

The common organization of the amygdaloid complex in tetrapods: New concepts based on developmental, hodological and neurochemical data in anuran amphibians

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Abstract

Research over the last few years has demonstrated that the amygdaloid complex in amniotes shares basic developmental, hodological and neurochemical features. Furthermore, homolog territories of all main amygdaloid subdivisions have been recognized among amniotes, primarily highlighted by the common expression patterns for numerous developmental genes. With the achievement of new technical approaches, the study of the precise neuroanatomy of the telencephalon of the anuran amphibians has been possible, revealing that most of the structures present in amniotes are recognizable in these anamniotes. Thus, recent investigations have yielded enough results to support the notion that the organization of the anuran amygdaloid complex includes subdivisions with origin in ventral pallial and subpallial territories, a strong relationship with the vomeronasal and olfactory systems, abundant intra-amygdaloid connections, a main output center involved in the autonomic system, profuse amygdaloid fiber systems, and distinct chemoarchitecture. When all these new data about the development, connectivity and neurochemistry of the amygdaloid complex in anurans are taken into account, it becomes patent that a basic organization pattern is shared by both amniotic and anamniotic tetrapods.

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Abbreviations: A, anterior nucleus of the dorsal thalamus; AA, anterior amygdala; ac, anterior commissure; Acc, nucleus accumbens; Ad, anterodorsal tegmental nucleus; Av, anteroventral tegmental nucleus; AOB, accessory olfactory bulb; Apl, amygdala pars lateralis; Apm, amygdala pars mediales; BDA, biotinylated dextran amine; BLA, basolateral amygdala; BMA, basomedial amygdala; BST, bed nucleus of the stria terminalis; C, central nucleus of the dorsal thalamus; CeA, central amygdala; CLD, area corticoidea dorsolateralis; CoAa, anterior cortical amygdala; CoApl, posterolateral cortical amygdala; CoApm, posteriomedial cortical amygdala; CPi, cortex piriformis; DB, diagonal band of Broca; DCN, dorsal column nucleus; DP, pallidum dorsal; DLA, dorsolateral amygdala; dStr, dorsal striatum; FDA, fluoresceine conjugated dextranamine; Hp, hippocampus; Hv, hyperstriatum ventrale; La, lateral thalamic nucleus; LA, lateral amygdala; Lc, locus coeruleus; LC, lateral cortex; LDT, laterodorsal tegmental nucleus; lfb, lateral forebrain bundle; LGE, lateral ganglionic eminence; LH, lateral hypothalamus; lot, lateral olfactory tract; LP, lateral pallium; Lpv, lateral posteroventral thalamic nucleus; LPv, lateral pallium ventralis; Ls, lateral septum; Ma, mamillar area; MC, medial cortex; MeA, medial amygdala; MGE, medial ganglionic eminence; MOB, main olfactory bulb; Mp, medial pallium; Ms, medial septum; NCL, caudolateral nidopallium; NS, nucleus Sphericus; Nsol, nucleus of the solitary tract; oc, optic chiasm; OT, optic tectum; PA, pallidum; PB, parabrachial nucleus; PC, precommissural pretecal nucleus; PDVR, posterodorsal ventricular ridge; PN, precommissural pretecal neuropil; Pir, piriform cortex; PoA, posterior nucleus of pallial amygdala; POa, anterior preoptic area; PPN, pedunculopontine tegmental nucleus; Pv, posteroventral tegmental nucleus; RC, retrochiasmatic nucleus; Ri, nucleus reticularis inferior; RM, retromamillary nucleus; S, septum; SAT, strio-amygdaloid transition area; SC, suprachiasmatic nucleus; Sd, septum dorsalis; Sl, septum lateralis; Sm, septum medialis; SP, subpallium; SpA, subpallial amygdala; st, stria terminalis; Str, striatum; Th, thalamus; Tor, torus semicircularis; TPdm, posterior tubercle; dorsomedial portion; TnA, nucleus taeniae amygdalae; TPO, area temporo-parieto-occipitalis; v, ventricle; VAA, ventral anterior amygdala; VH, ventral hypothalamus; VL, ventrolateral thalamic nucleus; VM, ventromedial thalamic nucleus; vp, ventral pallidum; VP, ventral pallium; vStr, ventral striatum

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1. Introduction

The identification of the amygdala as an almond shaped mass of gray matter through the temporal pole of the human cerebral hemispheres was done by Burdach in the early 19th century. Subsequent technical advances allowed the microscopic examination of histological sections that led to the observation of an intricate amygdaloid network. In addition, developmental studies attempted to unravel the embryological origin of the different portions of the amygdala. As a consequence of all these studies it became clear that the amygdala is more complicated than previously thought, and its actual outer border and the number and classification of its subdivisions (“amygdaloid complex”) are still a matter of debate.

Many authors have regarded the amygdaloid complex as an extended continuum within the basal telencephalon that rostrally reaches the caudal tip of the shell portion of the nucleus accumbens (Alheid et al., 1995; Martínez-García et al., 2002a). However, on the basis of its heterogeneous origin, chemoarchitecture, and hodology, other authors have proposed that the amygdaloid complex represents a number of different, unrelated anatomical structures, with pallial and subpallial derivatives, belonging to four different functional systems: (1) the main olfactory, (2) the accessory olfactory (vomeronasal), (3) the autonomic, and (4) the frontotemporal cortical systems (Swanson and Petrovich, 1998; Puelles et al., 2000). Moreover, several studies about the characterization of the amygdaloid complex in diverse amniotes (reptiles, birds and mammals) demonstrated that the different divisions of the amygdala show a common basic histochemical and hodological organization that includes an intricate set of intra-amygdaloid connections (Bruce and Neary, 1995c; Lanuza et al., 1997, 1998; Martínez-García et al., 2002a; Moreno and González, 2003, 2004, 2005a) and a common embryological origin among vertebrates (Smith-Fernández et al., 1998; Puelles et al., 2000; Brox et al., 2003, 2004; Stenman et al., 2003; Medina et al., 2004, 2005; Moreno et al., 2004; Remedios et al., 2004; Tole et al., 2005). These

evidences strongly supported the notion that the amygdala is a highly conserved structure in the telencephalon of vertebrates.

As new data were gathered about the common organization of the amygdaloid complex in amniotes, the situation in anamniotes (fish and amphibians) remained to be clarified. Only with the achievement of new technical approaches in the study of development and connectivity of tiny regions in the brain of anamniotes, have emerging hypothesis on the conservative structure of the amygdala between anamniotes and amniotes been proposed. In particular, the study of the amygdala in amphibians seems of special interest to understand the evolution of these structures in tetrapods (Bruce and Neary, 1995c; Marín et al., 1998a,b,c; Brox et al., 2004; Moreno and González, 2003, 2004, 2005a; Moreno et al., 2004; Roth et al., 2004; Mühlenbrock-Lenter et al., 2005a,b).

In the following sections we will focus on the major advances made in the last few years that led to change the ideas about the organization of the amygdaloid complex. The comparison of data obtained in different classes of amniotes with new information about the organization of the amygdaloid complex in amphibians will serve to highlight the degree of conservation of this important telencephalic region in all tetrapods. Through this comparative approach we attempt to frame the main basic features of amygdaloid organization shared by all tetrapods.

2. The amygdaloid complex of amniotes

A major problem when studying the comparative anatomy of the amygdaloid complex has been the delineation of the boundaries of the amygdaloid nuclei in non-mammalian vertebrates. In fact, many studies have been accomplished in different amniotes dealing with the connectivity, chemoarchitecture or, recently, the origin of the distinct amygdaloid nuclei (Martínez-García et al., 1993, 2002a; Lanuza et al., 1997, 1998; Martínez-Marcos et al., 1999; Swanson and Petrovich, 1998; Puelles et al., 2000; Sah et al., 2003; Medina et al., 2004;

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