

Neuronal Typology of the Thalamic Area Triangularis of *Gallotia galloti* (Reptilia, Sauria)

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ABSTRACT In a Golgi study of the area triangularis (AT), a rostral nucleus of the ventral thalamus of *Gallotia galloti*, we have identified four major neuronal types on the basis of their morphological characteristics: medium-sized fusiforms with two processes, medium-sized fusiforms with three or four processes, small bipolars, and small and medium-sized multipolars. These neurons are characterized by a simple morphology and radial arrangement. Cell size varies from small to medium, and all axons project laterally. These characteristics distinguish AT neurons from those of neighboring nuclei. In addition, we found some evidence of differential topographic distribution of each neuronal type within the nucleus. Medium-sized fusiform neurons with two processes are located in the most ventral part, where they constitute the ventral nuclear limit. Small multipolar neurons prevail in the dorsal and ventromedial parts, and in the rest of the nucleus medium-sized neurons, including both fusiform with three or four processes and multipolar types, are normally found. Finally, we discuss a putative homology of the reptilian AT with a part of the mammalian zona incerta.

The area triangularis (AT) is a nucleus located in the anterior part of the reptilian ventral thalamus (Fig. 1). It was first described by Huber and Crosby in 1926 in *Alligator mississippiensis*. Several subsequent authors have described it under other names, e.g., nucleus dorsolateralis anterior thalami (Shanklin, '30, in *Chamaeleo vulgaris*), nucleus suprapeduncularis (Frederikse, '31, in *Lacerta vivipara*), or the anterior part of the nucleus ventralis thalami (Kuhlenbeck, '31). Nevertheless, the nomenclature of Huber and Crosby ('26) has been most widely accepted (Papez, '35; Ariens Kappers et al., '36; Knapp and Kang, '68a,b; Campos-Ortega, '71; Butler and Northcutt, '73; Repérant, '73; Senn and Northcutt, '73; Cruce, '74; Trujillo and López, '77). A detailed review of the literature reveals that some confusion exists on the delimitation of the nucleus. For instance, Knapp and Kang ('68a,b) considered the caudal part of AT as belonging to the lateral geniculate body, and Repérant ('73) considered a dorsal part of AT as belonging to the nucleus ovalis.

The confusion increased when connection studies were carried out on this region. In type I and type II lizards, neither visual afferents (Butler and Northcutt, '71, in *Iguana* and *Anolis*; Northcutt and Butler, '74, in *Gekko*; Butler and Northcutt, '78, in *Iguana* and *Gekko*; Repérant

et al., '78, in *Scincus*, *Acanthodactylus*, *Tarentola*, *Uromastix* and *Zonosaurus*), nor brainstem afferents (Hoogland, '82, in *Varanus*) nor spinal cord afferents (Ebbesson, '67; Lohman and van Woerden-Verkley, '78, in *Tupinambis*; Hoogland, '81, in *Varanus*) have been found to the AT. In addition, visual afferents to this nucleus have not been encountered in snakes (Repérant, '73). In contrast, visual afferents to AT were reported in the turtles *Chelydra* and *Podocnemis* (Knapp and Kang, '68a,b) and *Emys* and *Testudo* (Belekhova, '79) but not in the turtles *Pseudemys* and *Chrysemys* (Hall et al., '77; Bass and Northcutt, '81; Kunzle and Snyder, '83). *Pseudemys* does have spinal afferents to the AT via the optic tectum (Künzle and Woodson, '82; Künzle and Snyder, '83). Among snakes, *Thamnophis* has afferents from the optic tectum (Dacey and Ulinski, '86) and from the trigeminal nuclei (Molenaar and Fizaan-Oostveen, '80). Lizards lack efferent connections from AT to the cortex (Bruce and Butler, '84a, in *Gekko* and *Iguana*) as do turtles (Hall et al., '77, in *Pseudemys* and *Chrysemys*). Lizards do have AT projections to the thalamic nucleus dorso-

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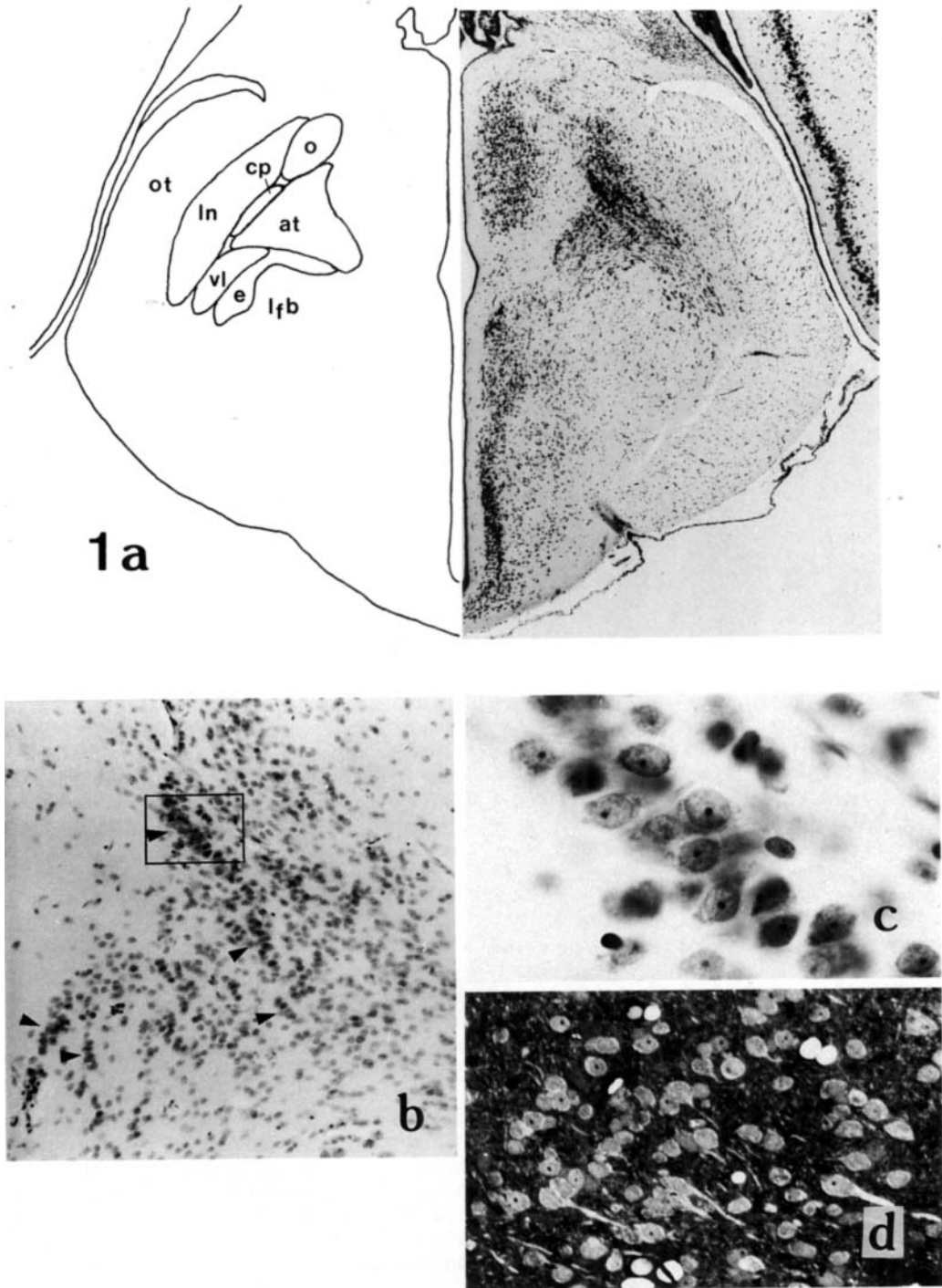


Fig. 1. **a:** Drawing and transverse section of halves of the diencephalon at the AT level, showing the close proximity of this nucleus to other nuclei of the ventral thalamus. **b:** Enlargement of AT region in a, showing cellular columns (arrow heads). **c:** Detail of a cell column. **d:** Semithin section showing cell columns. at, area triangularis; cp, cellular plate of the

nucleus geniculatus lateralis pars ventralis; e, entopeduncularis; lfb, lateral forebrain bundle; ln, lateral neuropile of the nucleus geniculatus lateralis pars ventralis; o, ovalis; ot, optic tract; vl, ventrolateralis pars dorsalis. a, $\times 50$; b, $\times 250$; c, $\times 1,200$; d, $\times 470$.

medialis and to the habenular region (Hoogland, '82, in *Varanus*).

The differences in AT connectivity of various reptiles are perhaps due to species-specific peculiarities. However, the imprecise cytoarchitectonic delimitation of the nucleus obscures the boundaries between AT and neighboring nuclei, ovalis (O), ventromedialis (VM), and entopeduncularis (E). Moreover, we cannot distinguish these neighboring nuclei on the basis of connections, because one class of afferents may reach several of these nuclei (Kunzle and Schnyder, '83). Accordingly, studies that provide a more accurate knowledge of the characteristics of each nucleus, including its neuronal typology, are needed. This is the aim of the present report. We have studied the AT in the lacertid lizard *Gallotia galloti*, which is endemic to Tenerife Island (Canary Islands) and which shows type I characteristics (Butler, '80).

MATERIALS AND METHODS

Forty-three adult brain specimens of *Gallotia galloti* (Reptilia, Lacertidae) were processed according to several variants of the Golgi technique: Kopsch, rapid Golgi, Rio-Hortega (Regidor, '78), and Colonnier ('64). The animals were anaesthetized with ethyl-ether and perfused transcardially, usually with 5% glutaraldehyde in 0.1 M phosphate buffer. When the chloralhydrate variant (Rio-Hortega) was used, we perfused the animals with Lillie's buffered formalin or 10% formol. Whole brains were dissected out and processed following one of the previously mentioned Golgi methods. Impregnated brains were embedded in 5% agar and sectioned (60–100 μm thick) with a tissue slicer in the transverse or sagittal planes. The sections frequently were stabilized by Lavilla's technique (Ramón y Cajal and Castro, '42) to avoid the loss of impregnation and to obtain a slight counterstaining, helpful for cytoarchitectonic delimitation. In other cases, sections were counterstained with cresyl-violet and then dehydrated and mounted in Canada balsam or Araldite. We studied the preparations with a Leitz microscope (Dialux) and used a camera lucida attachment for the drawings.

RESULTS

Most of the neurons composing the area triangularis have a simple fusiform or bipolar shape with small to medium somata (Fig. 6). Four major neuronal types can be distinguished on the basis of somatic shape and polarity, pattern of dendritic arborization, orientation and location within the nucleus: 1) medium-sized fusiforms with two processes; 2) medium-sized fusi-

forms with three or four processes; 3) small bipolar; and 4) small and medium-sized multipolars.

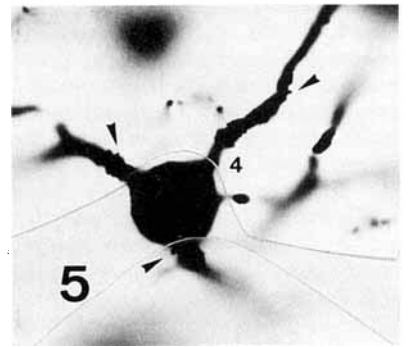
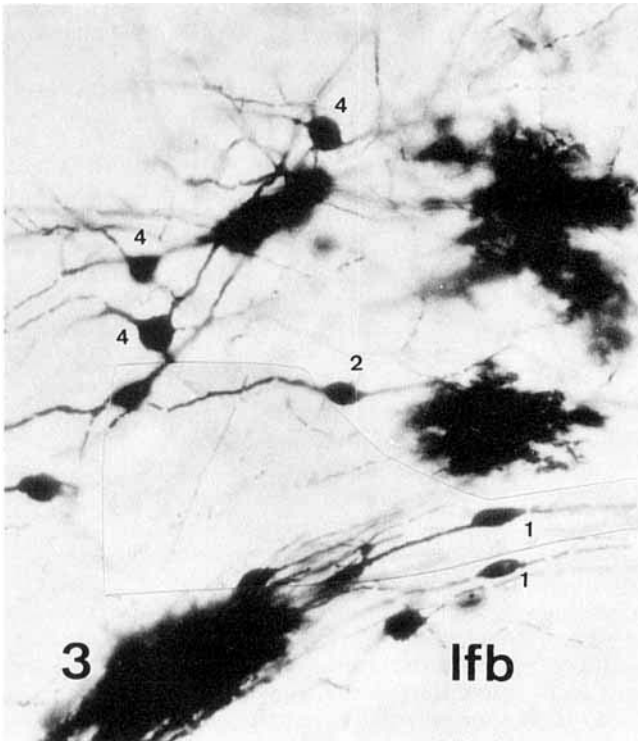
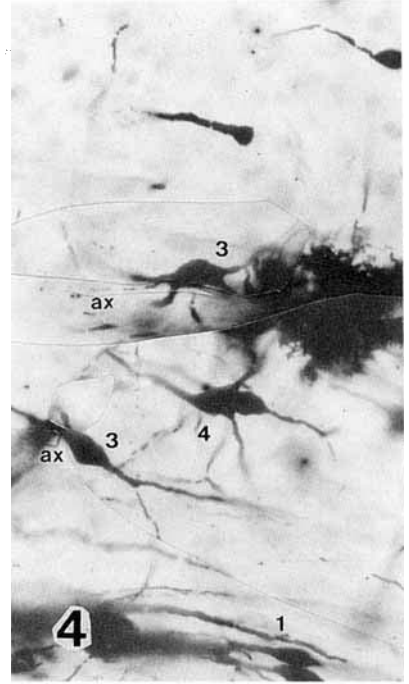
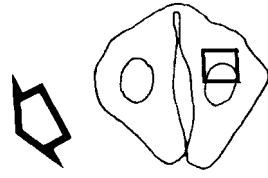
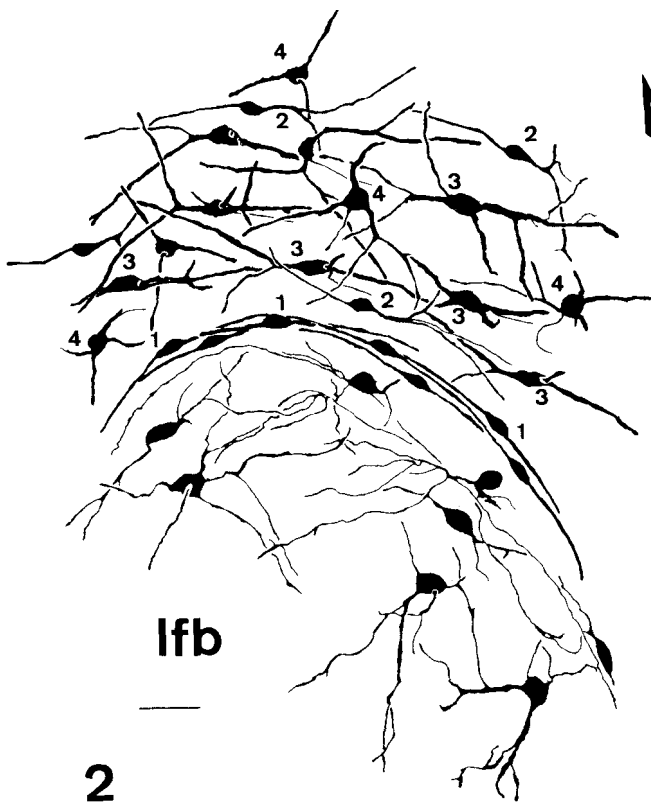
In Nissl material, the neurons of the AT characteristically form columns, especially in the center of the nucleus (Fig. 1b–d). The Golgi method also indicates some evidence of this organization in the form of the association of two intertwined, impregnated neurons (Fig. 9).

Medium-sized fusiform neurons with two processes

Neurons of this type (Figs. 2, 3, 4.1, 8) are the only ones located at the most ventral limit of the nucleus, aligned with the convex surface of the lateral forebrain bundle, and limited by the entopeduncular nucleus. They represent about 14% of the neurons in the nucleus and show a soma with a spindle shape. The somatic size ranges between 19 and 20 μm (long axis). Two opposite processes sprout from the soma; they tend to be disposed in parallel to the dorsal surface of the lateral forebrain bundle. The two dendritic trunks are slender and sometimes branch even farther from the soma than twice the length of the long somatic axis. The secondary dendrites follow the same direction as the primary trunks. We never have observed tertiary dendrites. This neuronal type does not show spines on the soma, but a few spines may be found on dendrites. Thus, fusiform neurons are extremely simple, a fact that may be useful in order to resolve problems of delimitation with the nearby grisea.

Small bipolar neurons

These neurons (Figs. 2, 3.2) lie throughout the nucleus, except in the most ventral limit. They represent about 20% of the neurons in the nucleus and show an ellipsoidal, usually smooth or almost smooth soma, ranging from 12 to 14 μm (long axis). Two dendritic processes grow from the cell body in opposite directions. Their disposition is generally radial. The lateral dendrite is the main cell process, being slightly thicker. Both primary dendritic processes usually branch closer than one and a half lengths relative to the long somatic axis. Sometimes lateral tertiary dendrites are formed. Spines are observed across the dendritic surface, being more numerous over the lateral dendrites. Some are thin pedicles that finish with a terminal bouton. Others are thick, short appendages. The axon usually grows either from the soma or from the lateral dendrite and courses radially in lateral direction.



Figures 2-5

Medium-sized fusiform neurons with three or four processes

These neurons (Figs. 2, 4, 3, 7), the most numerous type (36%) in the AT, are located throughout the nucleus, except in the most ventral limit. However, only a few are found dorsally and ventromedially (5%). They have an ellipsoidal soma, ranging from 19 to 20 μm (long axis), the surface of which is rough and displays some spinous appendages. Some of these cells are the largest neurons found in the nucleus. Three or four dendritic processes grow from opposite poles of the soma, two generally directed laterally and one or two directed medially. The overall orientation of this neuronal type is radial. Lateral dendrites usually are thicker than the others. Their ramification is proximal, usually closer than one length of the long somatic axis, and it is more intense in lateral dendrites than in medial ones. Lateral dendrites show a rough aspect with spines, whereas the surface of medial dendrites is smoother. The spines can be either thin or thick, short appendages that can have a terminal bouton or can be thin pedicles of various lengths, sometimes crooked or showing a terminal bouton. The axon grows either from the soma, or near to it from a dendrite, and it courses laterally.

Small and medium-sized multipolar neurons

These neurons (Figs. 2, 3, 4, 5, 10) are located throughout the nucleus except in its most ventral limit. Together they represent about 30% of the neurons. Most (80%) of the small ones are found within dorsal and ventromedial parts, whereas most (90%) of the medium-sized neurons are found within remaining parts of the nucleus. The surface of their soma is generally very rough and spinous and shows a nearly spherical shape, with sizes ranging between 9 and 12

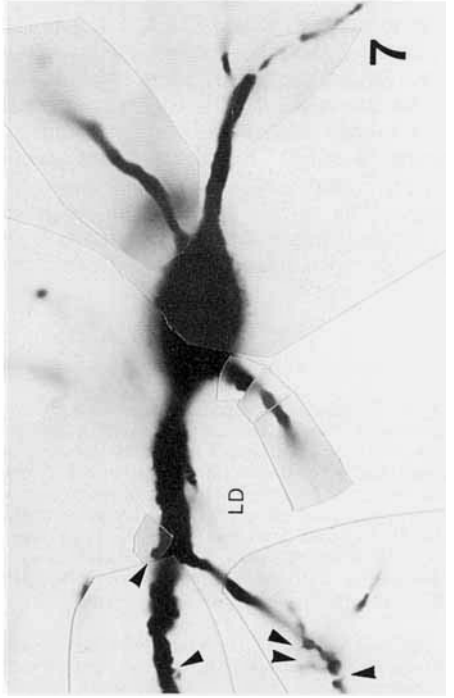
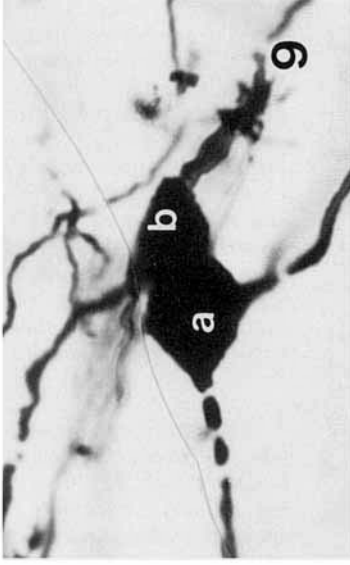
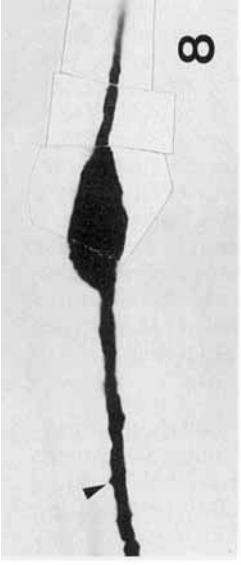
μm for small neurons, and between 14 and 19 μm for medium ones. The several emerging dendritic processes are arranged in different directions. Usually they ramify at a distance between one-half and twice the length of the long somatic axis. The dendritic surface shows some rough zones and several types of spines. Some have thin, long pedicles with a terminal bouton; others are thick, short protuberances that generally end with an enlargement. Also, short appendages of intermediate thickness are found. The axon can sprout laterally from a process near the soma. Sometimes we could see the associated impregnation of two multipolar neurons, one small and the other medium-sized (Fig. 9).

DISCUSSION

In this work we have established the characteristic neuronal cell types of the area triangularis of *Gallotia galloti*. Most neurons of this nucleus are radially orientated bipolars or fusiforms, showing a very simple dendritic tree with scanty ramifications and a small number of spines and with neuronal size varying within the small to medium range. All of these peculiarities differentiate AT neurons from those of the other adjacent nuclei, with which delimitation problems had become apparent. Thus, for instance, AT neurons may be distinguished from those of nucleus ovalis (O), immediately dorsal to AT, mainly by their different orientation, because the O neurons often show a circumferential disposition. Furthermore, GLpV neurons, lying lateral to AT, are generally larger and more complex than those of AT, and some GLpV cells are orientated tangentially (Franzoni and Fasolo, '82; Martin, '86), and can therefore be rejected as AT components. The ventrolateral aspect of the caudal part of AT adjoins the nucleus ventrolateralis pars dorsalis (VLpD). The neuronal typology of the latter is rather different from that of the AT, due to a generally oblique disposition of its cells and/or to their far larger size, distinct morphology, and greater complexity (unpublished observations). Ventral to the AT lies the nucleus entopeduncularis (E), interstitial within the lateral forebrain bundle. Neuronal typology unmistakably separates AT and E. Neurons of E are organized as a more compact cell group (Fig. 2), show a larger cell size than most AT neurons, and have a more complex dendritic morphology. Indeed, E nucleus shows many multipolar neurons with numerous branched processes that grow out from the soma (Brauth and Kitt, '80, in *Caiman*; personal unpublished observations). Thus, the present study attempts to resolve the delimitation problems of the AT and is to be followed by studies of development of this nu-

Fig. 2. Diagram of section through the diencephalon and camera lucida drawing showing neurons in boxed area. AT neurons (in numbered region) are mainly bipolar, radially disposed, and simple, and are localized above E neurons, which are more dispersed and more complex and which ramify between the fibers of the lateral forebrain bundle (lfb). Some AT neuronal types are identified: 1, medium-sized fusiforms with two processes; 2, small bipolars; 3, medium-sized fusiforms with three or four processes; 4, small and medium-sized multipolars. Scale bar = 35 μm .

Figs. 3-5. Some AT neuronal types: 1, medium-sized fusiforms with two processes; 2, small bipolars; 3, medium-sized fusiforms with three or four processes; 4, small and medium-sized multipolars. Arrowheads, spines; ax, axon. Fig. 3, $\times 390$; Fig. 4, $\times 400$; Fig. 5, $\times 1,000$.



Figures 6-10

cleus (see accompanying paper on neuronal differentiation).

The distribution of neuronal types within AT shows regional differences. Medium-sized fusiform neurons with two processes and a simple aspect are located at the most ventral border of the nucleus, dorsally surrounding the lateral fore-brain bundle and separating the rest of the AT from the E nucleus. The other neuronal types are distributed throughout the nucleus, even though small-sized multipolars prevail dorsally and ventromedially, whereas medium-sized multipolars and fusiforms with three or four processes predominate in the rest of the AT. Knapp and Kang ('68a,b) described an area triangularis, which is constituted of small, poorly differentiated cells in a rostral thalamic zone of turtles. Fusiform radially disposed cells have been reported to appear caudal and dorsal to those small cells. At these levels, both fusiform and small cells were grouped together as a part of the GLpV nucleus. However, some of these are placed clearly medial to the position of GLpV. We therefore think that they belong to the AT: thus, turtles also show a trend to a characteristic topographic distribution for distinct AT neuronal types. Moreover, Knapp and Kang ('68a,b) found a group of rounded cells that lie dorsal to the fusiform ones; they identify these as nucleus GLpD. Comparing their images with those of *Gallotia galloti*, we think that most ventral and rostral cells identified as GLpD may belong to the AT. Thus, dorsal and ventral parts of the turtle AT would be constituted by small, rounded cells, and the remaining nuclear zones would be composed of fusiform radially disposed cells. In any case, the AT of the lizard *Gallotia galloti* shows a marked segregation of distinct neuronal types to particular nuclear zones. This unequal arrangement may be related to differential connections.

Frequently, reptilian encephalic structures are evaluated to establish their putative homology with mammalian structures. The reptilian AT has been considered to be homologous to the mammalian zona incerta (Ariens Kappers et al., '36). Evaluation of this possibility must consider various kinds of criteria; one is neuronal typology. In a Golgi study of the cat subthalamic nucleus (STN), Iwahori ('78) showed some drawings of neuronal types in a nucleus dorsally located to STN, the zona incerta (ZI). In these images ZI neurons are mainly radially disposed bipolars, and their aspect, even if more complex than that of our AT neurons, is simpler than that of STN neurons. Exactly the same occurs for the neurons of AT of lizards with respect to those of the underlying nucleus entopeduncularis (E). Moreover, in mammals the STN and the ZI lie in the cerebral peduncle, and in reptiles the E and the AT are located above the lateral forebrain bundle, even though the E is partially enclosed within this fiber bundle. On the other hand, the reptilian E nucleus, named *entopeduncularis anterior* by some authors, has been considered homologous to the mammalian STN (Carpenter and Strominger, '66; Brauth and Kitt, '80). According to connection studies, some of the main paths through which basal ganglia control motor functions involve the STN (Carpenter and Strominger, '66; Kita and Kitai, '87; Beckstead and Cruz, '86) and the ZI (Ricardo, '81; Kita and Kitai, '87), which in their turn project to certain thalamic areas connected with the motor cortex and the neocortex (Herkenhan, '79, '80; Reiner et al., '80; Wiesendanger and Wiesendanger, '85a,b).

Both in birds and in reptiles, telencephalic areas considered equivalent to mammalian basal ganglia (the ventral striatum) project to the thalamic nuclei putatively homologous to STN of mammals, named the *ansa lenticularis anterior nucleus* in birds (Brauth and Kitt, '80) and the *nucleus entopeduncularis anterior* in reptiles (Reiner et al., '80; Brauth and Kitt, '80; González and Russchen, '88). Reptiles seem to lack connections of the AT with areas regarded as equivalents to mammalian basal ganglia, but efferents from AT to the thalamic nucleus dorsomedialis have been described (Hoogland, '82). The nucleus dorsomedialis projects to the anterior dorsal ventricular ridge, a zone regarded as homologous to parts of the mammalian neocortex from a homologic point of view (Ulinski, '83; Bruce and Butler, '84a,b) and related to other cortical areas (Bruce and Butler, '84a,b). Thus, even though AT connections are practically unexplored, this thalamic nucleus perhaps has a role

Fig. 6. Neurons in the AT showing the mainly radial disposition and the bipolar or fusiform shape. $\times 820$.

Fig. 7. Enlarged view of a fusiform neuron with four processes. Note the thicker and rougher aspect of the lateral dendrites (LD) compared with the medial pair. Arrowheads, spines, $\times 1,600$.

Fig. 8. Enlarged view of a fusiform neuron with two processes, showing an almost smooth surface. Arrowhead, spine $\times 1,600$.

Fig. 9. Two intertwined neurons (a,b). $\times 1,500$.

Fig. 10. Enlarged view of multipolar neurons, showing dendrites with spines (arrowheads) $\times 1,600$.

as a modulator in some telencephalic feedback mechanisms, equivalent to what has been supposed for the zona incerta of mammals (Ricardo, '81). Moreover, both AT and ZI have projections to the hypothalamus, which are direct in mammals (Nauta and Haymaker, '69; Ricardo, '81) and indirect in lizards, here passing through the thalamic nucleus dorsomedialis and the habenular nuclei (Belekhova and Nemova, '87). On the other hand, both the mammalian zona incerta (Peschanski, '84) and a ventral thalamic zone in snakes, which seems to be the AT (Molenaar and Fizaan-Oostveen, '80), receive trigeminal afferents.

Greater confidence in assessing the equivalence of two putative homologous zones requires consistency with embryologic data. This approach should offer clarification, as both the reptilian AT (Trujillo, '82) and the mammalian ZI (Keyser, '72) originate from the area rostralis thalami (Bergquist, '54).

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LITERATURE CITED

- Ariens Kappers, C.U., G.C. Huber, and E.C. Crosby (1936) The Comparative Anatomy of the Nervous System of Vertebrates, Including Man. New York: Hafner.
- Bass, A.H., and R.G. Northcutt (1981) Retinal recipient nuclei in the painted turtle, *Chrysemys picta*: An autoradiographic and HRP study. *J. Comp. Neurol.* 199:97-112.
- Beckstead, R.M., and C.J. Cruz (1986) Striatal axons to the globus pallidus, entopeduncular nucleus and substantia nigra come mainly from separate cell populations in cat. *Neuroscience* 19:147-158.
- Belekhova, M.G. (1979) Neurophysiology of the forebrain. In C. Gans, R.G. Northcutt, and P.S. Ulinski (eds): *Biology of the Reptilia*. Vol. 10. London: Academic Press, pp. 287-359.
- Belekhova, M.G., and G.V. Nemova (1987) Study of connection of supposed limbic diencephalic nuclei in lizards using the axonic HRP transport. *Neurofiziol. (Kiev)* 19:110-119.
- Bergquist, H. (1954) Ontogenesis of diencephalic nuclei in vertebrates: A comparative study. *Kungl. Fysiograf. Sällskaps Handlingar N. F.* 65:1-34.
- Brauth, S.E., and C.A. Kitt (1980) The paleostriatal system of *Caiman crocodilus*. *J. Comp. Neurol.* 189:437-465.
- Bruce, L.L., and A.B. Butler (1984a) Telencephalic connections in lizard. I. Projections to cortex. *J. Comp. Neurol.* 229:585-601.
- Bruce, L.L., and A.B. Butler (1984b) Telencephalic connections in lizard. II. Projections to anterior dorsal ventricular ridge. *J. Comp. Neurol.* 229:602-615.
- Butler, A.B., and R.G. Northcutt (1971) Ascending tectal efferent projections in the lizard *Iguana iguana*. *Brain Res.* 35:597-601.
- Butler, A.B., and R.G. Northcutt (1973) Architectonic studies of the diencephalon of *Iguana iguana* (Linnaeus). *J. Comp. Neurol.* 149:439-462.
- Butler, A.B., and R.G. Northcutt (1978) New thalamic visual nuclei in lizard. *Brain Res.* 149:469-476.
- Butler, A.B. (1980) Cytoarchitecture and connectional organization of the lacertilian telencephalon with comments on vertebrate forebrain evolution. In S.O.E. Ebbesson (ed.): *Comparative Neurology of the Telencephalon*. New York: Plenum Press, pp.297-329.
- Campos-Ortega, J.A. (1971) Estudios cito y mieloarquitectonicos en el diencefalo de algunos reptiles. *An. Anat.* 20:221-259.
- Carpenter, N.B., and N. Strominger (1966) Efferent fibers of the subthalamic nucleus in the monkey: a comparison of the efferent projections of the subthalamic nucleus, substantia nigra and globus pallidus. *Am. J. Anat.* 121:41-72.
- Colonnier, M. (1964) The tangential organization of the visual cortex. *J. Anat.* 98:327-344.
- Cruce, J.A. (1974) A cytoarchitectonic study of the diencephalon of the Tegu Lizard, *Tupinambis nigropunctatus*. *J. Comp. Neurol.* 153:215-238.
- Dacey, D.M., and P.S. Ulinski (1986) Optic tectum of the eastern garter snake, *Thamnophis sirtalis*. I. Efferent pathways. *J. Comp. Neurol.* 245:1-28.
- Ebbesson, S.O.E. (1967) Ascending axon degeneration following hemisection of the spinal cord in the Tegu lizard (*Tupinambis nigropunctatus*). *Brain Res.* 5:178-206.
- Franzoni, M.S., and A. Fasolo (1982) A golgi study on neuronal morphology of the ventral lateral geniculate nucleus of the lizard. *J. Hirnforsch.* 23:245-256.
- Frederikse, A. (1931) The Lizard's Brain. An Investigation on the Histological Structure of the Brain of *Lacerta vivipara*. Holland: C.C. Callenbach-Nijkerk.
- González, A., and F.T. Russchen (1988) Connections of the basal ganglia in the lizard *Gekko gekko*. In W.K. Schwerdtfeger and W.J.A.J. Smeets (eds): *The Forebrain of Reptiles*. Current Concepts of Structure and Function. Basel: Karger, pp. 50-59.
- Hall, J.A., R.E. Foster, R.F. Ebner, and W.C. Hall (1977) Visual cortex in a reptile, the turtle (*Pseudemys scripta* and *Chrysemys picta*). *Brain Res.* 130:197-216.
- Herkenham, M. (1979) The afferent and efferent connections of the ventromedial thalamic nucleus in the rat. *J. Comp. Neurol.* 183:487-518.
- Herkenham, M. (1980) Laminar organization of thalamic projections to the rat neocortex. *Science* 207:532-535.
- Hoogland, P.V. (1981) Spinothalamic projections in a lizard, *Varanus exanthematicus*: an HRP study. *J. Comp. Neurol.* 198:7-12.
- Hoogland, P.V. (1982) Brainstem afferents to the thalamus in a lizard, *Varanus exanthematicus*. *J. Comp. Neurol.* 210:152-162.
- Huber, G.C., and E.C. Crosby (1926) On thalamic and tectal nuclei and fiber paths in the brain of the American alligator. *J. Comp. Neurol.* 40:97-227.
- Iwahori, N. (1978) A Golgi study on the subthalamic nucleus of the cat. *J. Comp. Neurol.* 182:383-398.
- Keyser, A. (1972) The development of the diencephalon of the chinese hamster. *Acta Anat.* 83:1-181.
- Kita, H., and S.T. Kitai (1987) Efferent projections of the subthalamic nucleus in the rat: Light and electron microscopic analysis with the PHA-L method. *J. Comp. Neurol.* 260:435-452.
- Knapp, H., and D.S. Kang (1968a) The visual pathways of the snapping turtle (*Chelydra serpentina*). *Brain Behav. Evol.* 1:19-42.
- Knapp, H., and D.S. Kang (1968b) The retinal projections of the side-necked turtle (*Podocnemis unifilis*) with some notes on the possible origin of the pars dorsalis of the lateral geniculate body. *Brain Behav. Evol.* 1:369-404.
- Kuhlenbeck, H. (1931) Über die Grundbestandteile des Zwischenhirnsbauplans bei Reptilien. *Morphol. Jahrb.* 66:244-317.
- Künzle, H., and H. Schnyder (1983) Do retinal and spinal projections overlap within the turtle thalamus? *Neuroscience* 10:161-168.
- Künzle, H., and W. Woodson (1982) Mesodiencephalic and other target regions of ascending spinal projecting in the

- turtle, *Pseudemys scripta elegans*. *J. Comp. Neurol.* 212: 349-364.
- Lavilla, J. (1942) Estabilización de las coloraciones cromoar-genéticas. *Arch. Hist. Norm. Pat.* 1:441.
- Lohman, A.H., and T. van Woerden-Verkley (1978) Ascending connections to the forebrain in the Tegu lizard. *J. Comp. Neurol.* 182:553-594.
- Martin, A. (1986) Formación y Citodiferenciación del núcleo Geniculado Lateral pars Ventralis en *Gallotia galloti*: Estudio Golgi. España: Tesina. Univ. La Laguna.
- Molenaar, G.J., and J.L.F.P. Fizaan-Oostveen (1980) Ascending projections from the lateral descending and common sensory trigeminal nuclei in *Python*. *J. Comp. Neurol.* 189:555-572.
- Nauta, W.J.H., and W. Haymaker (1969) Hypothalamic nuclei and fiber connections. In W. Haymaker, E. Anderson, and W.J.H. Nauta (eds): *The Hypothalamus*. Springfield, Illinois: Charles C. Thomas, pp. 136-209.
- Northcutt, R.G., and A.B. Butler (1974) Evolution of reptilian visual systems: Retinal projections in a nocturnal lizard, *Gekko gekko* (Linnaeus). *J. Comp. Neurol.* 157:435-466.
- Papez, J.W. (1935) Thalamus of turtles and thalamic evolution. *J. Comp. Neurol.* 61:433-475.
- Peschaski, M. (1984) Trigeminal afferents to the diencephalon in the rat. *Neuroscience* 12:465-487.
- Ramón y Cajal, S., and F. de Castro (1942) Elementos de técnica micrográfica del sistema nervioso. Barcelona: Salvat.
- Regidor, J. (1978) Tipología neuronal y organización de la corteza cerebral de *Lacerta galloti* (Dum. y Bib.). Estudio con los métodos de Golgi. Las Palmas Exma. Mancomunidad de Cabildos Plan Cultural.
- Reiner, A., S.E. Brauth, C.A. Kitt, and H.J. Karten (1980) Basal ganglionic pathways to the tectum: studies in reptiles. *J. Comp. Neurol.* 193:365-389.
- Repérant, J. (1973) Les voies et les centres optiques primaires chez la vipère (*Vipera aspis*). *Arch. Anat. Microsc. Morphol. Exp.* 62:323-352.
- Repérant, J., J. Rio, D. Miceli, and M. Lemire (1978) A radioautographic study of retinal projections in type I and type II lizards. *Brain Res.* 142:401-411.
- Ricardo, J.A. (1981) Efferent connections of the subthalamic region in the rat. II. The zona incerta. *Brain Res.* 214:43-60.
- Senn, D.G., and R.G. Northcutt (1973) The forebrain and midbrain of some squamates and their bearing on the origin of snakes. *J. Morphol.* 140:135-152.
- Shanklin, W.M. (1930) The central nervous system of *Chamaeleon vulgaris*. *Acta Zool.* 11:425-491.
- Trujillo, C.M. (1982) Ontogénesis de los Núcleos Talámicos en *Gallotia galloti* (Reptil, Lacertidae): Estudio Estructural y Ultraestructural. Doctoral Thesis. & Univ. La Laguna, España.
- Trujillo, C.M., and C. López (1977) Citoarquitectura de los núcleos talámicos en los reptiles *Lacerta galloti* y *Chalcides viridanus*. *Trab. Inst. Cajal de Inv. Biol.* 69:223-238.
- Ułinski, P.S. (1983) Dorsal Ventricular Ridge: A Treatise on Forebrain Organization in Reptiles and Birds. New York: Wiley.
- Wiesendanger, R., and M. Wiesendanger (1985a) The thalamic connections with medial area 6 (supplementary motor cortex) in the monkey (*Macaca fascicularis*). *Exp. Brain Res.* 59:91-104.
- Wiesendanger, R., and M. Wiesendanger (1985b) Cerebellocortical linkage in the monkey as revealed by transcellular labelling with the lectin wheat germ agglutinin conjugated to the marker horseradish peroxidase. *Exp. Brain Res.* 59:105-117.