventrolaterally to occupy a position within the lateral forebrain bundle. Due to the gradual increase in the size of the neurons as they pass into the lateral forebrain bundle, they are believed to constitute the nucleus entopeduncularis (fig. 4). Caudal to the interventricular foramen, a new cellular population, pars lateralis of the amygdala, begins to expand ventrally as the pars ventralis of the striatum enters the lateral forebrain bundle. This new population forms a cup-shaped nucleus whose

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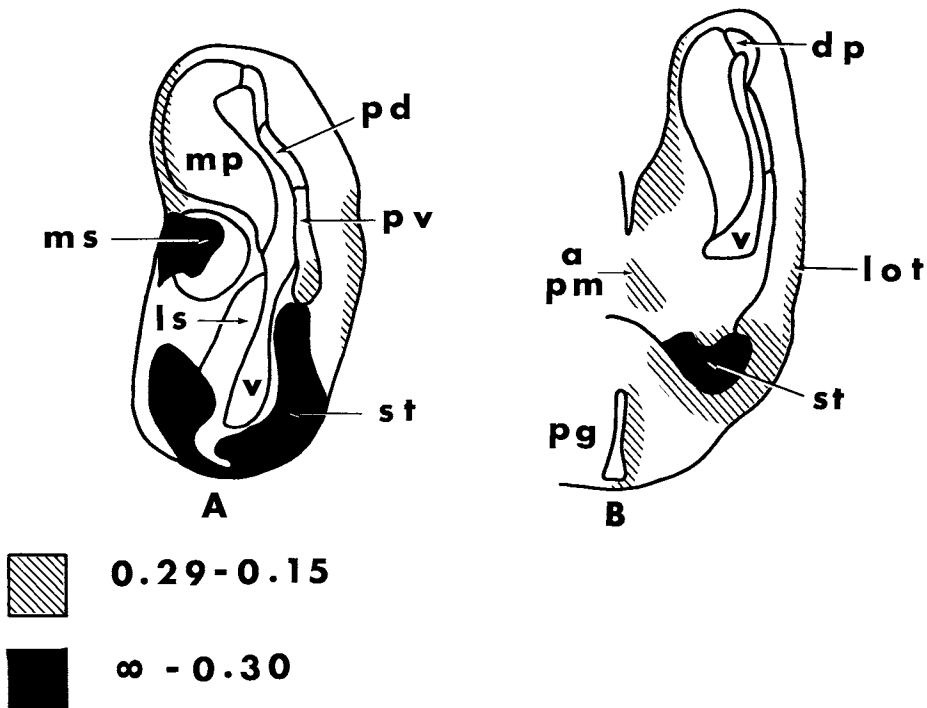


Fig. 5 Plot of regional distribution and relative intensity of acetylcholinesterase in the bullfrog telencephalon. Intensity plotted as relative optical absorbance. The most intense absorbance regions are confined to the subpallium.

cell-free opening is directed rostro-laterally (fig. 4). The pars lateralis occupies the entire caudal ventrolateral hemispheric wall and finally becomes continuous with the periventricular preoptic grey at rostral diencephalic levels. The topographical position of pars lateralis as a ventral continuation of the lateral pallium and its lack of direct continuity with the cellular population which continues into the lateral forebrain bundle suggests that the pars lateralis may be pallial in origin.

*Histochemistry*

AChE absorbance values greater than 0.30 are found throughout the length of nucleus accumbens, pars dorsalis and ventralis of the striatum, pars medialis of the amygdala and the medial septal nuclei (fig. 5). In addition lower O.D. values are seen in a medial zone of neuropil in the medial pallium and throughout the entire

rostro-caudal extent of the pars ventralis of the lateral pallium.

MAO absorbance values greater than 0.22 are restricted to the pars dorsalis of the striatum, the septal nuclei, the pars medialis of the amygdala and the preoptic area of the hypothalamus (fig. 6). Particularly noticeable are a group of fibers which appear to interconnect the septal region with the medial pallium (fig. 6A). Lower intensities are also observed in the outermost part of the pallial zones and in the pars lateralis of the amygdala (fig. 6B).

SDH absorbance values greater than 0.22 are found throughout the length of the medial pallium, in the rostral dorsal pallium and the pars dorsalis of the lateral pallium, in the caudal medial septal nuclei and the pars ventralis of the striatum and in both the divisions of the amygdala. Lower intensities are restricted to the nucleus accumbens, the lateral

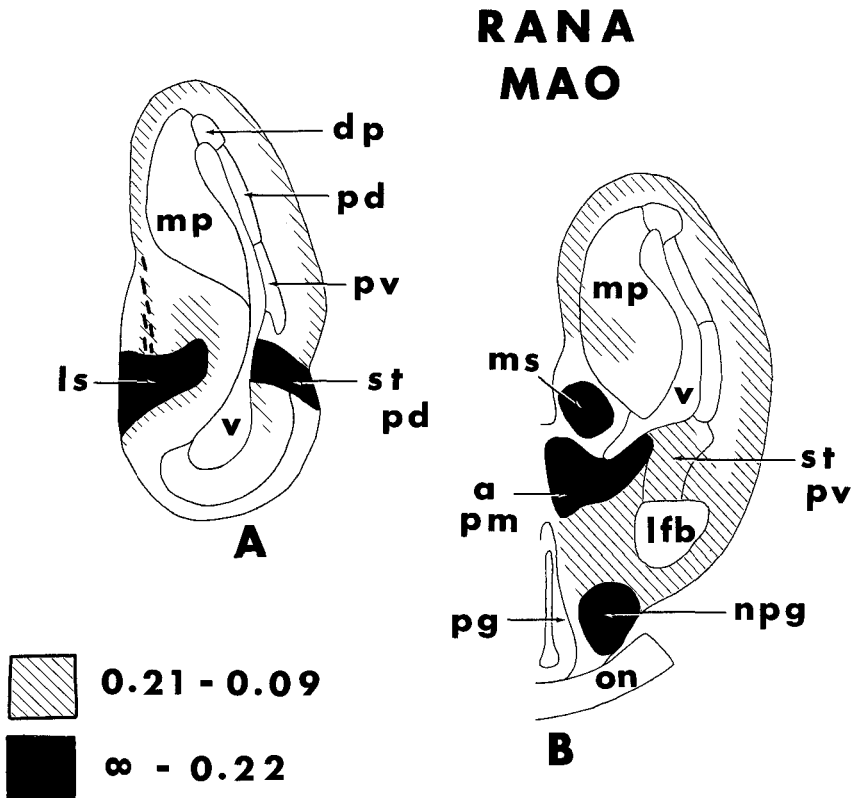


Fig. 6 Plot of regional distribution and relative intensity of monoamine oxidase in the bullfrog telencephalon. Intensity plotted as relative optical absorbance.

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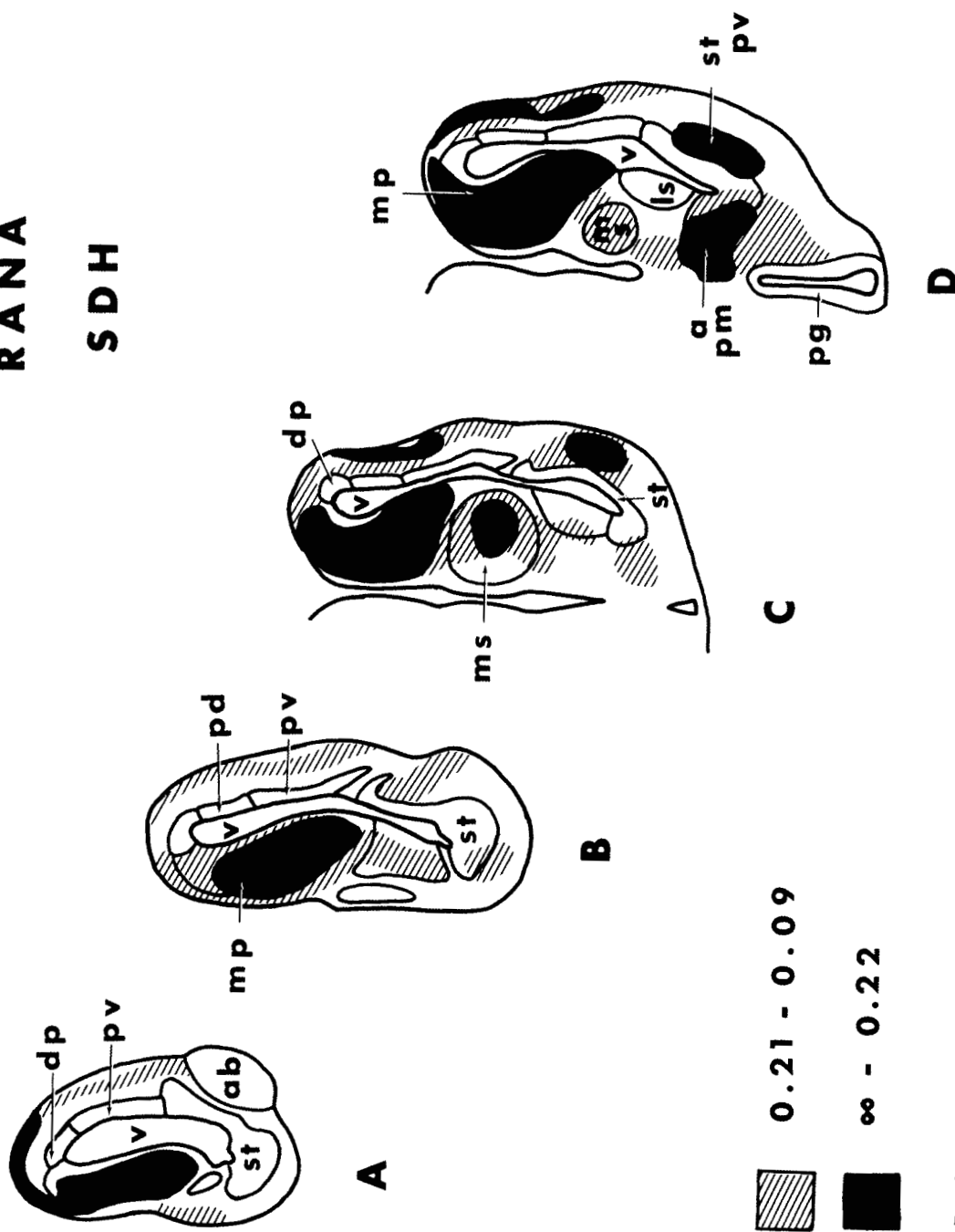


Fig. 7 Plot of regional distribution and relative intensity of succinate dehydrogenase in the bullfrog telencephalon. Intensity plotted as relative optical absorbance.

septal nuclei and the lateral olfactory tract (fig. 7).

#### DISCUSSION

In all vertebrate taxa so far examined, the telencephalic subpallial regions can be differentiated from the pallial regions by higher concentrations of both acetylcholinesterase and biogenic monoamines (Koelle, '54; Shen et al., '55; Dahlstrom and Fuxe, '65; Juorio and Vogt, '67; Kusunoki, '69, '71; Parent and Oliver, '70; Parent, '71, '73; Karten and Dubbeldam, '73; Terlouw and Ploemacker, '73). In *Rana esculenta* high concentrations of biogenic monoamines in the telencephalon are restricted to the lateral septal nucleus, the preoptic area and the striatum (Braak, '70). Thus the classically recognized divisions in anurans of pallium and subpallium based on cytological and topographical criteria are corroborated by the histochemical studies.

In amniotes, the septal nuclei occupy the medial subpallial wall of the telencephalon and are characterized by high concentrations of AChE, MAO and SDH (Friede, '66; Northcutt, personal observations). This region also receives an ascending sensory pathway from the isthmal reticular formation (Nauta and Kuypers, '58; Hedreen, '73). In *Rana* degenerating fibers have been traced to the ventromedial striatum and the septal nuclei following hemisections of the isthmal brain stem (Northcutt, '72). All available data related to topography, histochemistry and afferent connections suggest that the anuran septum is homologous to the amniotic septum.

At present, analysis of the anuran lateral subpallium is less complete. The highest concentration of AChE and monoamines in the anuran telencephalon like that of amniotes is located in the lateral subpallium. Likewise anurans possess ascending projections to the lateral subpallium from the ventral neural fields of the diencephalon and mesencephalon (Carpenter and Peter, '71; Hedreen, '71; Northcutt, '72; Rubinson and Colman, '72). These data suggest that the rostral, lateral subpallium should be regarded as homologous to the amniotic corpus striatum. The data further suggest that the pars lateralis of the amygdala may be homologous to the cortico-medial group of the mammalian amygdala. In anurans, as well as mammals,

these areas stain weakly by the AChE method. This similarity is further strengthened by the observation that the anuran accessory olfactory bulb (Scalia, '72) like that of mammals (Winans and Scalia, '70) projects solely to part of this region.

The cellular population recognized as the pars medialis of the amygdala may be homologous to the baso-lateral group of the mammalian amygdala. Both occupy a comparable topographical position within the telencephalon and in both anurans and mammals (Hall and Geneser-Jensen, '71) these regions stain strongly by the AChE method.

The amniotic hippocampus and adjacent limbic pallial fields primitively occupy a dorsomedial position in the telencephalic wall. In the few taxa examined high concentrations of SDH and MAO characterize these areas (Shimiyu et al., '59; Kusunoki, '69; Geneser-Jensen, '71). These medial pallial areas in amniotes also demonstrate moderate to high concentrations of AChE (Mathisen and Blackstad, '64; Geneser-Jensen and Blackstad, '71; Kusunoki, '71). This is particularly pronounced in reptiles (Kusunoki, '71; Northcutt, personal observations). Anuran medial pallia are characterized by low to moderate concentrations of AChE and MAO, and by high concentrations of SDH. Thus both topographically and histochemically the medial pallium of *Rana* is more similar to amniotic medial limbic cortices than are the other pallial fields in anurans. The similarity is particularly striking when connections are also considered. Both anurans and amniotes possess medial pallial fields that receive ascending projections from the mesencephalon via the medial forebrain bundle (Dahlstrom et al., '62; Northcutt, '70b, '72; Hedreen, '73). These pallial fields also project to septal and preoptic nuclei in both anurans and amniotes (Northcutt, '70a; Kokoros, '72; Lohman and Mentink, '72).

In mammals, isocortex and piriform cortex are characterized by low concentrations of MAO and by high concentrations of SDH restricted to cellular laminae that primarily receive sensory projections (Shimiyu et al., '59; Friede, '60). Low concentrations of AChE also are associated with isocortices (Friede, '66). In reptiles the dorsal cortex and dorsal ventricular ridge (DVR) demonstrate marked similarities to



different segments of mammalian isocortex. Both the dorsal cortex and DVR possess low concentrations of MAO and high concentrations of SDH (Kusunoki, '71; Northcutt, personal observations). These SDH rich areas are restricted to neural fields that receive thalamic projections (Baker-Cohen, '68; Pritz, '72, '73)) and these same fields also possess low concentrations of AChE (Kusunoki, '69; Northcutt, personal observations) and are in fact visual and auditory areas.

In *Rana* the dorsal and lateral pallia possess low concentrations of MAO. The pars ventralis of the lateral pallium is the only division of these pallial formations that demonstrates even low concentrations of AChE (fig. 3A). Both the dorsal and lateral pallia demonstrate moderate to high concentrations of SDH confined to the molecular zone. On the basis of histochemistry and topography it is possible to suggest that the pars ventralis of the lateral pallium might be the homologue of the sauropsid dorsal ventricular ridge. This hypothesis is further reinforced by the observation that the pars ventralis of the lateral pallium also receives an ipsilateral projection from the thalamus via the lateral forebrain bundle (Northcutt, '72; Kicliter and Northcutt, manuscript in preparation). Additionally, the ventral part of the pars dorsalis and all of the pars ventralis of the lateral pallium in *Rana* also receive a major projection from the main olfactory bulb (Scalia et al., '68; Royce and Northcutt, '69). This certainly suggests that the pars ventralis should also be considered homologous to the piriform cortex of amniotes.

Phylogenetically it is possible that the pars ventralis is the *field homologue* of both the amniotic piriform cortex and part of isocortex. Pars ventralis may contain two neuronal populations that have very different evolutionary fates in amniotes. The amphibian-reptilian transition may have been characterized by very different selective pressures on these two neuronal populations. One population may have migrated laterally to form the reptilian piriform cortex while the second population proliferated in situ to form the dorsal ventricular ridge. Recent studies on the embryogenesis of the reptilian telencephalon would support such a conclusion (Källén, '51; Kirsche, '72). This hy-

pothesis would predict that mammalian isocortex arose from two adjacent cytological fields. The most dorsal of these fields would be represented in modern anurans by the dorsal pallium (the pars dorsalis of the lateral pallium of this study) and in ancestral amphibians would give rise to primary visual isocortex. The second more ventral field would be represented in modern anurans by the pars ventralis of the lateral pallium and in ancestral amphibians would give rise to a lateral piriform cortex and a medial dorsal ventricular ridge in sauropsid amniotes or to secondary visual, auditory and primary sensorimotor isocortices in therapsid amniotes. Detailed information on the nature of telencephalic connections in anurans, and further information on the embryonic development of the reptilian dorsal ventricular ridge should greatly speed the resolution of this problem.

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