

The pallial amygdala of amniote vertebrates: Evolution of the concept, evolution of the structure

Fernando Martínez-García,^{1*} Alino Martínez-Marcos² and Enrique Lanuza³

¹Departament de Biologia Animal, Facultat de Ciències Biològiques, Universitat de València, València, Spain;

²Departamento de CC. Médicas, Fac. Medicina, Campus de Albacete, Universidad de Castilla-La Mancha, Albacete, Spain; and ³Departament de Biologia Cel·lular, Facultat de Ciències Biològiques, Universitat de València, València, Spain

ABSTRACT: Embryological studies indicate that the amygdala includes pallial structures, namely the cortical amygdala (olfactory and vomeronasal) and the basolateral complex deep to it. In squamate reptiles, the cortical amygdala includes secondary olfactory (the ventral anterior amygdala) and vomeronasal centres (the nucleus sphericus). In birds, the situation is far less clear, due to the relative underdevelopment of the chemosensory systems. The basolateral amygdala of squamate reptiles includes two ventropallial structures: the posterior dorsal ventricular ridge and the lateral amygdala. Like their mammalian counterparts, these centres give rise to glutamatergic projections to the striatal (centromedial) amygdala and the ventromedial hypothalamus. Using the same criteria, the caudal neostriatum and the ventral intermediate archistriatum may represent the ventral pallial amygdala of birds. The basal nucleus of the mammalian amygdala is a lateropallial territory. In reptiles, the lateral pallium includes the dorsolateral amygdala, which, like the mammalian basal nucleus, projects bilaterally to the striatum/accumbens and receives distinct cholinergic and dopaminergic innervations. In the avian brain, the same embryological, hodological, and histochemical criteria are met by the area temporo-parieto-occipitalis, the caudolateral neostriatum and the dorsal intermediate archistriatum. Therefore, the projections from these structures to the paleostriatum and the lobus paraolfactorius are amygdalostriatal, rather than corticostriatal connections. © 2002 Elsevier Science Inc.

KEY WORDS: Limbic system, Cortex, Striatum, Birds, Reptiles, Mammals, Comparative neuroanatomy, Homology.

INTRODUCTION

The organization of the mammalian amygdala is, currently, the centre of intense debate. Following Johnston [21], many authors consider that the amygdala extends rostrally within the basal telencephalon, and reaches the caudal tip of the shell of the nucleus accumbens [2]. On the other hand, Swanson and Petrovich [58] proposed that the amygdala is simply the sum of different, unrelated anatomical structures, including the cortex/claustrum (the basolateral amygdala), the striatum (the central and medial amygdaloid nuclei), and the olfactory cortex (cortical amygdala and cortex-amygdala transition zone). These authors suggested that the term amygdala should be abandoned because its components belong to four different functional systems, namely the main olfac-

tory, the accessory olfactory (vomeronasal), the autonomic and the frontotemporal cortical systems. This view has received some support from studies of the expression of homeotic genes during development [50,57], indicating that the amygdala contains derivatives of the lateral pallium, the ventral pallium, the striatum, and the pallidum. Thus, Puelles et al. [50] stated that “. . . the term ‘amygdaloid’ no longer conveys clearcut meaning. . . .” and instead proposed the use of “the unambiguous terms ‘ventral pallium’ or ‘ventropallial’ versus lateropallial, dorsopallial, mediopallial, or striatal, pallidal”.

Despite their heterogeneous embryological origin, the different divisions of the amygdala of reptiles, birds, and mammals show a common histochemical and hodological organization that includes an intricate set of intra-amygdaloid connections. This suggests that the amygdala is not an arbitrary concept but a true functional system in the telencephalon of amniote vertebrates whose role in the control of behaviour and physiology is only beginning to be understood.

ORGANIZATION AND CONNECTIONS OF THE MAMMALIAN PALLIAL AMYGDALA

The mammalian amygdala displays two kinds of pallial structures (Fig. 1). The superficial areas that show a laminar organization, are dominated by massive inputs from the olfactory bulbs, and are called the *cortical amygdala*. On the other hand, those pallial derivatives deep to the cortical amygdala constitute the *basolateral amygdala* [21,37]. From a comparative viewpoint, it would be very useful to assign each of these pallial amygdaloid nuclei to either the lateral or ventral pallium [50].

The cortical amygdala includes secondary olfactory and vomeronasal areas (see [37] for review). The main olfactory bulbs project to the anterior cortical amygdala (COAa) and the periamygdaloid cortex, which some authors further subdivide into the posterolateral cortical amygdala (COApI) and the cortex-amygdala transition (CxA) [58]. Rostrally, the olfactory projection also terminates in the nucleus of the lateral olfactory tract (NLOT). On the other hand, the posteromedial cortical amygdala (COApm) is the cortical target of the projection from the accessory olfactory bulb (the medial amygdala and the bed nucleus of the stria terminalis also receive this projection but are subpallial). Most of the cortical amygdala probably belongs to the ventral pallium because it is interposed between the piriform cortex and striatal territories.

* Address for correspondence: Fernando Martínez-García, Ph.D., Unitat de Morfologia Microscòpica, Departament de Biologia Animal, Facultat de Ciències Biològiques, Universitat de València. C. Dr. Moliner, 50, 46100 Burjassot, Spain. Fax: +34-96-386-4372; E-mail: martinfe@uv.es

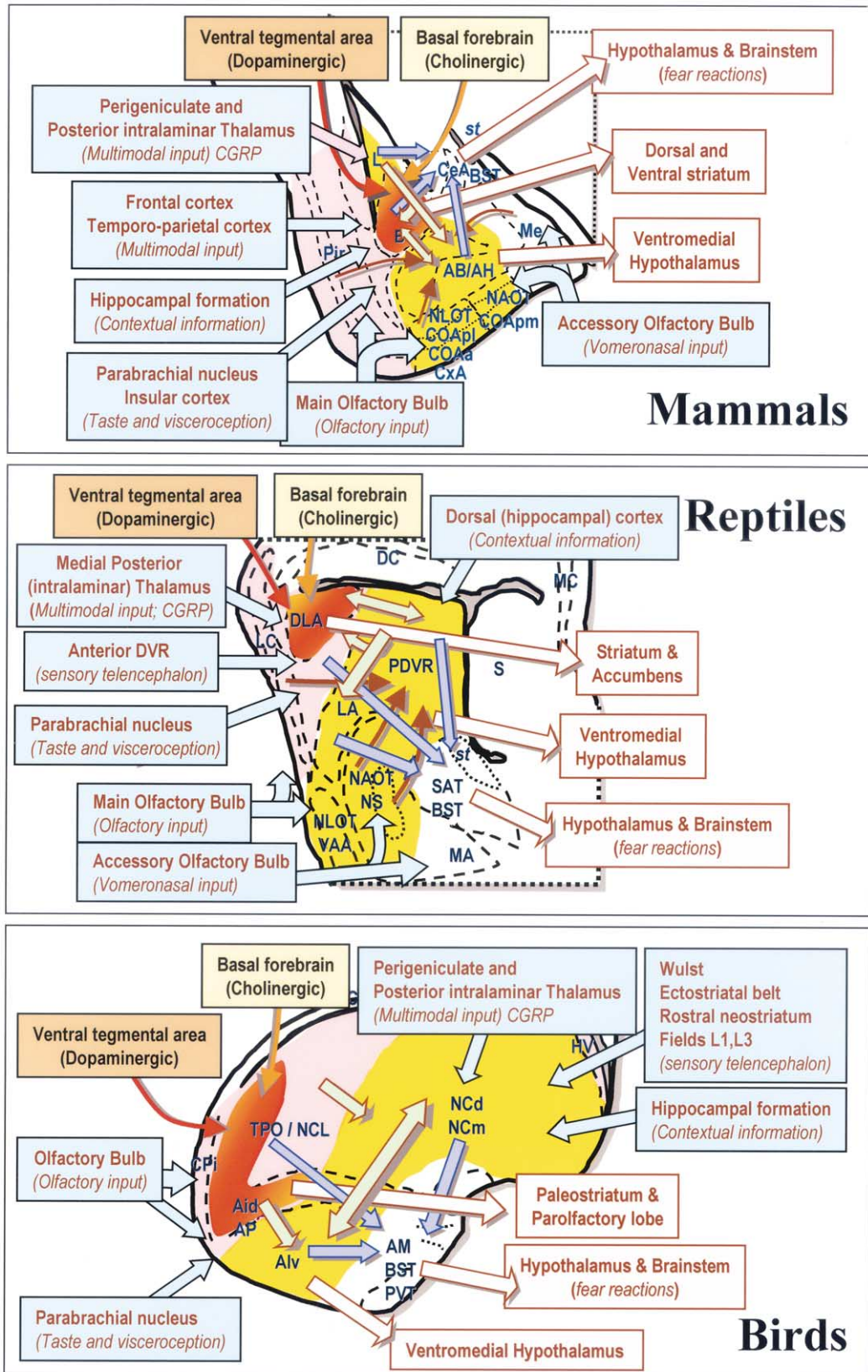


FIG. 1. Schematic drawing of the mammalian, reptilian and avian amygdalae, indicating the lateral (pink) and ventral (yellow) pallial territories and their main connections. See List of Abbreviations.

The basolateral amygdala (deep pallial amygdala) includes the basal (B), accessory basal (AB), and lateral (L) nuclei. Besides a given profile of genetic expression, the defining features of the ventral pallium are its position deep to the lateral olfactory tract and topologically dorsal (contiguous) with striatal territories, criteria that are met by the lateral nucleus [50]. Puelles et al. [50] ascribed the accessory basal amygdaloid nucleus to the striatum, but connectional and histochemical data suggest it to be a ventropallial structure [58]. First, it is the main source of projections from the basolateral to the central amygdala, which are usually considered atypical palliostriatal projections. As a general rule, cortical projections are glutamatergic, in contrast to the GABAergic nature of the main projections from striatal and pallidal centres [58]. The accessory basal nucleus contains few GABAergic neurones [58] and, together with the amygdalo-hippocampal area (AH) [49], is the source of glutamatergic (zinc-enriched) projections to the ventromedial hypothalamus via the stria terminalis [5,45,55]. These data indicate that the amygdalo-hippocampal area (included in the posterior amygdaloid nucleus [5]) is also a pallial structure belonging to the basolateral amygdala. The intercalated cell masses of the amygdala have been suggested to be ventropallial [58] and, in fact, the paracapsular interstitial nuclei, appear to form a bridge of ventral pallial tissue connecting the accessory basal and lateral nuclei.

The anterior amygdaloid area (AAA) lies rostral to the accessory basal amygdala and deep to the nucleus of the lateral olfactory tract [37], thus resembling a ventropallial structure. However, the anterior amygdaloid area is usually further subdivided into dorsal and ventral parts, so that a dual (striatal [58] and cortical) embryological origin of this ill-defined area cannot be disregarded.

Pitkänen et al. [48] reviewed the intra-amygdaloid circuitry in the context of fear conditioning and fear expression. They considered that the lateral nucleus is a sensory interface receiving both thalamic and cortical inputs, whereas the central amygdala (CeA) gives rise to projections subserving the expression of fear behaviour. Inputs from the hippocampus and frontal cortex to the lateral, basal, and accessory basal nuclei would constitute further highly processed sensory inputs to this functional system [37]. The intrinsic connections of the basolateral amygdala (mainly from the lateral nucleus to the basal and accessory basal nuclei) and its projections to the central amygdala appear to constitute the basic circuitry underlying fear conditioning and conditioned fear expression. Although widely accepted, this scheme neglects important amygdaloid afferents and efferents. Cholinergic cells in the basal forebrain innervate the basal nucleus, amygdalo-hippocampal area and nucleus of the lateral olfactory tract [7,19]. These nuclei also receive a relatively dense dopaminergic innervation from the lateral ventral tegmental area and the medial substantia nigra [33]. Other major inputs of the basolateral amygdala come from the superficial cortical amygdala and from other sources of chemosensory information including taste. Olfactory inputs arise from the piriform cortex [37] and posterolateral cortical amygdala [5], which project to parts of the accessory basal nucleus, anterior cortical amygdala, and anterior amygdaloid area. Vomeronasal stimuli may be conveyed to the accessory basal nucleus and amygdalo-hippocampal area from the posterior medial amygdala [6,14]. The parabrachial complex (directly and indirectly) and the insular cortex, convey a mixture of viscerosceptive and gustatory information to the central and basolateral amygdala [37,53]. In turn, the basolateral amygdala not only projects to the central and medial amygdala [8,24,47], but also to the ventromedial hypothalamus, and the dorsal (caudatus-putamen) and ventral striatum (nucleus accumbens). The projection to the hypothalamus courses through the stria terminalis and arises mainly from the accessory basal nucleus and amygdalo-hippocampal area [5,47,49], whereas

the basal nucleus is the main source of amygdalo-striatal projections [16,22].

THE REPTILIAN PALLIAL AMYGDALA

The pallial amygdala of reptiles can be identified using the same criteria that define it in mammals. Thus, it would include both superficial and deep nuclei that belong to either the lateral or ventral pallium. The superficial cortical amygdala would receive important inputs from the main and accessory olfactory bulbs, and the structures topographically deep to these nuclei would constitute the reptilian basolateral amygdala (Fig. 1).

Studies carried out on several species of reptiles [27,34] have identified two cortical (superficial and layered) structures of the caudal telencephalon that receive a massive projection from the main olfactory bulb: the caudal portion of the lateral cortex (LCC) and the ventral anterior amygdala (VAA). They are caudal to the rostral "piriform" cortex (rostral lateral cortex) and nucleus of the lateral olfactory tract, respectively. Moreover, squamate reptiles (lizards and snakes) possess a noteworthy structure known as the *nucleus sphericus* (NS), which constitutes the main target for the accessory olfactory bulb. The cortical nature of the NS has been recognised by several authors [44,59] and is supported by its laminar organization in which projection neurones occupy the cellular layer and most GABAergic neurones occur in the molecular layers (Fig. 2A).

If the caudal lateral cortex is the assumed to be the reptilian caudal "piriform" cortex, the ventral anterior amygdala would constitute the superficial ventral pallium of the reptilian amygdala, thus being the homologue of the mammalian anterior and posterolateral cortical amygdala. On the other hand, the nucleus sphericus is the most likely homologue for the mammalian posteromedial cortical amygdala. In fact, both the reptilian nucleus sphericus [17,26,34,35] and the mammalian posteromedial cortical amygdala [5] give rise to similar projections: (1) back to the accessory olfactory bulb; (2) to their contralateral counterpart through the anterior commissure; (3) to the piriform and endopiriform area; (4) to parts of the hippocampal (ammonic) cortex; (5) to the basolateral amygdala (see below); (6) to the medial amygdala and bed nucleus of the stria terminalis; and (7) to the ventral striatum (olfacto-striatum [26]).

Deep to the nuclei of the olfactory tracts, the nucleus sphericus and the ventral anterior amygdala, three main nuclei would make up the basolateral amygdala of reptiles: the posterior dorsal ventricular ridge (PDVR), the lateral amygdaloid nucleus and the dorsolateral amygdala (DLA [29]). Tracer injections into the dorsal ventricular ridge of lizards, encompassing the ependymal layer (Fig. 2B), usually result in labelling of radial glia cells, which run within the lateral amygdaloid nucleus to reach olfactory structures of the ventral pallium (e.g., the nucleus of the lateral olfactory tract; Fig. 2C). The ventropallial nature of the reptilian DVR is further supported by the expression pattern of homeotic genes in turtle embryos [57]. On the other hand, radial glia crossing the dorsolateral amygdaloid nucleus [42] seem to reach the pia mater at the level of the caudal lateral cortex, suggesting a lateropallial nature for this deep nucleus.

The ventropallial nature of the reptilian PDVR and the lateral amygdala suggests that these nuclei are homologous of the mammalian lateral and accessory basal amygdaloid nuclei and the amygdalo-hippocampal area. On the other hand, the deep lateropallial amygdala of lizards, the DLA, is the most likely candidate for the reptilian homologue of the mammalian basal amygdaloid nucleus. Data about the connections and histochemistry of the reptilian brain strongly support these homologies [29] (Fig. 1). Tracer injections into the PDVR and/or DLA [15,28,35] antero-

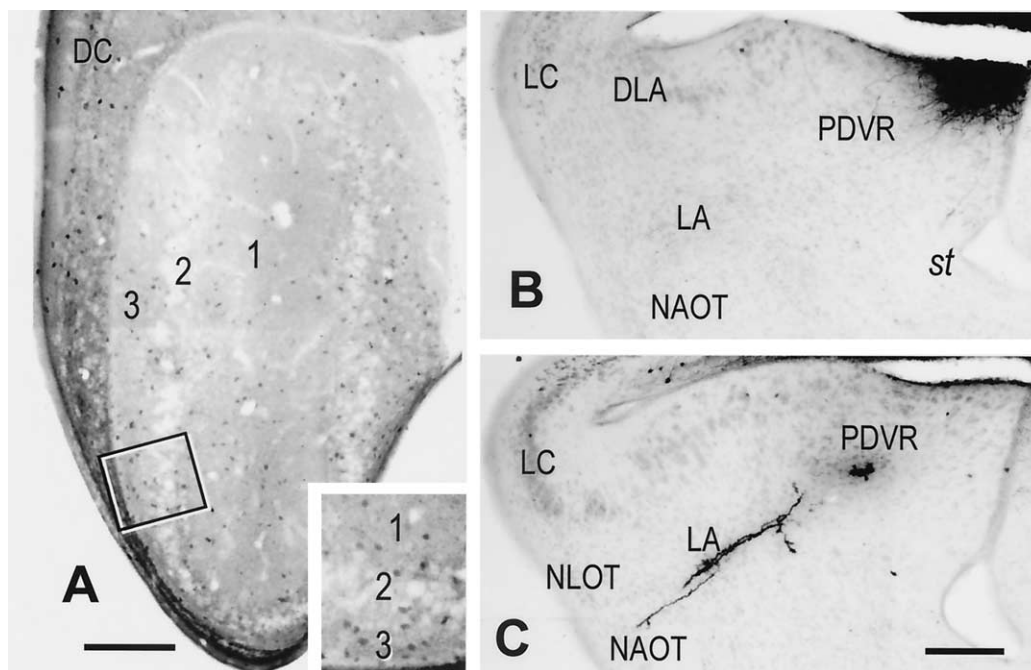


FIG. 2. (A) Distribution of γ -aminobutyric acid (GABA)-immunoreactive cells in the nucleus sphericus (NS) of the lizard *Podarcis hispanica*. Most of the GABAergic cells are present in the hilus (1) and marginal layer (3), whereas most of the neurones in the cell or mural layer (2) are non-immunoreactive (for detail, see inset). This distribution pattern is typical, but inverted, of the cortical telencephalon (see layering and distribution of GABAergic cells in the overlying dorsal cortex), thus supporting the (ventro)pallial nature of the nucleus sphericus. (B) and (C) An injection of biotinylated dextranamine, involving the ependymal layer of the medial posterior dorsal ventricular ridge (PDVR) (B) resulted in labelling of tanicytes, whose processes can be followed through the PDVR and LA (C), and reach the pial surface at the level of the nuclei of the lateral and accessory olfactory tracts. Scale bars in A and C (valid also for B): 200 μ m. See List of Abbreviations.

gradely labelled the striato-amygdaloid transition area (SAT), the most likely reptilian homologue of the central amygdala [28,52]. Thus, the basolateral amygdala of reptiles (PDVR, lateral amygdala, and DLA), like its mammalian homologue, projects massively to the central amygdala. The DLA of lizards receives distinctive dopaminergic [3,56] and cholinergic innervations [28, 38] and is the main source of amygdaloid projections to both the dorsal and ventral (nucleus accumbens) striatum [35,46], which are characteristic features of the mammalian basal amygdaloid nucleus (see above).

The third main output of the basolateral amygdala runs in the stria terminalis to reach the ventromedial hypothalamus, and in reptiles also seems to contain histochemically detectable zinc [44]. In squamate reptiles [4,28,36] this projection mainly arises from the ventral PDVR and lateral amygdaloid nucleus (although in snakes part of the DLA may also contribute to the stria terminalis [36]). These data strongly support the homology of parts of the PDVR and the lateral amygdala of reptiles with the mammalian accessory basal amygdaloid nucleus and amygdalo-hippocampal area.

It should be stressed that, like the mammalian basolateral amygdala, its reptilian counterpart receives: (1) non-chemosensory afferents from the thalamus and telencephalic sensory centres (anterior DVR), (2) highly processed sensory information from the hippocampal cortex (dorsal cortex), (3) olfactory information from the (ventral and caudal) lateral cortex [20,29,36], and (4) vomeronasal inputs from the nucleus sphericus [26].

THE AVIAN PALLIAL AMYGDALA

Two features of the avian brain have hindered the identification of the avian pallial amygdala (Fig. 1): first, the presence of a huge dorsal ventricular ridge of uncertain comparative significance and, second, the relatively poorly developed olfactory system and the virtual absence of vomeronasal system [51]. This second feature makes the superficial cortical structures of the avian amygdala very difficult to identify with certainty. However, it is worth mentioning that in mammals and reptiles the input from the main olfactory bulb is not an exclusive feature of the piriform cortex (lateral pallium) but also reaches superficial ventropallial structures (nucleus of the lateral olfactory tract and cortical amygdala).

Our strategy has been to use the brain of extant reptiles as a 'bridge' for comparing the avian and mammalian brains. Both birds and reptiles exhibit a DVR, although the avian DVR is more developed and displays two clear-cut divisions, the ventral hyperstriatum (HV) and neostriatum (N), which are not evident in reptiles. Light has been shed on the comparative significance of the avian DVR by studies of gene expression during development [50,57], indicating that it includes lateral (HV) and ventral pallial (N) derivatives. In the caudal telencephalon these pallial territories also include portions of the archistriatum: the dorsal intermediate (AI_d) and the posterior archistriatum (AP) belong to the lateral pallium, whereas the ventral intermediate archistriatum (AI_v) is ventropallial [50]. Topological congruence suggests that there should be a bridge of lateral pallial tissue in the intermediate-to-caudal neostriatum joining the two main lateral pallial derivatives

(ventral hyperstriatum and dorsal intermediate and posterior parts of the archistriatum). This zone would include the area temporoparieto-occipitalis (TPO), which seems lateropallial since it lies just deep to the cortex piriformis [51].

These data suggest a new view of the comparative neuroanatomy of the sauropsidian telencephalon (see Fig. 1). The deep, caudal lateral pallial derivatives, namely the reptilian DLA and the avian TPO and dorso-intermediate and posterior archistriatum, would be homologous to each other and to the mammalian basal amygdaloid nucleus. On the other hand, ventropallial structures like the reptilian PDVR/lateral amygdala and the caudal neostriatum and ventro-intermediate archistriatum of birds, would be the sauropsid counterparts of the lateral and accessory basal nuclei and amygdalo-hippocampal area of the mammalian amygdala. Histochemical and connectional data support some of these proposed homologies for the avian amygdala. Thus, the dorso-intermediate archistriatum and the TPO receive dopaminergic [61] and cholinergic innervations [39], reminiscent of the mammalian basal nucleus and its reptilian counterpart (DLA). Another feature of the basolateral amygdala, its projection to the central amygdala, is difficult to ascertain in birds due to the uncertain identity of the avian central amygdala. In their report of the pigeon corticostriatal projections Veenman et al. [60] described important projections from the dorso-intermediate archistriatum and TPO to both the dorsal (paleostriatum augmentatum) and ventral striatum (lobus parolfactorius) (see also [25]). The data discussed above lead us to reinterpret these connections as amygdalo-striatal. Therefore, in all studied amniote vertebrates amygdalo-striatal projections mainly arise from the deep lateropallial amygdala.

The third projection system characteristic of the basolateral amygdala of mammals and reptiles is the zinc-containing projection to the ventromedial hypothalamus via the stria terminalis that arises from ventral pallial structures. A similar projection exists in birds, where also appears to be rich in heavy metals [13] but, to the best of our knowledge, it has only been traced anterogradely [9,11,62]. Preliminary results in our laboratory confirm that this projection mainly arises from the ventro-intermediate and anterior archistriatum (see also [9,11]). These data suggest that in birds as in mammals and reptiles, the ventropallial amygdala includes a sensory interface (caudal neostriatum) that projects to the output region (AIv) [25,60]. The caudal neostriatum receives sensory information from associative portions of the DVR [25,40] as well as a multimodal thalamic input [23] rich in calcitonin-gene related peptide [30], which is reminiscent of the lateral amygdala of mammals [30].

Although our hypothesis does not fit the proposed homology of the TPO (lateral pallium) with the mammalian prefrontal cortex (dorsal and/or medial pallium), it might explain why lesions of both structures render similar behavioral deficits (impaired delayed alternation [41]). In the mammalian brain, the basolateral amygdala (more specifically the basal nucleus [37]) and prefrontal cortex are deeply interconnected and functionally interdependent (making up what Swanson and Petrovich [58] call the frontotemporal system). If the avian TPO is homologous to the mammalian basal nucleus, TPO lesions might well result in behavioural deficits similar to those of frontal cortex lesions in mammals.

THE AMYGDALA AS A FUNCTIONAL SYSTEM AND ITS ROLE IN THE EVOLUTION OF THE BRAIN

As discussed above, the amygdalae of mammals, birds and reptiles, show a common pattern of connections that include an intricate set of intrinsic connections. This suggests that the amygdala is indeed a functional system that has undergone a conserva-

tive evolution in amniote phylogeny and, therefore, should play a key role in survival and reproduction.

Functional studies of the pallial amygdala, virtually restricted to the mammalian basolateral amygdala, suggest it to have two main functions. First, it is involved in fear conditioning [10,31]. The anatomical pathway mediating this kind of conditioned response would be composed of the projection from the basolateral to the central amygdala and the descending projection systems of the latter. On the other hand, there is compelling evidence to suggest that the amygdalo-ventral striatal projections are involved in stimulus-reward association [12]. As described above, the basolateral amygdala of amniotes is an associative area receiving inputs of diverse sensory significance. Synaptic plasticity in the basolateral amygdala might mediate the association of aversive/attractive stimuli with neutral ones, which would result in the transfer of the emotional significance of the former to the latter (in a case of Pavlovian conditioning).

It is important to emphasise that chemosensory information reaches the pallial amygdala (cortical) directly from the olfactory bulbs. Moreover, both the piriform cortex and the cortical olfactory amygdala project massively to the basolateral amygdala, as do the vomeronasal portion of the amygdala in both mammals and reptiles (see above). However, the role of the basolateral amygdala in olfaction or vomeronasal function requires elucidation. Pheromones, which are detected by the vomeronasal organ in a very specific way [32], play a critical role in intra-species communication [18], and apparently have an innate emotional value. For instance, male sex pheromones attract conspecific females but are aversive to conspecific males [43]. Convergence of projections from the vomeronasal and olfactory systems in the basolateral amygdala might allow for an association of pheromones with odours, thus resulting in an emotional labelling of odours [1]. Indeed, many neurones in the basolateral amygdala respond to a particular odour depending on whether it was paired with a pleasant or unpleasant outcome [54]. This type of association would confer a predictive value to odours, allowing the animal to anticipate its reaction to the pheromone (which usually are non-volatile), leading to trailing the sources of attractive pheromones and to avoiding aversive ones. Afferents to the amygdala from the thalamus, both direct and indirect through the sensory telencephalon, appear to have arisen early in vertebrate evolutionary history (at least in ancestral amniotes). These pathways, together with the chemosensory inputs to the basolateral amygdala described above, allowed for the occurrence of associations between chemical (pheromones and odours) and non-chemical stimuli, as well as between different types of non-chemical stimuli. In this way, the vertebrate amygdala could have become a neural centre involved in the emotional labelling of any kind of novel stimuli by association with either attractive or aversive ones.

Processing of sensory information in the telencephalon prior to its relay to the amygdala, would have been strongly selected during the evolutionary history of amniotes, because it allows the animal to react differently to stimuli with a similar configuration but a different emotional value. This could have instigated a selection of bigger and more complex sensory telencephalic centres, a phenomenon that seems to have occurred independently in two different taxa, in a clear case of evolutionary convergence. In therapsid reptiles, leading to mammals, sensory processing possibly took place mainly in the mediodorsal pallium, which developed into a complex neocortex with associative regions that provide highly processed sensory information to the amygdala. In sauropsids, this sensory processing occurred in ventral and lateral pallial territories, thus resulting in the development of the DVR, which, at least in birds, includes associative areas that project to the amygdala.

ACKNOWLEDGEMENTS

This work has been supported by the *Conselleria de Cultura, Educació i Ciència* (GV00-161-05) and the Acciones Integradas Hispano-Británicas (HB-1997-0211). The authors are indebted to Dr. José F. Pertusa, Dr. Cristian Font, Dr. Adoración Hernández, Amparo Novejarque, Amparo Romero and José Moncho for their invaluable help during the experimental work, and to Dr. Ceri Davies for critically reading and commenting on the manuscript.

REFERENCES

- Aggleton, J. P. The amygdala—What's happened in the last decade? In: Aggleton, J. P., ed. *The amygdala*, 2nd ed.: A functional analysis. Oxford: Oxford University Press; 2000:1–30.
- Alheid, G. F.; de Olmos, J. S.; Beltramino, C. A. Amygdala and extended amygdala. In: Paxinos, G., ed. *The rat nervous system*, 2nd ed. San Diego: Academic Press; 1995:495–578.
- Andreu, M. J.; Dávila, J. C.; de la Calle, A.; Guirado, S. Monoaminergic innervation patterns in the anterior dorsal ventricular ridge of a lacertid lizard, *Psammodromus algerus*. *Brain Behav. Evol.* 44:175–186; 1994.
- Bruce, L. L.; Neary, T. J. Afferent projections to the ventromedial hypothalamic nucleus in a lizard *Gekko gecko*. *Brain Behav. Evol.* 46:14–29; 1995.
- Canteras, N. S.; Simerly, R. B.; Swanson, L. W. Connections of the posterior nucleus of the amygdala. *J. Comp. Neurol.* 324:143–179; 1992.
- Canteras, N. S.; Simerly, R. B.; Swanson, L. W. Organization of projections from the medial nucleus of the amygdala: A PHAL study in the rat. *J. Comp. Neurol.* 360:213–245; 1995.
- Carlsen, J.; Záborsky, L.; Heimer, L. Cholinergic projections from the basal forebrain to the basolateral amygdaloid complex: A combined retrograde fluorescent and immunohistochemical study. *J. Comp. Neurol.* 234:155–167; 1985.
- Christensen, M. K.; Frederickson, C. J. Zinc-containing afferent projections to the rat corticomedial amygdaloid complex: A retrograde tracing study. *J. Comp. Neurol.* 400:375–390; 1998.
- Davies, D. C.; Csillag, A.; Székely, A. D.; Kabai, P. Efferent connections of the domestic chick archistriatum: A *Phaseolus* lectin anterograde tracing study. *J. Comp. Neurol.* 389:679–693; 1997.
- Davis, M. Neurobiology of fear responses: The role of the amygdala. *J. Neurophysiol. Clin. Neurosci.* 9:382–402; 1997.
- Dubbeldam, J. L.; den Boer-Visser, A. M.; Bout, R. G. Organization and efferent connections of the archistriatum of the mallard, *Anas platyrhynchos* L.: An anterograde and retrograde tracing study. *J. Comp. Neurol.* 388:632–657; 1997.
- Everitt, B. J.; Parkinson, J. A.; Olmstead, M. C.; Arroyo, M.; Robledo, P.; Robbins, T. W. Associative processes in addiction and reward. The role of amygdala-ventral striatal subsystems. *Ann. N.Y. Acad. Sci.* 877:412–438; 1999.
- Faber, H.; Braun, K.; Zuschratter, W.; Scheich, H. System-specific distribution of zinc in the chick brain. A light- and electron-microscopic study using the Timm method. *Cell Tissue Res.* 258:247–257; 1989.
- Gómez, D. M.; Newman, S. W. Differential projections of the anterior and posterior regions of the medial amygdaloid nucleus in the Syrian hamster. *J. Comp. Neurol.* 317:195–218; 1992.
- González, A.; Russchen, F. T.; Lohman, A. H. M. Afferent connections of the striatum and the nucleus accumbens in the lizard *Gekko gecko*. *Brain Behav. Evol.* 36:39–58; 1990.
- Groenewegen, H. J.; Becker, N. E.; Lohman, A. H. M. Subcortical afferents of the nucleus accumbens septi in the cat, studied with retrograde axonal transport of horseradish peroxidase and bisbenzimid. *Neuroscience* 5:1903–1916; 1980.
- Halpern, M. The telencephalon of snakes. In: Ebbesson, S. O. E., ed. *Comparative neurology of the telencephalon*. New York: Plenum Press; 1980:257–294.
- Halpern, M. The organization and function of the vomeronasal system. *Annu. Rev. Neurosci.* 10:325–362; 1987.
- Hecker, S.; Mesulam, M. M. Two types of cholinergic projections to the rat amygdala. *Neuroscience* 60:383–397; 1994.
- Hoogland, P. V.; Vermeulen-Vanderzee, E. Efferent connections of the lateral cortex of the lizard *Gekko gecko*: Evidence for separate origins of medial and lateral pathways from the lateral cortex to the hypothalamus. *J. Comp. Neurol.* 352:469–480; 1995.
- Johnston, J. B. Further contributions to the study of the evolution of the forebrain. *J. Comp. Neurol.* 35:337–481; 1923.
- Kelley, A. E.; Domesick, V. B.; Nauta, W. J. H. The amygdalostriatal projection in the rat: An anatomical study by anterograde and retrograde tracing methods. *Neuroscience* 7:615–630; 1982.
- Korzeniewska, E.; Güntürkün, O. Sensory properties and afferents of the N. dorsolateralis posterior thalami of the pigeon. *J. Comp. Neurol.* 292:457–479; 1990.
- Krettek, J. E.; Price, J. L. A description of the amygdaloid complex in the rat and cat with observations on intra-amygdaloid axonal connections. *J. Comp. Neurol.* 178:255–280; 1978.
- Kröner, S.; Güntürkün, O. Afferent and efferent connections of the caudolateral neostriatum in the pigeon (*Columba livia*): A retro- and anterograde pathway tracing study. *J. Comp. Neurol.* 407:228–260; 1999.
- Lanuza, E.; Halpern, M. Afferent and efferent connections of the nucleus sphericus in the snake *Thamnophis sirtalis*: Convergence of olfactory and vomeronasal information in the lateral cortex and the amygdala. *J. Comp. Neurol.* 385:627–640; 1997.
- Lanuza, E.; Halpern, M. Efferents and centrifugal afferents of the main and accessory olfactory bulbs in the snake *Thamnophis sirtalis*. *Brain Behav. Evol.* 51:1–22; 1998.
- Lanuza, E.; Font, C.; Martínez-Marcos, A.; Martínez-García, F. Amygdalo-hypothalamic projections in the lizard *Podarcis hispanica*: A combined anterograde and retrograde tracing study. *J. Comp. Neurol.* 384:537–555; 1997.
- Lanuza, E.; Belekova, M.; Martínez-Marcos, A.; Font, C.; Martínez-García, F. Identification of the reptilian basolateral amygdala: An anatomical investigation of the afferents to the posterior dorsal ventricular ridge of the lizard *Podarcis hispanica*. *Eur. J. Neurosci.* 384:537–555; 1998.
- Lanuza, E.; Davies, D. C.; Landete, J. M.; Novejarque, A.; Martínez-García, F. Distribution of CGRP-like immunoreactivity in the chick and quail brain. *J. Comp. Neurol.* 421:515–532; 2000.
- LeDoux, J. E. *The emotional brain*. New York: Simon and Schuster; 1996.
- Liman, E. R. Sex and the single neuron: Pheromones excite. *Trends Neurosci.* 24:2–3; 2001.
- Loughlin, S. E.; Fallon, J. H. Substantia nigra and ventral tegmental area projections to cortex: Topography and collateralization. *Neuroscience* 11:425–435; 1984.
- Martínez-García, F.; Olucha, F. E.; Teruel, V.; Lorente, M. J.; Schwedtfeger, W. K. Afferent and efferent connections of the olfactory bulbs in the lizard *Podarcis hispanica*. *J. Comp. Neurol.* 305:337–347; 1991.
- Martínez-García, F.; Olucha, F. E.; Teruel, V.; Lorente, M. J. Fiber connections of the amygdaloid formation of the lizard *Podarcis hispanica*. *Brain Behav. Evol.* 41:156–162; 1993.
- Martínez-Marcos, A.; Lanuza, E.; Halpern, M. Organization of the ophidian amygdala: Chemosensory pathways to the hypothalamus. *J. Comp. Neurol.* 412:51–68; 1999.
- McDonald, A. Cortical pathways to the mammalian amygdala. *Prog. Neurobiol.* 55:257–332; 1998.
- Medina, L.; Smeets, W. J. A. J.; Hoogland, P. V.; Puelles, L. Distribution of choline acetyltransferase immunoreactivity in the brain of the lizard *Gallotia galloti*. *J. Comp. Neurol.* 331:261–285; 1993.
- Medina, L.; Reiner, A. Distribution of choline acetyltransferase immunoreactivity in the pigeon brain. *J. Comp. Neurol.* 342:497–537; 1994.
- Metzger, M.; Jiang, S.; Braun, K. Organization of the dorsocaudal neostriatal complex: A retrograde and anterograde tracing study in the domestic chick with special emphasis on pathways relevant to imprinting. *J. Comp. Neurol.* 395:380–404; 1998.
- Mogensén, J.; Divac, I. The prefrontal 'cortex' in the pigeon. Behavioral evidence. *Brain Behav. Evol.* 21:60–66; 1982.
- Monzon-Mayor, M.; Yanes, C.; Tholey, G.; De Barry, J.; Gombos, G. Immunohistochemical localization of glutamine synthetase in mesen-

- cephalon and telencephalon of the lizard *Gallotia galloti* during ontogeny. *Glia* 3:81–97; 1990.
43. Mucignat-Caretta, C.; Caretta, A.; Baldini, E. Protein-bound male urinary pheromones: Differential responses according to age and gender. *Chem. Senses* 23:67–70; 1998.
 44. Pérez-Clausell, J. Organization of zinc-containing terminal fields in the brain of the lizard *Podarcis hispanica*: A histochemical study. *J. Comp. Neurol.* 267:153–171; 1988.
 45. Pérez-Clausell, J.; Frederickson, C. J.; Danscher, G. Amygdaloid efferents through the stria terminalis in the rat give origin to zinc-containing boutons. *J. Comp. Neurol.* 290:201–212; 1989.
 46. Pérez-Santana, L.; Marín, O.; Smeets, W. J. A. J. Afferent connections of the nucleus accumbens of the snake, *Elaphe guttata*, studied by means of in vitro and in vivo tracing techniques in combination with TH immunohistochemistry. *Neurosci. Lett.* 225:101–104; 1997.
 47. Petrovich, G. D.; Risold, P. Y.; Swanson, L. W. Organization of projections from the basomedial nucleus of the amygdala: A PHAL study in the rat. *J. Comp. Neurol.* 374:387–420; 1996.
 48. Pitkänen, A.; Savander, V.; LeDoux, J. E. Organization of intra-amygdaloid circuitries in the rat: An emerging framework for understanding functions of the amygdala. *Trends Neurosci.* 20:517–523; 1997.
 49. Price, J. L.; Slotnick, B. M.; Revial, M. F. Olfactory projections to the hypothalamus. *J. Comp. Neurol.* 306:447–461; 1991.
 50. Puelles, L.; Kuwana, E.; Puelles, E.; Bulfone, A.; Shimamura, K.; Keleher, J.; Smiga, S.; Rubenstein, J. R. L. Pallial and subpallial derivatives in the embryonic chick and mouse telencephalon, traced by the expression of the genes, *Dlx-2*, *Emx-1*, *Nkx-2.1*, *Pax-6*, and *Tbr-1*. *J. Comp. Neurol.* 424:409–438; 2000.
 51. Reiner, A.; Karten, H. J. Comparison of olfactory bulb projections in pigeons and turtles. *Brain Behav. Evol.* 27:11–27; 1985.
 52. Russchen, F. T.; Jonker, A. J. Efferent connections of the striatum and the nucleus accumbens in the lizard *Gekko gekko*. *J. Comp. Neurol.* 276:61–80; 1987.
 53. Saper, C. B.; Loewi, A. D. Efferent connections of the parabrachial nucleus in the rat. *Brain Res.* 197:291–317; 1980.
 54. Schoenbaum, G.; Chiba, A. A.; Gallagher, M. Neural encoding in orbitofrontal cortex and basolateral amygdala during olfactory discrimination learning. *Neuroscience* 19:1876–1884; 1999.
 55. Slomianka, L.; Danscher, G.; Frederickson, C. J. Labeling of the neurons of origin of zinc-containing pathways by intraperitoneal injections of sodium selenite. *Neuroscience* 38:843–854; 1990.
 56. Smeets, W. J.; Hoogland, P. V.; Voorn, P. The distribution of dopamine immunoreactivity in the forebrain and midbrain of the lizard *Gekko gekko*: An immunohistochemical study with antibodies against dopamine. *J. Comp. Neurol.* 253:46–60; 1986.
 57. Smith-Fernández, A.; Pieau, C.; Repérant, J.; Boncinelli, E.; Wassef, M. Expression of *Emx-1* and *Dlx-1* homeobox genes define three molecularly distinct domains in the telencephalon of mouse, chick, turtle and frog embryos: Implications for the evolution of telencephalic subdivisions in amniotes. *Development* 125:2099–2111; 1998.
 58. Swanson, L. W.; Petrovich, G. D. What is the amygdala? *Trends Neurosci.* 21:323–331; 1998.
 59. Ulinski, P. S.; Kanarek, D. A. Cytoarchitecture of nucleus sphericus in the common boa, *Constrictor constrictor*. *J. Comp. Neurol.* 151:159–174; 1973.
 60. Veenman, C. L.; Wild, J. M.; Reiner, A. Organization of the avian corticostriatal projection system: A retrograde and anterograde pathway tracing study in pigeons. *J. Comp. Neurol.* 354:87–126; 1995.
 61. Waldmann, C.; Güntürkün, O. The dopaminergic innervation of the pigeon caudolateral forebrain: Immunocytochemical evidence for a “prefrontal cortex” in birds? *Brain Res.* 600:225–234; 1993.
 62. Zeier, H.; Karten, H. J. The archistriatum of the pigeon: Organization of afferent and efferent connections. *Brain Res.* 31:313–326; 1971.

LIST OF ABBREVIATIONS

Mammals

AAA,	anterior amygdaloid area
AB,	accessory basal amygdaloid nucleus
AH,	amygdalo-hippocampal area
B,	basal amygdaloid nucleus
BST,	bed nucleus of the <i>stria terminalis</i>
CeA,	central amygdaloid nucleus
COAa,	anterior cortical amygdala
COApl,	posterolateral cortical amygdala
COApm,	posteromedial cortical amygdala
CxA,	cortex-amygdala transition
L,	lateral amygdaloid nucleus
Me,	medial amygdala
NAOT,	nucleus of the accessory olfactory tract
NLOT,	nucleus of the lateral olfactory tract
Pir,	piriform cortex

Reptiles

BST,	bed nucleus of the <i>stria terminalis</i>
DC,	dorsal cortex
DLA,	dorsolateral amygdaloid nucleus
DVR,	dorsal ventricular ridge
LA,	lateral amygdala
LCC,	caudal portion of the lateral cortex
MA,	medial amygdala
MC,	medial cortex
NAOT,	nucleus of the accessory olfactory tract
NLOT,	nucleus of the lateral olfactory tract
NS,	Nucleus sphericus
PDVR,	posterior dorsal ventricular ridge
S,	septum
SAT,	reptilian striato-amygdaloid transition
st,	stria terminalis
VAA,	ventral anterior amygdala

Birds

AA,	anterior archistriatum
AId,	dorsal intermediate archistriatum
AIV,	ventral intermediate archistriatum
AM,	medial archistriatum
AP,	posterior archistriatum
BST,	bed nucleus of the <i>stria terminalis</i>
CPI,	cortex piriformis
HV,	ventral hyperstriatum
N,	Neostriatum
NCd,	neostriatum dorsocaudale
NCL,	neostriatum dorsolaterale
NCm,	neostriatum caudomediale
PVT,	ventral paleostriatum
TPO,	area temporo-parieto- occipitalis