2.07 Do Birds and Reptiles Possess Homologues of Mammalian Visual, Somatosensory, and Motor Cortices?

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Glossary

amniote Group of vertebrates that develop an amniotic membrane around the embryo; includes reptiles, birds, and mammals.

arcopallium A caudal (or posterior) subdivision of the dorsal ventricular ridge in birds.

cortex A laminar brain structure consisting of cells arranged in layers parallel to the ventricular/pial surfaces and generally orthogonal (perpendicular) to radial glial fibers.

developmental regulatory gene A gene encoding a transcription factor (or a cofactor) or a signaling protein that is expressed during development in specific patterns, and is able to control expression of other genes and regulate patterning and morphogenesis of specific body parts.

DVR Dorsal ventricular ridge: a large region of the ventrolateral pallium of the telencephalon of birds and reptiles.

hippocampal formation Derivative of the medial pallium in different vertebrates. In mammals it includes the dentate gyrus, the hippocampus proper (Ammon's fields), and the subiculum. In birds it includes the hippocampus and the area parahippocampalis, whereas in reptiles it includes the medial and dorsomedial cortices.

homologous Having the same relative position (topological position), embryonic origin, and common ancestor; exhibiting biological homology.

homologue The same organ in different animals under every variety of form and function (Owen's definition, in 1843; see A History of Ideas in Evolutionary Neuroscience and Field Homologies on this concept).

homology A similarity attributed to common evolutionary origin (see 'homologous').

hyperpallium A dorsal region of the avian telencephalon that develops from the dorsal pallium. It typically forms a bulge on the dorsal surface of the telencephalon. It was often called Wulst.

M1 Primary motor area of the mammalian neocortex.

mesopallium A dorsal subdivision of the DVR in birds.

neocortex Derivative of the dorsal pallium in mammals, that typically shows a six-layered organization. It is also known as isocortex.

nidopallium A ventral subdivision of the DVR in birds.

pallial thickening A lateral expansion of the dorsal cortex of reptiles, showing a non-cortical organization. It is generally considered a lateral part of the dorsal cortex. However, only part of it may be a dorsal pallial derivative, and more comparative and developmental studies of this structure are needed before reaching any conclusion.

pallium A major dorsocaudal division of the telencephalon in all vertebrates, which in mammals gives rise to the cortical regions, claustrum, and part of the amygdala (including the cortical areas plus the basolateral complex). It is subdivided into four parts, called medial, dorsal, lateral, and ventral pallia.

piriform cortex Olfactory cortex of different vertebrates. It derives from the ventrolateral pallium. In reptiles, it is also known as lateral cortex.

S1 Primary somatosensory area of the mammalian neocortex.

sauropsid Group of vertebrates that includes reptiles and birds.

subpallium A major ventrorostral (or basal) division of the telencephalon in all vertebrates, that in mammals gives rise to most of the septum, the basal ganglia, part of the amygdala (including the intercalated and centromedial nuclei), and other cell groups of the basal telencephalon, such as the cholinergic corticopetal groups. It is subdivided into striatal, pallidal, and anterior entopeduncular parts.

telencephalon Bilateral evaginations of the rostral forebrain. It shows two major divisions in all vertebrates: pallium and subpallium.

tetrapod Group of vertebrates having two pairs of limbs, that includes amphibians, reptiles, birds, and mammals.

thalamus Forebrain structure that derives from the alar plate of the diencephalon (in particular, from prosomeres 2 to 3). It is subdivided into a ventral thalamus (also called prethalamus, which derives from prosomere 3), and a dorsal thalamus (or simply thalamus, which derives from prosomere 2). The dorsal thalamus contains cell groups that typically relay sensory information to the subpallium and pallium in vertebrates. In amniotic vertebrates, the dorsal thalamus contains specific cell groups that relay unimodal sensory and/or motor information to specific areas of the dorsal pallium.

topology Geometric configuration of any given structure (such as the brain) according to internal coordinates, which remain unaltered independent of deformations or differential growth of subdivisions that occur during development. According to this, the topological position of any subdivision within the structure, and its relation to neighbors, remains the same throughout ontogeny. Further, in organisms sharing the same configuration and basic organization plan (for example, vertebrates), the topological position of homologous subdivisions should be the same across species.

V1 Primary visual area of the mammalian neocortex.

Wulst German term previously employed to name the hyperpallium. It literally means bulge, making reference to the swollen or protuberant appearance of this subdivision of the avian telencephalon.

2.07.1 Introduction

One of the most challenging questions in brain evolution is to ascertain the origin of neocortex and to know whether a comparable cortical (pallial) region is present in extant birds and reptiles, which would

mean that a primordium of this structure was already present in stem amniotes. This question has been addressed by researchers since the end of the nineteenth century and continues to be discussed nowadays (for example, see article by Aboitiz *et al.*, 2003, and commentaries on it). However, many issues related to this question still remain uncertain and controversial. Nevertheless, the combination of developmental, paleontological, and adult anatomical plus functional data, analyzed using a cladistic approach, has proven to be very useful for evolutionary studies; this combined approch has helped to clarify some aspects of cortical evolution and has offered some light on what direction to follow in this research (for example, Northcutt and Kaas, 1995; Striedter, 1997, 2005; Medina and Reiner, 2000; Puelles, 2001; Butler and Molnár, 2002; Aboitiz *et al.*, 2003). Here I will review evidence based on this approach that suggests that: (1) the pallium of birds and reptiles contains a sector that is homologous as a field to the mammalian neocortex (i.e., they evolved from the same primordium present in stem amniotes); (2) this pallial sector contains a primary visual and a primary somatosensory area that might be homologous to V1 and S1, respectively, of mammalian neocortex; and (3) the frontal part of this pallial sector contains a somatomotor control area in birds (apparently overlapped with the somatosensory field) and mammals (M1), but these areas likely evolved independently and are, therefore, nonhomologous (see Evolution of the Nervous System in Reptiles, Visual Cortex of Turtles, The Origin of Neocortex: Lessons from Comparative Embryology, Reconstructing the Organization of Neocortex of the First Mammals and Subsequent Modifications, The Evolution of Motor Cortex and Motor Systems).

2.07.2 Finding the Homologue of Neocortex in the Pallium of Nonmammals

The neocortex is a six-layered structure located in the dorsolateral part of the telencephalon in mammals, above the ventricle, and it covers the central and basal region that is occupied by the basal ganglia and other basal telencephalic cell groups (Figure 1a). The neocortex is also located above the rhinal fissure, which separates it from the piriform cortex and olfactory tract. In contrast to the neocortex, the basal ganglia and other basal telencephalic cell groups show a nuclear (nonlaminar) organization. The difference between laminar versus nuclear organization together with the relative position of the cell masses with respect to the ventricle was once considered a criterion to identify cortical (pallial) and basal (subpallial) regions in the telencephalon of nonmammals, and based on it the telencephalon of birds and reptiles was thought to be made of a very large basal ganglia and a very tiny cortical region (reviewed in Medina and Reiner, 1995; Striedter, 1997; Reiner *et al.*, 1998; Jarvis *et al.*, 2005). This is now known to be wrong, and there is a large amount of evidence showing that the telencephalon of birds and reptiles contains a large pallial region, a major part of which shows a nuclear organization and is located below the lateral ventricle (Figures 1b–1d) (Karten and Hodos, 1970; Reiner, 1991, 1993; Butler, 1994b; Striedter, 1997, 2005; Smith-Fernández *et al.*, 1998; Medina and Reiner, 2000; Puelles *et al.*, 2000; Jarvis *et al.*, 2005). The evidence showing this includes developmental and adult anatomical and functional data, and it has mainly been obtained after the development of modern techniques that allowed detection of gene products (such as enzymes, proteins and, more recently, mRNAs), tracing of axonal pathways, fate mapping, and functional studies of the brain.

The cortical region of mammals is subdivided into medial, dorsal, and lateroventral units during development and in the adult (Figures 1a and 2c), and the neocortex derives from the dorsal subdivision (Holmgren, 1925; Striedter, 1997). The cortical region (pallium) of birds and reptiles is also subdivided into medial, dorsal, and lateroventral units (Figure 1) (Reiner, 1991, 1993; Butler, 1994b; Striedter, 1997; Puelles *et al.*, 2000). The problem comes when trying to compare one-to-one these subdivisions of the avian/reptilian pallium with those of mammals. Some authors employing only adult anatomical and functional data (including connectivity patterns) believe that the dorsal subdivision of the avian/reptilian pallium is homologous to the dorsomedial part of the neocortex, whereas a large part of the lateroventral pallium of birds/reptiles (called dorsal ventricular ridge or DVR; in particular, its ventral part in birds) is homologous to the dorsolateral part of the neocortex or to specific cell groups of it (Karten, 1969, 1997; Reiner, 1993; Butler, 1994b). However, homologous structures must originate from the same embryonic primordium (Striedter, 1997; Puelles and Medina, 2002; see Field Homologies). In this sense, developmental studies indicate that only the dorsal subdivision of the avian/reptilian pallium can be compared to the neocortex, but not the DVR (in particular, its ventral part, which includes the nidopallium in birds) (Striedter, 1997; Puelles *et al.*, 2000). Rather, both developmental and some adult connectivity data suggest that the avian/reptilian DVR is homologous to the claustrum and pallial

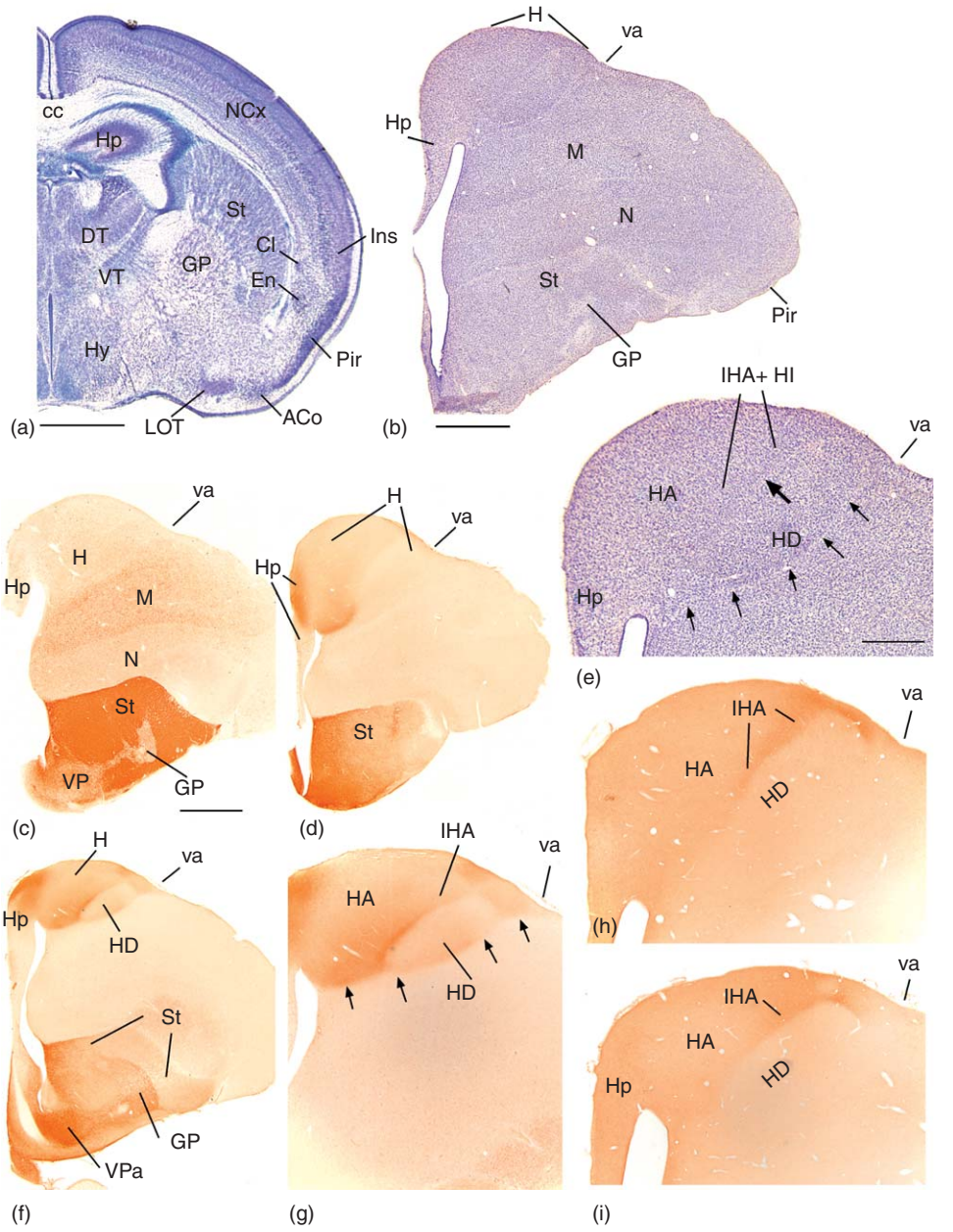

Figure 1 Photomicrographs of frontal sections through the telencephalon of a postnatal mouse (a) or adult pigeon (b–i), showing the general cytoarchitecture, as observed in Nissl staining (a), (b), (e), and some subdivisions based on immunostaining for tyrosine hydroxylase (c), substance P (d), (f), (g), of choline acetyltransferase (h), (i). Note the typical lamination in the cerebral cortex of mouse (a), that differs from the nuclear-like organization in the basal ganglia (striatum and pallium). In pigeon (b), as in other birds and reptiles, most of the telencephalon is not laminated. Nevertheless, neurochemical data help to locate the main intratelencephalic boundary in birds and reptiles, separating subpallium and pallium. The subpallium is relatively rich in tyrosine hydroxylase (c) and substance P (d), (f), and includes the basal ganglia (striatum and pallidum). The avian pallium includes four major subdivisions, including the hippocampal formation (medially), the hyperpallium (dorsally), the mesopallium (laterodorsally), and the nidopallium (lateroventrally). At caudal levels, the avian lateroventral pallium includes the arcopallium and part of the amygdala. The avian hyperpallium appears to be the only derivative of the dorsal pallium and is therefore comparable (homologous as a field) to the mammalian neocortex (see Figure 2). The avian hyperpallium (H) has four mediolateral subdivisions, called apical (HA), interstitial nucleus of apical (IHA), intercalated (HI), and densocellular (HD) hyperpallium (e–i). These subdivisions are not comparable to neocortical layers, although they show some functional features that resemble them. The lateral extension of the hyperpallium coincides with a cell-free lamina called superior frontal lamina (arrows in (e) and (g)), and generally relates to a superficial groove called vallecula (va), although this is not true at rostral levels. See text for more details. ACo, anterior cortical amygdalar area; cc, corpus callosum; Cl, claustrum; DT, dorsal thalamus; En, endopiriform nucleus; GP, globus pallidus; H, hyperpallium; HA, apical hyperpallium; HD, densocellular hyperpallium; HI, intercalated hyperpallium; Hp, hippocampal formation; Hy, hypothalamus; IHA, interstitial nucleus of the apical hyperpallium; Ins, insular cortex; LOT, nucleus of the lateral olfactory tract; M, mesopallium; N, nidopallium; NCx, neocortex; Pir, piriform cortex; St, striatum; va, vallecula; VPa, ventral pallidum; VT, ventral thalamus. Scale bars: 1 cm (a, b); 0.5 cm (c, d, f; scale in c); 1 cm (e, h, i; scale in e).

amygdala (Bruce and Neary, 1995a, 1995b, 1995c; Striedter, 1997; Guirado *et al.*, 2000; Puelles *et al.*, 2000; Puelles, 2001; Dávila *et al.*, 2002; Martínez-García *et al.*, 2002). Below I review the evidence that supports that the dorsal part of the avian/reptilian cortical region is homologous as a field to the mammalian neocortex, and that both evolved from a similar pallial subdivision present in the telencephalon of stem amniotes.

2.07.2.1 Developmental Evidence: Histogenetic Origin and Transcription Factors

During development, the telencephalon of vertebrates becomes parcellated into radial histogenetic divisions and subdivisions that are comparable across species (Striedter, 1997; Puelles and Medina, 2002). Each division/subdivision shows a unique molecular profile and produces specific cell groups, most of which stay within the radial domain, except for some selective cell populations that undergo tangential migration across boundaries (Striedter and Beydler, 1997; Striedter *et al.*, 1998; Puelles *et al.*, 2000; Cobos *et al.*, 2001; Marín and Rubenstein, 2001, 2002; Puelles and Medina, 2002). This conclusion is strongly supported by data on developmental regulatory genes (encoding transcription factors or signaling proteins that regulate the expression of other genes), which are expressed in specific and generally comparable spatiotemporal patterns in the telencephalon of different vertebrates during development (Smith-Fernández *et al.*, 1998; Puelles *et al.*, 2000; Brox *et al.*, 2003, 2004; Medina *et al.*, 2005), and play key roles in the regional specification and formation of telencephalic divisions and subdivisions (Marín and Rubenstein, 2002).

2.07.2.1.1 Pallial subdivisions in mammals and neocortical origin Classical and modern developmental studies, including data on developmental regulatory genes, indicate that the mammalian neocortex derives from the pallium, one of the major divisions of the telencephalon (Figure 2c) (Holmgren, 1925; Källén, 1951b; Puelles *et al.*, 2000). During development, the pallium shows specific expression of numerous transcription factor-expressing genes, including *Pax6*, *Emx1/2*, *Tbr1/2,* and several *LIM-homeobox* (*Lhx*) genes (Simeone *et al.*, 1992; Stoykova and Gruss, 1994; Bulfone *et al.*, 1995, 1999; Rétaux *et al.*, 1999; Puelles *et al.*, 2000; Bulchand *et al.*, 2001, 2003; Medina *et al.*, 2004), which play key roles in pallial specification and parcellation, cell proliferation, and/or cell differentiation (Stoykova *et al.*, 1996, 2000; Zhao *et al.*, 1999; Bulchand *et al.*, 2001; Hevner *et al.*, 2001, 2002; Yun *et al.*, 2001; Bishop *et al.*, 2002, 2003; Muzio *et al.*, 2002; Campbell, 2003). For example, *Pax6, Emx1,* and *Emx2* are involved in pallial specification and parcellation (Bishop *et al.*, 2002, 2003; Muzio *et al.*, 2002). *Emx1* and *Emx2* are also involved in pallial growth (cell proliferation) (Bishop *et al.*, 2003). On the other hand, *Tbr1* appears to be involved in the differentiation of glutamatergic neurons, which are typical in the pallium (Hevner *et al.*, 2001).

What part of the pallium gives rise to the neocortex? Classical developmental studies and studies on the expression and function of developmental regulatory genes indicate that the pallium of mammals contains three main radial subdivisions (Figure 2c): (1) a medial pallium, giving rise to the hippocampal formation; (2) a dorsal pallium, giving rise to the neocortex; and (3) a lateroventral pallium, giving rise to the piriform cortex, claustrum, and pallial amygdala (the lateroventral pallium is sometimes referred to as the piriform lobe, and has the olfactory tract at the surface) (Holmgren, 1925; Striedter, 1997; Puelles *et al.*, 2000; Puelles, 2001). The lateroventral pallium is also subdivided into dorsal and ventral parts (called lateral and ventral pallia, respectively, by Puelles *et al.*, 2000), which show distinct expression of the several developmental regulatory genes, including *Emx1* and *Dbx1*, and give rise to different parts of the claustrum and pallial amygdala (Figure 2c) (Puelles *et al.*, 2000; Yun *et al.*, 2001; Medina *et al.*, 2004). During early development, the lateral pallium expresses strongly *Emx1* but not *Dbx1*, whereas the ventral pallium expresses *Dbx1* in the ventricular zone but only shows *Emx1* expression in the subpial surface (Puelles *et al.*, 2000; Yun *et al.*, 2001; Medina *et al.*, 2004). However, a recent fate-mapping study indicates the existence of numerous *Emx1*-expressing cells in both lateral pallial and ventral pallial parts of the amygdala around and after birth (Gorski *et al.*, 2002), suggesting that there may be a high degree of cellular mixing between these subdivisions (Figure 2c).

The pallial subdivisions are apparently formed by the early action of: (1) signaling proteins (such as Wnt proteins) that diffuse from organizer centers such as the cortical hem (Figure 2c), which, by way of receptors, apparently control the expression of downstream genes (including genes encoding transcription factors) in adjacent pallial areas in a concentration-dependent way (Ragsdale and Grove, 2001); (2) transcription factors that are expressed in opposing gradients in the pallium during early development, involved in regional specification, parcellation, cell proliferation, and/or cell differentiation of the pallium (for example, *Pax6, Emx2, Lhx2*; Donoghue and Rakic, 1999;

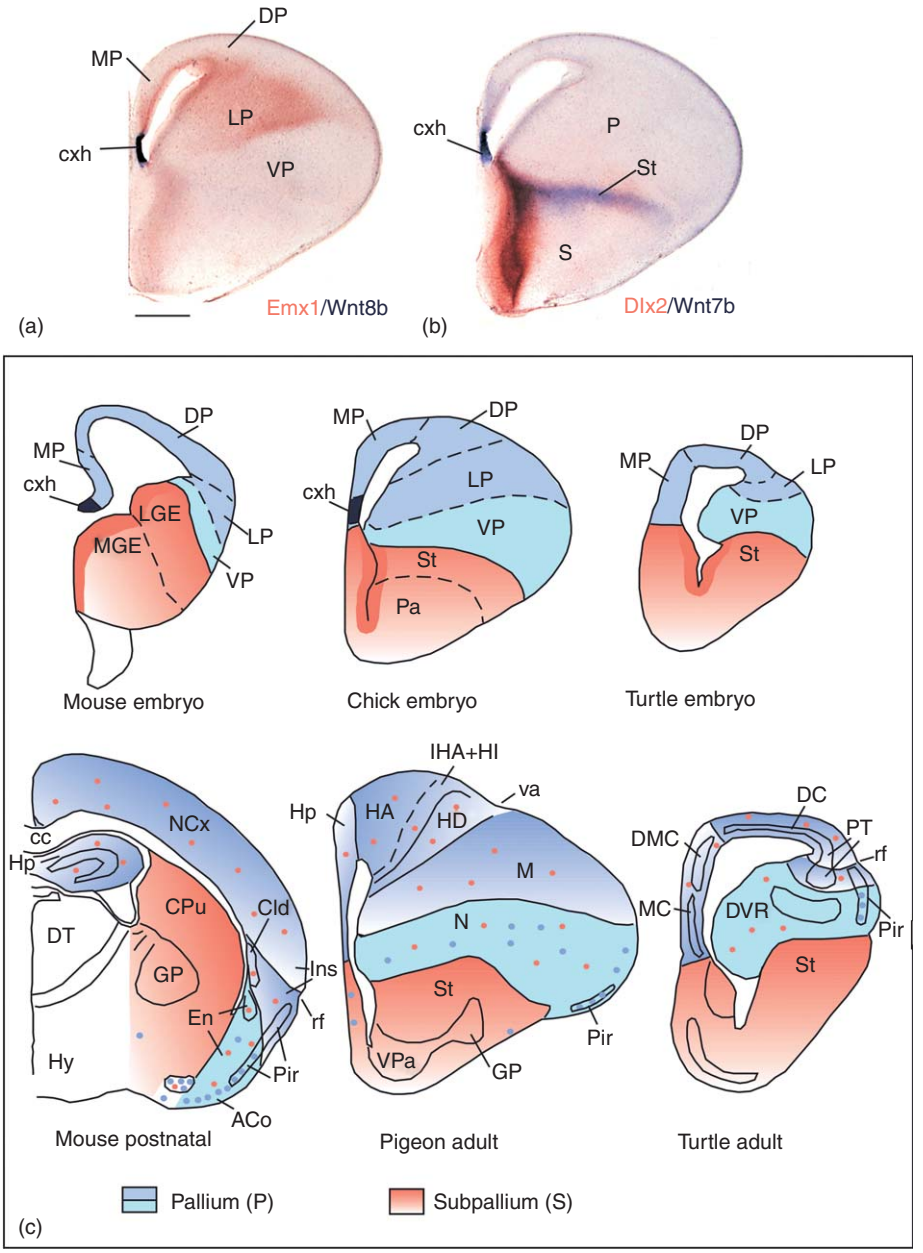

Figure 2 a and b, Photomicrographs of frontal sections through the telencephalon of chick embryos (10 days of incubation), showing expression of the chick genes *Emx1* (red in a), *Wnt8b* (blue in a), *Dlx2* (red in b), or *Wnt7b* (blue in b). The genes *Dlx2* and *Wnt7b* are expressed in the subpallium, either in the ventricular/subventricular zone of the whole subpallium (*Dlx2*) or the ventricular zone and mantle of the striatum (*Wnt7b*). Expression of *Emx1* helps to distinguish a ventral pallial (VP) subdivision, poor in *Emx1* expression and poor in subpallial marker genes. Note the expression of *Wnt* genes in the avian cortical hem, a putative secondary organizer comparable to the cortical hem of mammals. c, Schematics of the telencephalon of a mammal (mouse), a bird (chick or pigeon), and a reptile (turtle), as seen in frontal sections during development or in the adult. The pallial and the major subpallial subdivisions are represented in the different species, based on known expression patterns of developmental regulatory genes observed during development. Four major pallial subdivisions appear to exist in all groups, although the lateral and ventral subdivisions appear to have a large degree of cellular mixing in the adult (which occurs at the level of the ventral pallium). The dorsal pallium gives rise to the neocortex (NCx) in mammals, to the hyperpallium (H) in birds, and to the dorsal cortex (DC) in reptiles. The pallial thickening (PT) is often considered a lateral part of the dorsal cortex. However, available data suggest that only part of it may be a dorsal pallial derivative, and more studies are needed to know where the exact boundary between the dorsal and lateral pallium is, in reptiles. ACo, anterior cortical amygdalar area; cc, corpus callosum; Cld, dorsolateral claustrum; CPu, caudoputamen (dorsal striatum); cxh, cortical hem; DC, reptilian dorsal cortex; DMC, reptilian dorsomedial cortex; DP, dorsal pallium; DT, dorsal thalamus; DVR, dorsal ventricular ridge; En, endopiriform nucleus; GP, globus pallidus; H, hyperpallium; HA, apical hyperpallium; HD, densocellular hyperpallium; HI, intercalated hyperpallium; Hp, hippocampal formation; Hy, hypothalamus; IHA, interstitial nucleus of the apical hyperpallium; Ins, insular cortex; LGE, lateral ganglionic eminence; LP, lateral pallium; M, mesopallium; MC, reptilian medial cortex; MGE, medial ganglionic eminence; MP, medial pallium; N, nidopallium; NCx, neocortex; P, pallium; Pa, pallidum; Pir, piriform cortex; PT, pallial thickening; rf, rhinal fissure; S, subpallium; St, striatum; va, vallecula; VP, ventral pallium; VPa, ventral pallidum. Scale bar: 400μm.

Bulchand *et al.*, 2001; Bishop *et al.*, 2002); (3) cofactors (activators or repressors) and other regulatory proteins that regulate directly or indirectly the expression of specific transcription factors, that show sharp expression boundaries between subdivisions (for example, the LIM-only protein Lmo3, with a sharp expression boundary between dorsal and lateroventral pallial subdivisions; Bulchand *et al.*, 2003; Vyas *et al.*, 2003). The main pallial subdivisions are differentially affected by mutations targeting some of the above-mentioned developmental regulatory genes, supporting that they represent distinct histogenetic compartments. For example, a mutation in the LIM-homeobox gene *Lhx2* produces a severe malformation of the hippocampal formation and neocortex, but the piriform lobe appears unaffected (Bulchand *et al.*, 2001; Vyas *et al.*, 2003).

2.07.2.1.2 Pallial subdivisions in nonmammals: the dorsal pallium in birds and reptiles Since developmental regulatory genes generally show highly conserved sequences and expression patterns, they have become very useful tools for identifying comparable brain regions in different vertebrate species and for studies of brain evolution (Puelles *et al.*, 2000; Medina *et al.*, 2005). Classical and modern developmental studies, including radial glial analysis, fate-mapping studies, and expression of developmental regulatory genes, indicate that the telencephalic pallium in reptiles and birds contains three main radial divisions (Figure 2c): (1) a medial pallium, which gives rise to the medial/dorsomedial cortices in reptiles and to the hippocampal formation (hippocampus and parahippocampal area) in birds; (2) a dorsal pallium, which gives rise to the dorsal cortex in reptiles and the hyperpallium or Wulst in birds; and (3) a lateroventral pallium, which gives rise to the lateral or piriform cortex, to a large nuclear structure called the DVR and to some pallial amygdalar nuclei in reptiles and birds (Holmgren, 1925; Källén, 1951a, 1953, 1962; Striedter, 1997; Striedter and Beydler, 1997; Striedter *et al.*, 1998; Puelles *et al.*, 2000; Cobos *et al.*, 2001; Martínez-García *et al.*, 2002). As in mammals, the pallium of reptiles and birds shows specific expression of *Pax6*, *Tbr1/2,* and *Emx1* during development (Smith-Fernández *et al.*, 1998; Bulfone *et al.*, 1999; Puelles *et al.*, 2000; Garda *et al.*, 2002). Similarly to mammals, in birds there is an organizer center at the medial edge of the pallium expressing *Wnt*-family genes (the avian cortical hem; Figures 2a–2c), which may control the formation of the medial pallial subdivision (Garda *et al.*, 2002). This indicates that the specification and parcellation of the avian/reptilian pallium are controlled by many of the same regulatory genes and mechanisms that control pallial development in mammals.

Further, as in mammals, the lateroventral pallium of birds and reptiles is subdivided into a lateral pallium, showing broad and strong expression of *Emx1*, and a ventral pallium, which expresses *Emx1* only in a thin band of the subpial mantle (Figures 2a–2c) (Smith-Fernández *et al.*, 1998; Puelles *et al.*, 2000). These two pallial subdivisions of birds also differ by their distinct expression of *Dachsund* and several *Cadherin* genes during development (Redies *et al.*, 2001; Szele *et al.*, 2002). However, as in mammals, the derivatives of the lateral and ventral pallial subdivisions of birds apparently display a high degree of cellular mixing (Figure 2c), based on radial glial fiber disposition and fate-mapping analysis in chick embryos (Striedter and Beydler, 1997; Striedter *et al.*, 1998; Striedter and Keefer, 2000). The lateral pallium includes the so-called mesopallium and posterior amygdalar nucleus of birds, whereas in reptiles it appears to include a small dorsolateral part of the DVR plus the dorsolateral amygdalar nucleus (Smith-Fernández *et al.*, 1998; Guirado *et al.*, 2000; Puelles *et al.*, 2000; Martínez-García *et al.*, 2002). The ventral pallium includes the so-called nidopallium and arcopallium of birds, whereas in reptiles it appears to include most of the DVR plus the lateral and other amygdalar nuclei (Smith-Fernández *et al.*, 1998; Guirado *et al.*, 2000; Puelles *et al.*, 2000; Martínez-García *et al.*, 2002). The olfactory tract is located at the surface of the ventral pallium (or ventral DVR) in mammals, birds, and reptiles (Striedter, 1997; Guirado *et al.*, 2000; Puelles *et al.*, 2000; Puelles, 2001). Both the relative (topological) position and molecular profile of the pallial subdivisions (including expression of *Pax6, Tbr1,* and *Emx1*) suggest that the dorsal pallial subdivision of reptiles and birds, from which derive the reptilian dorsal cortex and avian hyperpallium, is comparable and possibly homologous as a field to the dorsal pallium of mammals, which gives rise to the neocortex (Striedter, 1997; Puelles *et al.*, 2000). As in mammals, in reptiles the rhinal fissure separates the dorsal cortex from the piriform cortex and olfactory tract (Figure 2c). These data also indicate that the ventral pallial part of the reptilian/avian DVR (which has the olfactory tract and piriform cortex at the surface, and is poor in *Emx1* expression) is not comparable and cannot be homologized to the neocortex, since they derive from different embryonic primordia (Striedter, 1997; Striedter and Beydler, 1997; Smith-Fernández *et al.*, 1998; Striedter *et al.*, 1998; Puelles *et al.*, 2000).

However, one important issue that developmental studies have not yet resolved is where to locate the exact boundary between the dorsal and lateral pallial subdivisions, since both subdivisions express many of the same developmental regulatory genes (for example, *Emx1*) and the morphological landmarks are not clear in birds and many reptiles. In other words, what is the exact lateral extension of the dorsal pallium in birds and reptiles? In mammals, some developmental regulatory genes are expressed differently in the lateral and dorsal pallium (for example, the LIM-only genes *Lmo2* and *Lmo3*), but, unfortunately, data on the orthologue genes are lacking in nonmammalian vertebrates (Medina *et al.*, 2005). I will return to this issue below.

2.07.2.2 Adult Anatomical Evidence: Morphological Landmarks, Molecular Markers, and Connections

2.07.2.2.1 Morphological landmarks and molecular markers: problematic delimitation of the dorsal pallium in birds and reptiles As noted above, the dorsal cortex of reptiles and the hyperpallium of birds appear to derive from the same pallial embryonic subdivision as the neocortex. In adult animals, these structures show cellular and molecular features typical of pallium. For example, they contain a majority of excitatory (glutamatergic) neurons (the principal or projection neurons) and only a relatively small subpopulation of inhibitory (GABAergic) interneurons (Ottersen and Storm-Mathisen, 1984; Reiner, 1993; Veenman and Reiner, 1994, 1996; Swanson and Petrovich, 1998; Fowler *et al.*, 1999; Medina and Reiner, 2000; Broman *et al.*, 2004). In mammals, birds, and reptiles, the principal pallial neurons have excitatory projections to the striatum and brainstem (Ottersen and Storm-Mathisen, 1984; Veenman and Reiner, 1996; Kenigfest *et al.*, 1998; Fowler *et al.*, 1999; Broman *et al.*, 2004). Some of the strongest evidence showing that the principal pallial neurons are glutamatergic has been provided recently by the localization of vesicular glutamate transporters VGLUT1 and VGLUT2, although data on these transporters exist only in mammals (Fujiyama *et al.*, 2001; Herzog *et al.*, 2001; Broman *et al.*, 2004; Fremeau *et al.*, 2004), but are lacking in birds and reptiles. The GABAergic interneurons of the mammalian neocortex and avian hyperpallium, as those of the rest of the mammalian and avian pallium, originate in the subpallium and migrate tangentially to the pallium during development (Figure 2c) (Anderson *et al.*, 1997, 2001; Pleasure *et al.*, 2000; Cobos *et al.*, 2001; Marín and Rubenstein, 2001; Nery *et al.*, 2002; Legaz *et al.*, 2005). This situation appears to be typical in all tetrapods, since it is also described in amphibians (Brox *et al.*, 2003).

In addition to these and other molecular and cellular features typical of the whole pallium, there are no comparative data on molecular markers that clearly distinguish the neocortex/dorsal pallium from other pallial subdivisions in adult animals. In mammals, the neocortex can be distinguished from the adjacent pallial subdivisions because of its typical six-layered structure and the presence of the rhinal fissure on its lateral egde. However, in birds and reptiles there are no clear morphological landmarks for distinguishing the lateral boundary of the dorsal pallium. The absence of dorsal pallial molecular markers has become an additional obstacule for delimiting the lateral extension of the dorsal pallium in adult birds and reptiles. As noted above, more comparative studies on the expression of developmental regulatory genes are also needed to resolve this issue. In reptiles, the dorsal cortex appears to include a rostrolateral extension called pallial thickening (reviewed in Reiner, 1993; Medina and Reiner, 2000). However, the identification of the pallial thickening varies between authors and reptilian species, and it appears that a ventral part of it is located deep to the piriform cortex and, thus, may be part of the lateral pallium (Figure 2c). Analysis of radial glial fiber disposition in that part of the reptilian pallium (Monzón-Mayor *et al.*, 1990) suggests that only the dorsal-most part of the pallial thickening may belong to the dorsal pallium (Figure 2c). This dorsal part of the pallial thickening appears located above the rhinal fissure (visible in only some reptiles), which is consistent with its dorsal pallial nature. As in reptiles, so also in birds, there is some confusion on where to locate the lateral boundary of the hyperpallium or Wulst. According to numerous studies, the hyperpallium includes the so-called apical, interstitial nucleus of apical, intercalated, and densocellular hyperpallium (HA, IHA, HI, and HD, respectively), and its lateral (or lateroventral) boundary coincides with both the superior frontal lamina and a superficial groove called vallecula (Figures 1b–1i and 2c) (Karten *et al.*, 1973; Shimizu and Karten, 1990; reviewed in Medina and Reiner, 2000). However, although this is generally true, the HD exceeds laterally the vallecula at rostral levels (Shimizu and Karten, 1990), and the superior frontal lamina appears to bend laterally when approaching the vallecula (Suárez *et al.*, 2006; see Figures 1e, 1g, and 2c). Further, the HD is sometimes misidentified and either confused

with the dorsal part of the mesopallium (a part of the DVR that belongs to the lateral pallium) or vice versa. This is partly due to the fact that the HD (or part of it) shares with the mesopallium expression of some molecular markers, such as some glutamate receptor subunits (Wada *et al.*, 2004). This has raised the question of whether the HD should or should not be considered part of the hyperpallium. However, the HD also differs from the mesopallium in many other molecular features, such as expression of calcium-binding proteins (Suárez *et al.*, 2006), expression of delta and mu opiate receptors (Reiner *et al.*, 1989), and expression of GluR1 glutamate receptor subunit, neurotensin receptors, or the neuropeptide substance P (Reiner *et al.*, 2004) (Figures 1f and 1g). Further, recent evidence indicates the existence of an additional pallial division (the laminar pallial nucleus) clearly located at the boundary between HD and mesopallium, showing distinct expression of calcium-binding proteins throughout development and in adult chicks (Suárez *et al.*, 2006). Thus, the questions raised on the identity and nature of HD may be partially due to the use of different species. Whereas all four subdivisions of the hyperpallium are clearly distinguished in birds with a large hyperpallium (such as the owl), it appears that the more lateral hyperpallial subdivisions, HI or HD, are difficult to distinguish in either pigeons/chicks or songbirds, respectively.

2.07.2.2.2 Connections One of the most typical features of the mammalian neocortex is that it contains unimodal sensory and motor areas that receive their input directly from specific nuclei of the dorsal thalamus (Northcutt and Kaas, 1995) (Figure 3). These primary functional areas of mammals show a detailed point-to-point representation of the body and/or world (Krubitzer, 1995). The presence of these primary, unimodal sensory and motor areas makes the neocortex unique and different from adjacent pallial divisions (such as the hippocampal formation, which typically receives multimodal thalamic input, and the piriform cortex, which typically receives olfactory input from the bulb), and this has been used for identifying the dorsal pallium or specific dorsal pallial functional areas in other vertebrates. Nevertheless, the use of connections (or any other single data) alone for identification of homologies is highly risky since they may have changed during the course of evolution (Striedter, 2005). For this reason, when searching for homologies and for evolutionary interpretations, data on connections need to be used in combination with other data, including embryological origin and/or topological position.

The neocortex contains: (1) a primary visual area (V1), receiving input from the retinorecipient dorsal lateral geniculate nucleus; (2) a primary somatosensory area (S1), receiving input from specific nuclei of the ventrobasal (or ventral posterior) thalamic complex (including the ventral posterolateral (VPL) and ventral posteromedial (VPM) nuclei in rodents), which in turn receive somatosensory information from the head and body via the trigeminal sensory and dorsal column nuclei; and (3) a primary motor area (M1), receiving input from specific nuclei of the ventrobasal thalamic complex (including the ventral anterior (VA) and ventral lateral (VL) nuclei in rodents) that receive motor information from the basal ganglia and deep cerebellar nuclei (Figure 3) (Krubitzer, 1995; Groenewegen and Witter, 2004; Sefton *et al.*, 2004; Tracey, 2004; Guy *et al.*, 2005). These primary functional areas are present in most groups of mammals and have a similar relative position within the neocortex, with M1 and S1 being always rostral to V1 (Krubitzer, 1995; Medina and Reiner, 2000; Kaas, 2004). This suggests that these areas (at least V1 and S1, as well as some other sensory areas) were likely present in the origin of the mammalian radiation (Krubitzer, 1995; Slutsky *et al.*, 2000). Further, it appears that the neocortex of early mammals had multiple somatosensory representations of the body, each one corresponding to a distinct area (Krubitzer *et al.*, 1995, 1997; Catania *et al.*, 2000a, 2000b; Kaas, 2004). However, current available data suggest that early mammals did not possess a separate motor cortical area (M1), and this possibly appeared with the origin of placental mammals (Kaas, 2004). In mammals with a small neocortex, the visual and somatomotor areas show a close spatial contiguity (for example, in monotremes or in the hedgehog). In mammals with a large neocortex, such as rodents, carnivores, and primates, V1 becomes secondarily displaced to the most caudal part of the neocortex (occipital lobe) by the development of novel cortical areas involved in higher-order or multimodal information processing. In these mammals, S1 is located in the parietal lobe (in the postcentral gyrus of the primate parietal lobe), whereas M1 is located in the frontal lobe (in the precentral gyrus of the primate frontal lobe). In rodents and primates, the initial parcellation of these functional areas during development is related (among other things) to their expression of specific ephrin ligands and receptors, some of which can be used as early markers of S1 (ephrinA5) or V1 (Ephrin receptor EphA6) (Donoghue and Rakic, 1999; Yun *et al.*, 2003).

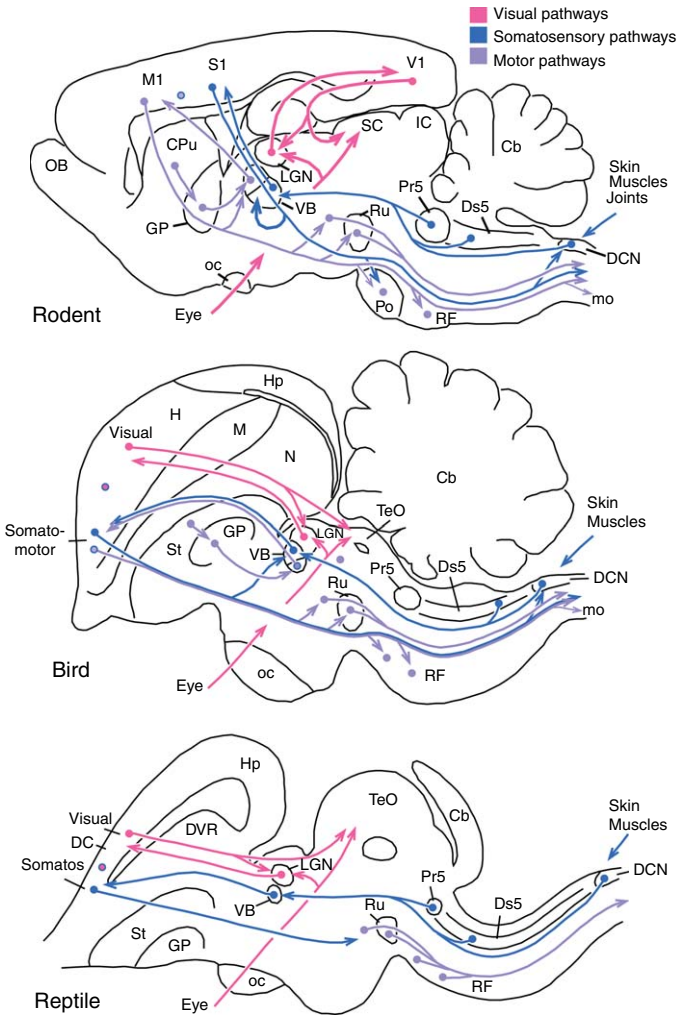

Figure 3 Schematics of lateral views of the brain of a rodent, a bird, and a reptile, showing the major connectivity patterns of the visual, somatosensory, and motor pathways. In mammals, birds, and reptiles, partially comparable visual and somatosensory pathways to the dorsal pallium are present. Visual information reaches a dorsal pallial primary visual area (V1 in mammals) by way of the lateral geniculate nucleus (LGN), located in the lemnothalamus. In turn, the visual cortical (dorsal pallial) area projects back to this thalamic nucleus and to the optic tectum. Somatosensory information reaches a dorsal pallial primary somatosensory area (S1 in mammals) by way of the ventrobasal complex of the lemnothalamus (VB). In birds, the body is mainly represented in the dorsal pallium, whereas in mammals and at least some reptiles, there is representation of both body and head. In birds and mammals, the ventrobasal complex has a motor subdivision that receives basal ganglia and cerebellar input, and projects to the dorsal pallium. In birds, this motor input ends in the somatosensory field (thus becoming a true somatomotor area). In placental mammals, such as rodents, the motor input ends mostly in a separate primary motor area (M1), although a small somatosensory–motor overlap occurs at the interface between M1 and S1. See text for details. In mammals, both S1 and M1 project back to the ventrobasal thalamic complex and to the brainstem and spinal cord by way of the pyramidal tract. S1 projections primarily end on precerebellar centers (such as the pontine nuclei) and somatosensory-relay centers (such as the dorsal column nuclei and the dorsal horn of the spinal cord). M1 projections primarily reach premotor precerebellar and reticulospinal centers (such as prerubral and rubral neurons), and also provide some input to motoneuron pools, such as those of the ventral horn of the spinal cord. In birds, the somatomotor dorsal pallial area shows descending projections resembling both S1 and M1 (especially in some avian species). In reptiles, the putative ventrobasal complex does not include any motor subdivision. The somatosensory area of the reptilian dorsal pallium only shows projections to diencephalic and midbrain tegmentum, reaching premotor precerebellar and reticulospinal cell groups, and suggesting that it may control or modulate motor behavior. However, this area lacks most of the connections typical of a true somatomotor area, suggesting that this likely evolved independently in birds and mammals. Cb, cerebellum; CPU, caudoputamen (dorsal striatum); DC, reptilian dorsal cortex; DCN, dorsal column nuclei; Ds5, descending sensory trigeminal nucleus; DVR, dorsal ventricular ridge; GLN, dorsal lateral geniculate nucleus; GP, globus pallidus; H, hyperpallium; Hp, hippocampal formation; IC, inferior colliculus; M, mesopallium; M1, primary motor area of neocortex; mo, motoneuron pools; N, nidopallium; OB, olfactory bulb; oc, optic chiasm; Po, pontine nuclei; Pr5, principal sensory trigeminal nucleus; RF, reticular formation; Ru, nucleus ruber; S1, primary somatosensory area of neocortex; SC, superior colliculus; St, striatum; TeO, optic tectum; V1, primary visual area of neocortex; VB, ventrobasal thalamic complex.

Are these areas present in the dorsal pallium of reptiles and/or birds? Data on ephrin ligands and receptors in the dorsal pallium of birds and reptiles are lacking but, in any case, the search for functional areas in the dorsal pallium of birds and reptiles requires the analysis of the thalamopallial projections in these vertebrate groups and/or electrophysiological recordings in the pallium.

Of interest, the adult hyperpallium of birds and dorsal cortex of reptiles show some patterns of connections with the dorsal thalamus similar to those of the neocortex (Figure 3). In particular, the patterns of connections suggest the existence of a primary visual area and a primary somatosensory area in the reptilian dorsal cortex and avian hyperpallium that are comparable and might be homologous to the primary visual (V1) and primary somatosensory (S1) areas of the mammalian neocortex (reviewed in Medina and Reiner, 2000; see also Wild and Williams, 2000). The somatosensory area found in the avian hyperpallium shows some connections, suggesting that it may represent a true somatomotor area, able to play a role in modulation of somatosensory input as well as in motor control, resembling aspects of mammalian S1+M1 (perhaps like the somatomotor area present in the origin of mammals). However, available data suggest that the motor control features of this avian hyperpallial area evolved independently from those found in M1.

The conclusion of homology of the visual and somatosensory cortical areas is partially based on assumption of homology of the thalamic nuclei of reptiles, birds, and mammals relaying the visual or somatosensory information to the dorsal pallium. But, for this to be true, these nuclei not only need to share similar connections, but also need to originate from the same embryonic primordium (or be located in the same histogenetic field). This will be analyzed in the following section.

2.07.3 Thalamopallial Projections and Sensory and Motor Areas in the Dorsal Pallium of Mammals, Birds, and Reptiles

2.07.3.1 Divisions of the Thalamus: Specific Relation of the Lemnothalamus with the Dorsal Pallium

To know whether the thalamic nuclei projecting to V1, S1, or M1 of mammalian neocortex are located in the same histogenetic unit as the avian and reptilian thalamic nuclei projecting to the hyperpallium/dorsal cortex, it is important to analyze the development and adult organization of the thalamus. In this sense, Butler (1994a) proposed the existence of two dorsal thalamic divisions, the lemnothalamus and the collothalamus, which receive sensory input through different systems and have different connections with the pallium (see The Dual Elaboration Hypothesis of the Evolution of the Dorsal Thalamus). The lemnothalamus includes nuclei receiving sensory input primarily from lemniscal systems and projecting to the medial and/or dorsal pallium (Butler, 1994a, 1994b). The collothalamus includes nuclei receiving a major collicular input and projecting to the lateroventral pallium (Butler, 1994a, 1994b). A similar but more complex subdivision of the thalamus was later proposed by other authors based on differential expression of cadherins or calcium-binding proteins by thalamic subdivisions during development or in the adult (Dávila *et al.*, 2000; Redies *et al.*, 2000). According to these authors, the dorsal thalamus is subdivided into three main histogenetic divisions, called dorsal, intermediate, and ventral tiers, each one showing a specific immunostaining profile and connections with a particular pallial subdivision (Dávila *et al.*, 2000; Redies *et al.*, 2000; Puelles, 2001). The dorsal tier corresponds roughly to the lemnothalamus, whereas the intermediate and ventral tiers roughly correspond to the collothalamus of Ann Butler (Butler, 1994a, 1994b; Dávila *et al.*, 2000; Redies *et al.*, 2000). Thus, the thalamic nuclei projecting to V1, S1, and M1 in mammals are all located in the dorsal tier or lemnothalamus (Puelles, 2001; Butler, 1994a). What about the visual and somatosensory/somatomotor thalamic nuclei projecting to the avian hyperpallium and reptilian dorsal cortex?

2.07.3.2 A Primary Visual Area in the Dorsal Pallium of Birds and Reptiles and Its Comparison to V1 of Mammals

In mammals, V1 (area 17) receives unimodal visual input from the dorsal lateral geniculate nucleus and projects back to this nucleus and to the superior colliculus (Figure 3) (Krubitzer, 1995; Sefton *et al.*, 2004). A comparable retinorecipient dorsal lateral geniculate nucleus is present in the lemnothalamus of birds and reptiles that projects to the avian hyperpallium and reptilian dorsal cortex (Figure 3) (Karten *et al.*, 1973; Hall *et al.*, 1977; Miceli and Repérant, 1982; Miceli *et al.*, 1990; Mulligan and Ulinski, 1990; Butler, 1994a, 1994b; Kenigfest *et al.*, 1997; Medina and Reiner, 2000; Zhu *et al.*, 2005). In lizards, this nucleus is sometimes called intercalatus (Bruce and Butler, 1984a) and apparently corresponds to the deeper part (cell plate) of the dorsal lateral geniculate nucleus of other authors (Kenigfest *et al.*, 1997; Dávila *et al.*, 2000). In lizards, the geniculate thalamic input only reaches a lateral extension of the dorsal cortex, called pallial

thickening (Bruce and Butler, 1984a; Kenigfest *et al.*, 1997). In birds, the geniculate thalamic input mainly reaches a hyperpallial subdivision called interstitial nucleus of the apical hyperpallium or IHA (Karten *et al.*, 1973; Watanabe *et al.*, 1983). As in mammals, the dorsal pallial area of birds and at least some reptiles (such as turtles) that receives visual input from the geniculate nucleus projects back to this thalamic nucleus and the optic tectum (Figure 3) (Karten *et al.*, 1973; Hall *et al.*, 1977; Miceli and Repérant, 1983, 1985; Reiner and Karten, 1983; Ulinski, 1986; Mulligan and Ulinski, 1990; Butler, 1994a, 1994b; Kenigfest *et al.*, 1998). Therefore, their similar position, histogenetic origin, and connections suggest that the visual lemnothalamic nuclei and related pallial areas of the neocortex, hyperpallium, and dorsal cortex of mammals, birds, and reptiles are homologous, and evolved from similar areas present in their common ancestor.

2.07.3.3 A Primary Somatosensory Area in the Dorsal Pallium of Birds and Reptiles and Its Comparison to S1 of Mammals

In the mammalian neocortex, S1 receives somatosensory input from the ventrobasal or ventral posterior thalamic complex (in particular, from VPL, receiving body information via the dorsal column nuclei, and from VPM, receiving head information via the principal sensory trigeminal nucleus; restricted parts of VPL/VPM also receive pain and temperature information directly from the spinal cord through the dorsal horn and spinal trigeminal nucleus) (Figure 3). In turn, S1 shows descending projections back to this thalamic complex and to the brainstem and spinal cord (reaching primarily precerebellar and/or somatosensory relay centers) (Weisberg and Rustioni, 1977; McAllister and Wells, 1981; Torigoe *et al.*, 1986; Krubitzer, 1995; Desbois *et al.*, 1999; Manger *et al.*, 2001; Martínez-Lorenzana *et al.*, 2001; Killackey and Sherman, 2003; Craig, 2004; Friedberg *et al.*, 2004; Gauriau and Bernard, 2004; Leergaard *et al.*, 2004; Oda *et al.*, 2004; Tracey, 2004; Waite, 2004; Guy *et al.*, 2005). Similarly to S1, the frontal part of the avian hyperpallium (Wulst) receives somatosensory input from the dorsointermediate ventral anterior thalamic nucleus (DIVA), which is a target of both the dorsal column nuclei (Wild, 1987, 1989, 1997; Funke, 1989a, 1989b; Korzeniewska and Güntürkün, 1990) and the spinal cord (Schneider and Necker, 1989) (Figure 3). The avian DIVA develops in the dorsal tier/lemnothalamus of the dorsal thalamus (Redies *et al.*, 2000) and, thus, appears comparable in position, histogenetic origin, and connections to the mammalian ventrobasal thalamic complex (mainly to VPL). In addition to receiving somatosensory input from DIVA, the frontal part of the Wulst (hyperpallium) projects back to this thalamic nucleus, to the brainstem, and, in some species of birds, to the cervical spinal cord (Figure 3) (Wild, 1992; Wild and Williams, 2000). As with S1, the frontal hyperpallial descending projections predominantly reach precerebellar areas and somatosensory relay areas, such as the thalamic DIVA, the dorsal column nuclei, and the vicinity of medial lamina V in the cervical spinal dorsal horn, which suggests that the frontal hyperpallium may be primarily concerned with the control/modulation of somatosensory input (Wild and Williams, 2000). This suggests that the avian frontal hyperpallium contains a primary somatosensory area that appears comparable to S1 of mammals (Wild, 1992; Medina and Reiner, 2000; Wild and Williams, 2000). However, unlike S1, a sensory trigeminal representation (with head information) has not been found in the hyperpallium (Wild *et al.*, 1985). To know whether these primary somatosensory areas of the avian hyperpallium and mammalian neocortex are homologous we need to analyze if a similar pallial area is present in the dorsal pallium of reptiles.

The frontal part of the reptilian dorsal cortex was previously thought to contain a somatosensory area based on input from a spinorecipient thalamic nucleus (Ebbesson, 1967, 1969, 1978; Hall and Ebner, 1970). Modern tract-tracing data in lizards indicate that the rostral dorsal cortex receives distinct ipsilateral input specifically from a ventral part of the dorsolateral thalamic nucleus (Guirado and Dávila, 2002), which receives somatosensory input from the dorsal column and trigeminal sensory nuclei as well as from the spinal cord (Figure 3) (Hoogland, 1982; Desfilis *et al.*, 1998, 2002). Of interest, the dorsolateral thalamic nucleus of lizards is located in the dorsal tier/lemnothalamus of the dorsal thalamus, and its ventral part DLV, which differs from the rest of the nucleus by its connections and calbindin immunostaining profile – shows a location that resembles that of avian DIVA and ventrobasal complex of mammals (Dávila *et al.*, 2000). The projection from the dorsal column and sensory trigeminal (both descending and principal) nuclei and from the spinal cord to the dorsolateral thalamic nucleus appears to reach specifically its ventrolateral part or DLV (plus the area adjacent to it, called intermediodorsal nucleus; Ebbesson, 1967, 1969, 1978; Hoogland, 1982). Thus, DLV of lizards appears to be a distinct subnucleus of the lemnothalamus that may be primarily involved in

somatosensory information processing. Using modern tract-tracing techniques, similar thalamocortical projections have also been described in crocodiles (Pritz and Stritzel, 1987; these authors also found a specific dorsolateral cell population projecting only ipsilaterally to the dorsal cortex) and in adult and developing turtles (Hall *et al.*, 1977; Cordery and Molnár, 1999). In turtles, the thalamocortical nucleus appears located in a perirotundal position, medially adjacent to the dorsal lateral geniculate nucleus and ventral to the dorsolateral thalamic nucleus (a position that resembles the DLV of lizards), and this perirotundal area is the site of termination of spinal and dorsal column nuclei (but not retinal) projections (Künzle and Schnyder, 1983; Siemen and Künzle, 1994). However, other authors studying turtles have not found any thalamic relay center projecting to the dorsal cortex other than the geniculate nucleus (Zhu *et al.*, 2005). This may be due to the more caudal location of the injections in the dorsal cortex (note that the somatosensory area is located at its rostral pole) or to the employment of *in vitro* tract-tracing techniques in the study done by Zhu *et al.* (2005). Based on the evidence presented above, two different thalamic relay centers conveying either visual or somatosensory information to the dorsal cortex are present in most reptilian groups, and were likely present in their common ancestor. Thus, the frontal part of the dorsal cortex of most reptiles contains a primary somatosensory area that is comparable and may be homologous to those present in the hyperpallium of birds and the neocortex of mammals. Consistent with this, the relative position of the primary somatosensory area in the dorsal pallium is similar in mammals, birds, and reptiles, being always located rostral (in a more frontal position) to the primary visual area.

2.07.3.4 Do Birds and/or Reptiles Possess a Somatomotor Dorsal Pallial Area Comparable to M1 of Mammals?

In the mammalian neocortex, M1 (area 4) receives motor input from a specific part of the lemnothalamic ventrobasal complex (VA/VL nuclei in rodents), and shows descending projections back to this thalamic complex, and to the brainstem and the spinal cord (Figure 3), where the projections reach precerebellar (including the red and pontine nuclei) and sensory-relay areas (including dorsal column nuclei and dorsal horn of the spinal cord), but also reach premotor reticulospinal cell groups (including the prerubral and rubral neurons) and, in some species (such as rodents and primates), motor neuron pools such as those of the ventral horn in the spinal cord (Weisberg and Rustioni, 1977; Humphrey *et al.*, 1984; Torigoe *et al.*, 1986; Liang *et al.*, 1991; Krubitzer, 1995; Song and Murakami, 1998; Kuchler *et al.*, 2002; Leergaard *et al.*, 2004). In general, the descending projections of M1 are similar to those of S1, and axons from both areas contribute to form the pyramidal tract. However, the descending projections of S1 and M1 are somewhat different. For example, in the brainstem, S1 projects significantly more heavily to the precerebellar pontine nuclei than M1 (Leergaard *et al.*, 2004), whereas M1 is the major source of corticorubral axons (Giuffrida *et al.*, 1991; Burman *et al.*, 2000) (Figure 3). Further, in the spinal cord, S1 axons primarily reach dorsal horn laminae, whereas M1 axons, but not S1 axons, also reach the motoneuron pools in the ventral horn (Figure 3) (Ralston and Ralston, 1985; Martín, 1996). Current available data suggest that early mammals lacked a separate motor cortical area (M1), and that a separate M1 likely evolved with the origin of placental mammals (Kaas, 2004). Thus, it appears that early mammals only had an S1 where somatosensory and motor attributes were overlapped, a situation which resembles that found in marsupials (Kaas, 2004).

Similarly to M1, the frontal part of the avian hyperpallium (Wulst) receives input from a putative motor thalamic nucleus, the ventrointermediate area (VIA), which receives input from the avian globus pallidus, substantia nigra pars reticulata, and deep cerebellar nuclei (Medina *et al.*, 1997) (Figure 3). The avian VIA resembles the motor part of the mammalian ventrobasal thalamic complex (VA/VL) in both its position (located in the lemnothalamus and adjacent to the somatosensory part of the avian ventrobasal complex or DIVA), and its connections (Medina *et al.*, 1997). Both DIVA and VIA project to the frontal part of the hyperpallium (Wild, 1987, 1989; Funke, 1989a, 1989b; Korzeniewska and Güntürkün, 1990; Medina *et al.*, 1997), where somatosensory and motor information may be completely overlapped (Medina and Reiner, 2000) (Figure 3). Of note, as S1 and M1 of mammals, the frontal hyperpallium of birds projects back to the thalamus (including DIVA), to the brainstem and, in some avian species, to the cervical spinal cord (Wild, 1989, 1992; Medina and Reiner, 2000; Wild and Williams, 2000) (Figure 3). In the brainstem and spinal cord, the frontal hyperpallial projections reach precerebellar (including pretectal and rubral nuclei), sensory-relay cell groups (including the dorsal column nuclei and the dorsal horn in the spinal cord), premotor reticulospinal neurons (such as rubrospinal neurons) and, in some birds, a few axons reach the ventral horn of the cervical spinal

cord, where motoneuron pools are located (Wild, 1992; Wild and Williams, 2000). Thus, the frontal hyperpallium contains a somatosensory/somatomotor area that appears at least partially comparable to the overlapped S1+M1 of marsupials, and possibly of early mammals. To know whether these areas are homologous we need to know if a similar sensorimotor field is present in the dorsal pallium of reptiles.

As noted above, in some reptiles (lizards), the frontal part of the dorsal cortex appears to receive somatosensory input from a specific subdivision of the dorsolateral thalamic nucleus, the DLV (Guirado and Dávila, 2002) (Figure 3). Further, this part of the reptilian dorsal cortex has descending projections to diencephalic and midbrain tegmetum (Hoogland and Vermeulen-vanderZee, 1989; Guirado and Dávila, 2002). In the prerubral tegmentum, these cortical projections reach at least the nucleus of the medial longitudinal fascicle, which is a well-known premotor precerebellar and reticulospinal cell group (Figure 3) (ten Donkelaar, 1976; Woodson and Künzle, 1982; Wolters *et al.*, 1986). This feature has been used to suggest that this part of the reptilian dorsal cortex may represent a rudimentary sensorimotor area, partially comparable to that in other amniotes (Medina and Reiner, 2000; Guirado and Dávila, 2002). However, this putative sensorimotor area of the reptilian dorsal cortex does not possess a distinct motor field comparable to M1 of mammals, since its thalamic input does not include a basal ganglia-recipient nor a cerebellar-recipient nucleus. No part of the dorsolateral thalamic nucleus and no part of the reptilian dorsal thalamus receives direct basal ganglia input (Reiner *et al.*, 1984, 1998; Medina and Smeets, 1991) nor input from the deep cerebellar nuclei (Künzle, 1985). Further, in some reptilian species (including the pond turtle) the descending projections of the dorsal cortex are rather modest and do not reach rubral and, perhaps, not even prerubral levels (Zhu *et al.*, 2005). Thus, at present it is unclear whether ancestral reptiles had a rudimentary somatomotor area in the dorsal cortex, and more data are needed in other reptilian species before any conclusion can be reached. If a rudimentary somatomotor area was present in the dorsal cortex of reptiles, this area lacked many of the connections that characterize the true somatomotor cortical area found in birds and mammals (including basal ganglia and cerebellar indirect input, or output to additional precerebellar and reticulospinal fields and to the spinal cord), meaning that these features likely evolved independently in the avian and mammalian radiations.

2.07.3.5 Other Functional Areas in the Pallium of Birds and Reptiles and Comparison to Mammals

In birds and reptiles, there are other sensory (visual, somatosensory, and auditory) areas in the pallium that are located in the DVR (Karten and Hodos, 1970; Dubbeldam *et al.*, 1981; Bruce and Butler, 1984b; Wild, 1987, 1994; Wild *et al.*, 1993, 1997; Guirado *et al.*, 2000; reviewed by Karten and Shimizu, 1989; Butler, 1994b; Reiner, 2000). These sensory areas are mainly located in the ventral pallial part of the DVR (called nidopallium in birds; Reiner *et al.*, 2004) and receive visual, somatosensory, or auditory input from specific nuclei of the collothalamus or directly from the brainstem (see above-cited references; this is described in detail in Evolution of the Nervous System in Reptiles, Visual Cortex of Turtles). In birds, some of these DVR areas appear to have a better (more detailed) sensory representation than those present in the hyperpallium, such as the nucleus basalis of the budgerigar, which shows a highly somatotopically organized representation of head and body (Wild and Farabaugh, 1996; Wild *et al.*, 1997). In addition, the caudal part of the DVR in birds (including the caudal nidopallium and the region called arcopallium) and reptiles contains associative and/or motor centers that project to the basal ganglia, hypothalamus, and/or, in birds, also to premotor brainstem centers (Zeier and Karten, 1971; Bruce and Neary, 1995a, 1995b, 1995c; Davies *et al.*, 1997; Dubbeldam *et al.*, 1997; Lanuza *et al.*, 1997, 1998; Kröner and Güntürkün, 1999; Bottjer *et al.*, 2000; Martínez-García *et al.*, 2002). Further, in songbirds and budgerigars, the caudal DVR (arcopallium) contains a specific motor area that projects directly to motor brainstem nuclei, the ambiguus, and/or hypoglossal motor nuclei, which control syringeal, respiratory, and tongue muscles (Nottebohm, 1991; Vicario, 1991a, 1991b; Wild, 1993; Brauth *et al.*, 1994; Striedter, 1994; Durand *et al.*, 1997; see details on this motor pallial area and its connections in The Evolution of Vocal Learning Systems in Birds). In songbirds and budgerigars, this motor area is well developed and plays a key role in vocalization (including vocal learning and vocal production), and apparently evolved independently in songbirds and budgerigars (Striedter, 1994). These sensory, associative, and motor areas of the DVR play very important roles in sensory processing, sensorimotor integration, and motor control, and in birds are also involved in cognitive tasks such as learning, memory, and spatial orientation, and they have been compared to specific areas or specific cell populations of the mammalian temporal,

frontal, and prefrontal neocortex (for example, Karten, 1969, 1997; Morgensen and Divac, 1993; Veenman *et al.*, 1995; Kröner and Güntürkün, 1999; see The Evolution of Vocal Learning Systems in Birds and Humans). Although this makes sense from a functional point of view, the different histogenetic origin of the DVR (lateroventral pallium) and neocortex (dorsal pallium) indicates that the similarities of such sauropsidian DVR and mammalian neocortical areas represent cases of analogy (homoplasy). Consistent with this, the thalamic nuclei that project to the DVR sensory areas are not comparable in location to those that project to the neocortex. Thus, the DVR receives sensory information via thalamic nuclei that are located in the intermediate and ventral tiers of the dorsal thalamus, whereas those that project to the neocortex are generally located in the dorsal tier or lemnothalamus (Dávila *et al.*, 2000, 2002; Puelles, 2001). Further, the avian motor area(s) of the caudal DVR projecting to the premotor and/or motor brainstem are not present in the caudal DVR of reptiles (some of them are not even present in all birds), which means that they evolved as novelties in some birds. Thus, it appears that, in contrast to mammals, the repertory of complex behaviors shown by birds and reptiles depends primarily (although not exclusively) on a large variety of cell groups that develop in the ventrolateral pallial histogenetic division, but the contribution of dorsal pallial areas to these behaviors is likely more modest (especially in reptiles).

2.07.4 Pallial Lamination in Birds and Mammals: Evidence for Independent Evolution

2.07.4.1 Different Development and Adult Organization of Neocortical Layers and Hyperpallial Subdivisions

In mammals, the neocortex shows a laminar structure of six layers, and each layer has a similar cytoarchitecture and general pattern of connections throughout all areas, including V1, S1, and M1 (Figure 4). Thus, the dorsal thalamic input mainly contacts cells in neocortical layer 4, a layer that is called granular layer because of its typical granule or stellate cells (Humphrey *et al.*, 1977; Kharazia and Weinberg, 1994). In this layer, thalamic axons contact granule cells as well as apical dendrites of pyramidal neurons located below, in layers 5/6 (Mountcastle, 1997). In addition, thalamocortical axons ending in layer 4 provide collaterals that terminate in layer 5 and/or 6, but other thalamocortical axons terminate in layer 1 (Figure 4) (Jones, 1975; Rausell *et al.*, 1992; Lu and Lin, 1993; Zhang and Deschenes, 1998; Groenewegen and Witter, 2004; Sefton *et al.*, 2004). Layers 2 and 3 are called supragranular layers, located superficially to layer 4, and typically contain small to medium-sized pyramidal neurons involved in corticocortical (associational) projections (Gilbert and Kelly, 1975; Jones and Wise, 1977; Swadlow and Weyand, 1981; Sefton *et al.*, 2004). Layers 5 and 6 are called infragranular layers, located deep to layer 4, and typically contain large pyramidal neurons that show descending projections to the striatum, thalamus, and brainstem (Figure 4). Layer 5 mainly projects to the striatum and brainstem (to the midbrain tectum in the case of V1 and to the brainstem tegmentum and spinal cord in the case of S1 and M1), whereas layer 6 typically projects to the thalamus (Gilbert and Kelly, 1975; Jones and Wise, 1977; Swadlow and Weyand, 1981; Sefton *et al.*, 2004; Tracey, 2004). The pyramidal neurons of the supra- and infragranular layers of the neocortex typically have a long apical dendrite that span the cortical layers above its cell body (Figure 4), which provides one of the anatomical bases for the columnar functional organization of the neocortex (Mountcastle, 1997; Lübke *et al.*, 2000).

In birds, the dorsal pallium (corresponding to the so-called hyperpallium) also shows cytoarchitectonic subdivisions, considered by some authors as the layers of the neocortex (for example, Karten *et al.*, 1973; Shimizu and Karten, 1990; reviewed by Medina and Reiner, 2000). From rostral (frontal) to caudal levels, each hyperpallial subdivision is characterized by a specific pattern of connections which partially resembles the connectivity organization of neocortical layers (Figure 4). For example, the thalamic input ends primarily in an intermediate hyperpallial subdivision called the IHA, in both the visual and somatomotor areas (Karten *et al.*, 1973; Watanabe *et al.*, 1983; Wild, 1987, 1997), resembling neocortical layer 4. Nevertheless, some thalamic axons appear to end in the hyperpallium outside IHA (Figure 4). Further, the descending projections to the striatum, thalamus, and brainstem mainly originate in the apical hyperpallium or HA (Reiner and Karten, 1983; Wild, 1992; Wild and Williams, 1999, 2000), resembling neocortical layers 5–6. Morever, the densocellular hyperpallium (HD) appears to be mainly involved in connections with other pallial and subpallial areas (Veenman *et al.*, 1995; Kröner and Güntürkün, 1999; Wild and Williams, 1999), thus partially resembling neocortical layers 2–3. In addition to the apparently similar laminar organization of both neocortex and hyperpallium, there is evidence suggesting that they also

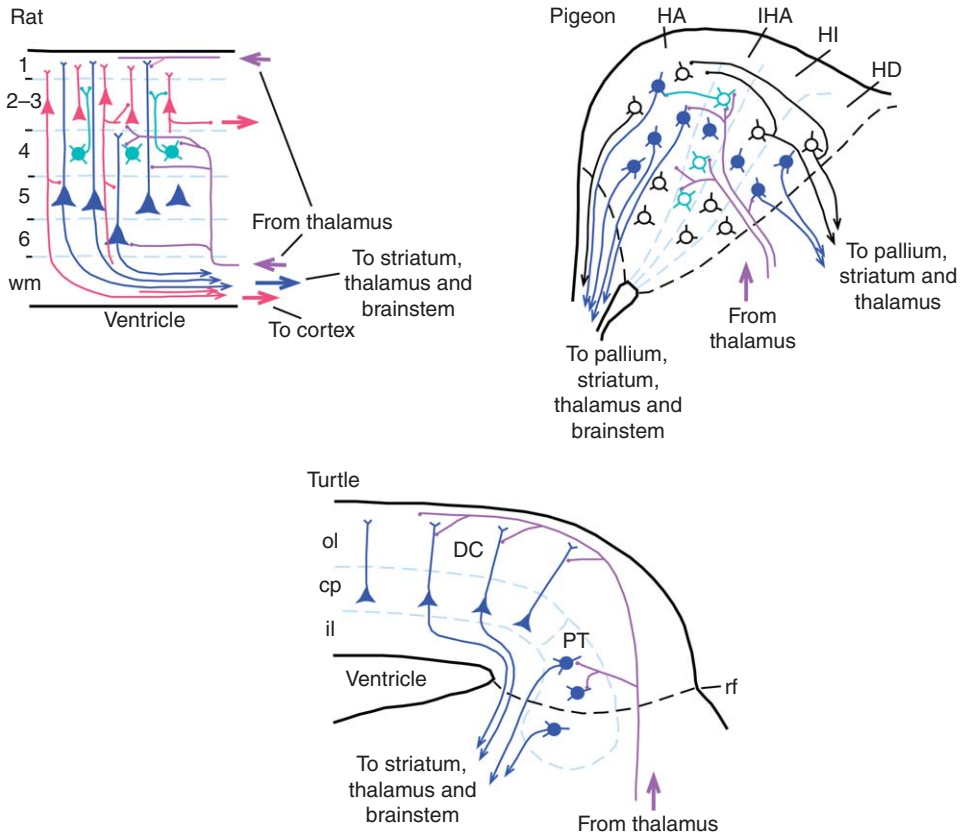

Figure 4 Schematics of the layers/subdivisions, cell types, and major connections of the mammalian neocortex, avian hyperpallium, and reptilian dorsal cortex. The mammalian neocortex shows a six-layered organization, and each layer shows specific cell types and connections. The thalamic input primarily reaches the intermediate layer 4 (also called granular layer, because of its typical granule or stellate cells). In this layer, thalamic axons contact stellate cells as well as apical dendrites of pyramidal neurons located in infragranular layers (layers 5 and 6). Some thalamic axons also reach layers 6 or 1. Infragranular layers contain large pyramidal neurons having apical dendrites that radially span the layers above, and give rise to descending projections to the striatum, thalamus, and brainstem. Supragranular layers contain small to medium pyramidal neurons involved in corticocortical (associational) connections. This anatomical and cellular organization, with radially oriented dendrites that span most layers, constitutes one of the basis of the functional columnar organization of neocortex. In contrast to this organization, the avian hyperpallium shows four mediolateral subdivisions that are formed and organized in a radically different way. These subdivisions contain multipolar or stellate-like neurons having star-like oriented dendrites that do not span adjacent subdivisions (i.e., they lack the translayer, radial dendritic organization typical of neocortex). In contrast to the neocortex, the connections between subdivisions occur by way of tangential projections, instead of the radial connections typical of neocortical columns. Nevertheless, the patterns of connections of hyperpallial subdivisions partially resemble those of neocortical layers. For example, thalamic input primarily ends in an intermediate subdivision (IHA), which is sandwiched between a subdivision (HA) giving rise to descending projections to the striatum, thalamus, and brainstem, and another subdivision (HD) giving rise to pallial projections. However, HA also projects to other pallial areas, whereas HD also projects to the striatum and thalamus, indicating that their similarity with specific neocortical layers in terms of connectivity is only partial. The reptilian dorsal cortex is very simple but resembles, in a very rudimentary way, both the laminar organization of neocortex and the mediolateral subdivisions of hyperpallium. Thus, the reptilian dorsal cortex contains a medial subdivision (dorsal cortex proper or DC) that resembles HA, and a lateral subdivision (pallial thickening or PT) that resembles HD. Further, the reptilian dorsal cortex shows a three-layered structure, with a main cell layer located between superficial and deep cell-sparse layers. The main cell layer contains pyramidal neurons having apical dendrites that span the superficial layer, where they are contacted by incoming thalamic axons. Further, these pyramidal neurons give rise to descending projections to the striatum, thalamus, and brainstem. This basic laminar and cellular organization partially resembles that of the neocortex, with pyramidal neurons located in deeper layers (5/6) giving rise to long descending projections, and thalamic axons contacting the apical dendrites of these cells. Cell types sharing these features and connections were likely present in the dorsal pallium of the common ancestor of mammals, birds, and reptiles (represented in dark blue in schematics). However, many of the cell types present in the mammalian neocortex and avian hyperpallium likely evolved independently in birds and mammals (such as the thalamorecipient stellate or stellate-like cells, or many of the neurons involved in corticocortical connections). cp, main cell layer; DC, reptilian dorsal cortex; HA, apical hyperpallium; HD, densocellular hyperpallium; HI, intercalated hyperpallium; IHA, interstitial nucleus of the apical hyperpallium; il, inner layer; ol, outer layer; PT, pallial thickening; wm, white matter.

share a similar functional columnar organization (Revzin, 1970). Both in the neocortex and the hyperpallium, the sensory input is topographically (retinotopically or somatotopically) organized (Pettigrew and Konishi, 1976; Wilson, 1980; Wild, 1987; Funke, 1989a; Manger *et al.*, 2002). In each single neocortical unit, the excitation reaches layer 4 by way of thalamocortical axons, and then spreads primarily in a columnar way first to supragranular and later to infragranular layers (Petersen and Sakmann, 2001), and this appears to be similar in the avian hyperpallium (Revzin, 1970).

However, the similarity of hyperpallial subdivisions and specific neocortical layers in terms of connectivity is only partial (Veenman *et al.*, 1995; Wild and Williams, 1999). More importantly, developmental and cellular analysis of the avian hyperpallium and mammalian neocortex indicates that the subdivisions of the avian hyperpallium are not true layers (as least, as defined from a developmental point of view, but see Striedter, 2005) and show important organizational differences with neocortical layers (reviewed in Medina and Reiner, 2000). For this reason, the subdivisions of avian hyperpallium have been called pseudolayers, meaning false layers (Medina and Reiner, 2000). This is based on the following facts. First, although the layers of the mammalian neocortex are aligned parallel to the ventricular surface and develop perpendicular to radial glial fibers, the hyperpallial subdivisions are generally organized parallel to radial glial fibers (Striedter and Beydler, 1997; Medina and Reiner, 2000). Since, during development, the majority of neurons migrate from ventricular to mantle positions following radial glial fibers (Rakic, 1972, 1995; Alvarez-Buylla *et al.*, 1988; Striedter and Beydler, 1997), the different disposition of neocortical layers and hyperpallial subdivisions with respect to the radial glial fibers likely reflects that they are formed in radically distinct ways (Medina and Reiner, 2000). Second, as a consequence of their apparently different development, whereas for any single neocortical area the majority of neurons of all layers are born in the same ventricular sector (except interneurons, which immigrate from the subpallium; Anderson *et al.*, 1997), in the avian hyperpallium the neurons of each subdivision (HA, IHA, and HD) are primarily born in different ventricular sectors (Medina and Reiner, 2000). Third, also as a consequence of their development, whereas many layers of the neocortex typically contain pyramidal neurons with an apical dendrite that span the layers above (where they can be contacted by axons of extrinsic origin ending in other layers, as well as by axon collaterals of local neurons of other layers; Mountcastle, 1997), the subdivisions of avian hyperpallium contain neurons showing multipolar or stellate-like morphology, with star-like oriented dendrites that generally do not cross subdivision boundaries (Figure 4) (Watanabe *et al.*, 1983; Tömbol, 1990; Medina and Reiner, 2000). This means that, whereas in the mammalian neocortex, the radial (translayer) disposition of dendrites allows functional integration of layers (and constitutes one of the anatomical basis of functional columns; Lübke *et al.*, 2000), the neuronal communication between subdivisions of the avian hyperpallium is apparently only possible by way of tangential, inter-area axonal connections (Figure 4) (Kröner and Güntürkün, 1999; Medina and Reiner, 2000; Wild and Williams, 2000).

2.07.4.2 Layers and Subdivisions of the Reptilian Dorsal Cortex. Possibilities and Uncertainties on Dorsal Pallial Evolution

How did the different pallial organizations found in neocortex and hyperpallium evolve and which was the primitive condition in stem amniotes? Extant reptiles have a very simple dorsal pallium, but this shows some features that partially resemble, in a very rudimentary way, both the medial–lateral subdivisions of avian hyperpallium and the lamination of mammalian neocortex (Figure 4). The reptilian dorsal pallium appears to have two parts that show different cytoarchitecture and connections: a medial part or dorsal cortex and a lateral part or pallial thickening (as noted above, only part of the pallial thickening may be part of the dorsal pallium) (Figure 4). In lizards, the thalamic input primarily reaches the pallial thickening, whereas the dorsal cortex gives rise to the descending projections to the striatum and brainstem (see references in previous section; reviewed in Medina and Reiner, 2000). In turtles, thalamic input reaches both the pallial thickening and the dorsal cortex (Mulligan and Ulinski, 1990), and extratelencephalic projections originate in the dorsal cortex (Hall *et al.*, 1977; Ulinski, 1986; Zhu *et al.*, 2005). In lizards and turtles, the pallial thickening shows important intratelencephalic connections (Medina and Reiner, 2000). Thus, the organization of the connections and the relative position of these two divisions in the reptilian dorsal pallium suggests a similarity of the reptilian dorsal cortex and avian HA and the reptilian pallial thickening and avian HD. As the dorsal cortex or pallial thickening, the avian HA and HD also appear to receive a minor direct input from the sensory thalamus (Karten *et al.*, 1973; Watanabe *et al.*, 1983; Wild, 1997; Wild and Williams, 2000). On the other hand, the reptilian dorsal cortex shows a simple three-layered structure, with a main, intermediate cell layer

containing pyramidal-like cells, flanked by a superficial and a deep cell sparse layer (Figure 4) (Reiner, 1993; Medina and Reiner, 2000; Colombe *et al.*, 2004). As neocortical layers, those of the reptilian dorsal cortex are disposed parallel to the ventricular surface and perpendicular to the radial glia. Further, the pyramidal cells of the main cell layer show apical dendrites that span the layer above, where they are contacted by thalamic afferent axons, and they give rise to long descending projections reaching the striatum and brainstem (Figure 4) (Mulligan and Ulinski, 1990; Colombe *et al.*, 2004). Thus, the reptilian dorsal cortex shares with the neocortex some aspects of its laminar and cellular organization. In both the neocortex and reptilian dorsal cortex, the thalamic axons contact the apical dendrites of deep pyramidal neurons, and in both these, deep pyramidal neurons are the source of long descending projections. Of interest, in the neocortex, some thalamic afferent axons travel tangentially in layer 1, where they contact apical dendrites of pyramidal neurons (Rausell *et al.*, 1992), resembling the trajectory of thalamic axons in the reptilian dorsal cortex. Further, analysis of chemically different neurons in the dorsal pallium of mammals, birds, and reptiles indicates that only the cell types present in neocortical layers 5–6 (which contain the deep pyramidal neurons giving rise to long descending projections) are found in birds and reptiles, suggesting that only layers 5–6 were present in the common ancestor (Reiner, 1991). Further, comparative developmental studies suggest that only the subpial layer 1 and the deepest neocortical layers may have been present in the common ancestor of extant reptiles, birds, and mammals (Marín-Padilla, 1998).

All these data together suggest that the pyramidal neurons found in the cell layer of the reptilian dorsal cortex may be homologous to the pyramidal cells of layers 5–6 of the mammalian neocortex, and possibly to some of the multipolar projection neurons of avian HA (at least including the neurons that, in addition to giving rise to long descending projections, receive thalamic input). In contrast, the thalamorecipient granule (or stellate) cells found in neocortical layer 4 have no counterpart in reptiles and are not homologous to the thalamorecipient stellate-like cells found in avian IHA (Figure 4). Stellate cells of neocortical layer 4 and stellate-like cells of IHA apparently evolved independently (and were produced as novelties) in the mammalian and avian radiations. On the other hand, the pyramidal neurons of neocortical layers 2–3 and part of the projection neurons of avian hyperpallium involved in corticocortical connections may also be newly evolved. Finally, it is unclear what part of the mammalian neocortex (if any) is comparable to avian HD and reptilian pallial thickening, both involved in intratelencephalic connections. As noted above, since the pallial thickening and apparently HD receive retinal input, they may be comparable to a lateral part of V1. In relation to this, V1 in rats contains medial and lateral subdivisions which differ in cyto-, myelo-, and chemoarchitecture (Palomero-Gallagher and Zilles, 2004). The medial subdivision represents a monocular subfield, whereas the lateral subdivision represents a binocular subfield. Nonplacental mammals, such as marsupials, also show similar medial–lateral V1 subdivisions in the neocortex, representing areas of either complex or simpler waveform processing (Sousa *et al.*, 1978). Thus, it is possible that such mediolateral subdivisions were present in the origin of mammals and, if so, the lateral V1 part may be comparable to HD/pallial thickening of birds and reptiles. Another possibility is that HD and/or the pallial thickening are not comparable to any part of V1, but rather to a more laterally located cortical or subcortical pallial area, such as the insular cortex (or part of it) or the claustrum (Striedter, 1997). The position of these structures at the lateral extreme of the neocortex, either abutting the lateral pallium or within it, resembles that of both HD and pallial thickening (Figure 2). In contrast to this possibility, the connectivity patterns of HD and pallial thickening are very different from those of the insular cortex or claustrum. For example, in contrast to HD and pallial thickening, neither the insular cortex nor the claustrum receive direct input from the dorsal lateral geniculate nucleus (Clascá *et al.*, 1997; Sefton *et al.*, 2004). More studies will be needed to resolve this issue. If the pallial thickening of reptiles were not homologous (as a field) to any part of V1, it would challenge the existence of a primary visual area in the dorsal pallium of the amniote common ancestor (since in lizards the geniculate projection only reaches the pallial thickening but not the dorsal cortex proper), opening new and important questions on neocortical evolution.

2.07.5 Functional Properties of the Visual and Somatosensory Areas of Neocortex and Sauropsidian Dorsal Pallium: Do Mammals, Birds, and Reptiles See and Feel the Same?

2.07.5.1 Visual Area: Retinotopy, Signal Types, Binocularity, and Perception

The mammalian V1 contains a detailed point-to-point retinal map, received through the retinogeniculocortical pathway, which subserves conscious

vision (Kahn *et al.*, 2000; Sefton *et al.*, 2004; Wässle, 2004). Neurons in V1 respond to orientation, direction, or color, and this information reaches the cortex through mostly segregated parallel pathways (Wässle, 2004). This information is then processed and combined (a process that involves higher-order areas), making possible animals' visual perception of the world. Visual signals are first detected by retinal photoreceptors, rods (involved in detection of low light levels), and cones (involved in detection of lights of different wavelengths; i.e., they are color-sensitive). The signals detected at the photoreceptor level are then processed and filtered through a complex retinal system involving several cell types (including horizontal, bipolar, amacrine, and ganglion cells), connected through specific circuitries (Lee, 2004; Wässle, 2004). At the end of this process, different types of retinal ganglion cells respond to orientation, direction, motion, or color, and this information is then transmitted to the brain through the retinofugal pathways (one of which is the retinogeniculate system). In primates, achromatic retinofugal signals mainly reach the visual cortex by way of the magnocellular layer of the geniculate nucleus, whereas chromatic retinofugal signals reach V1 mainly via either the koniocellular or the parvocellular geniculate cells, and each pathway mainly ends on a separate layer or sublayer in V1 (Chatterjee and Callaway, 2003; Lee, 2004).

In V1, orientation and direction signals represent a first step for analysis of form or movement, in which higher-order visual areas participate (Sincich and Horton, 2005; Saul *et al.*, 2005; Shmuel *et al.*, 2005; van Hooser *et al.*, 2005). Neurons responsive (or sensitive) to orientation or direction appear to be present in V1 of a large variety of mammals (including placental and marsupial species; Murphy and Berman, 1979; Parnavelas *et al.*, 1981; Crewther *et al.*, 1984; Orban *et al.*, 1986; Vidyasagar *et al.*, 1992; Ibbotson and Mark, 2003; Priebe and Ferster, 2005), and many mammals appear to have at least a second visual area (V2) involved in higher-order processing (Kaas, 2004; Sefton *et al.*, 2004), suggesting that some basic aspects of form and movement perception are common to all mammals. Nevertheless, in some mammals (such as marsupials) only a low percentage of V1 neurons respond to motion (Ibbotson and Mark, 2003), whereas other mammals possess multiple higher-order visual areas, one of which (V5/MT of primates) is specially involved in motion perception (Riecansky, 2004; Sincich *et al.*, 2005; Silvanto *et al.*, 2005). Thus, it appears that some mammals have a better visual perception of movement and form than others. Further, in mammals (such as primates, cats, and rats, as well as marsupials), some or many neurons of V1 are characterized by binocular convergence (depending on the degree of orbital convergence, which is maximal in primates), and are involved in perception of depth (stereoscopic vision) (Vidyasagar *et al.*, 1992; Barton, 2004; Grunewald and Skoumbourdis, 2004; Heesy, 2004; Menz and Freeman, 2004; Read, 2005). But again, some mammals show higher binocular convergence and have more visual cortical areas involved in its analysis, indicating that some species apparently have better depth perception than others. Nevertheless, in many mammals, several noncortical areas (including pretectum, superior colliculus, and other subcortical areas) are involved in motion processing (Ibbotson and Price, 2001; Price and Ibbotson, 2001; Sefton *et al.*, 2004). The superior colliculus appears to be involved in the spatial localization of biologically significant stimulus rather than its recognition (where it is rather than what it is) (Schneider, 1969), and can influence head/eye movements and guidance toward or away from a stimulus (reviewed by Sefton *et al.*, 2004). The visual cortex (with the participation of higher-order areas) appears to be involved in perception of both what the stimulus is (form and pattern discrimination) and where it is, among other aspects of visual perception.

Regarding color perception, the majority of mammals appear to have dichromatic vision, whereas – among placental mammals – only some primates have trichromatic vision. Among nonplacental mammals, it appears that some Australian marsupials may also have trichromatic vision. This depends on the pigment (opsin) variety found in retinal cone photoreceptors, and in the existence of color opponent systems. It appears that most mammals have two cone types: a majority of cones are sensitive to medium or long wavelengths (M/L-cones, sensitive to green or red), depending on the species; and a minority of cones are sensitive to short wavelengths (S-cones, sensitive to blue or ultraviolet (UV)), depending on the species (Peichl and Moutairou, 1998; Yokoyama and Radlwimmer, 1998, 2001; Shi and Yokoyama, 2003; Gouras and Ekesten, 2004). Among placental mammals, only some primates (including squirrel monkeys, New World monkeys, and humans) have a trichromatic color vision and their retina contains cones sensitive to green, red, or blue. Many marsupials also have M/L- and S-cones (Deeb *et al.*, 2003; Strachan *et al.*, 2004), and it seems that they were present in the retina of ancestral vertebrates well before the emergence of mammals (Shi and

Yokoyama, 2003). It has been suggested that the green-sensitive and red-sensitive cones present in mammals evolved from a single M/L cone present in the common ancestor well before the origin of mammals (Yokoyama and Radlwimmer, 1998). However, several species of Australian marsupials do have trichromatic retinas, with cones sensitive to short, medium, or long wavelengths (Arrese *et al.*, 2002, 2005), which appears to be due to retention from the ancestor (see below). It seems that the retina of ancestral placental mammals became dichromatic when these animals adopted nocturnality and some primates, subsequently, re-evolved trichromacy (Arrese *et al.*, 2002).

It seems that color perception involves a comparison of the relative activities of different cones by way of an opponent process, which starts in the retina and is conveyed to the visual cortex by parallel, anatomically segregated color-opponent systems (Dacey, 2000). In mammals having a dichromatic retina, only one opponent system exists, a blue–yellow system, in which signals from blue cones are opposed to signals from red or green cones. For trichromatic retinas (such as those of some primates), there are two color opponent systems, one for a red–green system, in which signals from red- and green-sensitive cones are opposed, and another one for a blue–yellow system, in which signals from blue cones are opposed to a combined signal from red and green cones (Dacey, 2000; Chatterjee and Callaway, 2003). Specific retinal ganglion cells exist for each color system. The blue–yellow information is conveyed to V1 through the koniocellular geniculate pathway, whereas the red–green information is conveyed by the parvocellular geniculate pathway (Lee, 2004). The information reaching V1 is later combined in higher-order visual areas. It is likely that ancestral placental mammals only had the blue–yellow system, and that the anatomical substrate for the red–green system evolved as a novelty in primates (Dacey, 2000; Lee, 2004).

In reptiles and birds, the retina contains cell types (including rod and cone photoreceptors, as well as horizontal, bipolar, amacrine, and ganglion cells) and circuitries in general similar to many of those present in mammals (Fernández *et al.*, 1994; Kittila and Granda, 1994; Ammermüller and Kolb, 1995; Haverkamp *et al.*, 1997, 1999; Luksch and Golz, 2003). Ganglion cells responsive to direction, motion, or color are found in the retina of both birds and reptiles, and cells responsive to orientation are also found in birds (Granda and Fulbrook, 1989; Guiloff and Kolb, 1994; Ammermüller *et al.*, 1995; Borg-Graham, 2001; Wilke *et al.*, 2001; Jones and Osorio, 2004). Retinal information is then conveyed to the dorsal pallium by way of a retinotopically organized retinogeniculodorsal pallial pathway (Bravo and Pettigrew, 1981; Miceli and Repérant, 1982; Ehrlich and Mark, 1984; Mulligan and Ulinski, 1990). This suggests that the dorsal pallium of birds and reptiles may be involved in some aspects of visual perception similar to those processed by V1 in mammals. Consistent with this, the visual hyperpallium of some birds (such as owls) contains neurons showing selectivity for orientation and movement direction (Pettigrew and Konishi, 1976), and has been shown to be involved in form discrimination, including some complex aspects such as subjective contour discrimination (Nieder and Wagner, 1999). In other birds (chicks or pigeons), the hyperpallium is involved in motion processing, far-field pattern discrimination, spatial discrimination acquisition, and in sun-compass associative learning (Gusel'nikov *et al.*, 1977; Leresche *et al.*, 1983; Britto *et al.*, 1990; Budzynski *et al.*, 2002; Watanabe, 2003; Budzynski and Bingman, 2004). Among birds, the complexity of visual processing by the hyperpallium appears to be higher in owls (which are frontal-eyed birds) than in other birds. In fact, the hyperpallium of owls shows a larger size, a more detailed retinotopic map, a much higher binocular convergence, and a more complex visual processing than that of lateral-eyed birds, such as pigeons (Pettigrew and Konishi, 1976; Nieder and Wagner, 1999, 2000, 2001; Liu and Pettigrew, 2003). Thus, the visual hyperpallium of owls is involved in depth perception and detection of visual illusions (subjective contours), exhibiting a functional complexity analogous to that of higher-order visual areas of highly visual mammals such as primates and cats (Nieder and Wagner, 1999, 2000, 2001; Liu and Pettigrew, 2003; van der Willigen *et al.*, 2003). In contrast, binocularity in pigeons is low (Martin and Young, 1983; McFadden and Wild, 1986; Holden and Low, 1989). Further, although the hyperpallium in pigeons is involved in motion perception and far-field discrimination, other brain areas, such as the optic tectum and the areas involved in the tectothalamo-DVR pathway, also play very important roles in motion processing or in other aspects of visual discrimination (Gusel'nikov *et al.*, 1977; Leresche *et al.*, 1983; Macko and Hodos, 1984; Britto *et al.*, 1990; Wang *et al.*, 1993; Laverghetta and Shimizu, 1999; Crowder *et al.*, 2004; Nguyen *et al.*, 2004). Among these areas, the thalamic nucleus rotundus and its DVR target play an important role in processing of ambient illumination, near-field discrimination, spatial-pattern vision, motion, and color (Wang *et al.*, 1993).

In reptiles, the visual dorsal cortex shows a coarse retinotopic map (Mulligan and Ulinski, 1990), and it appears involved in some aspects of visual processing, such as motion, discrimination acquisition, and spatial learning, but not in brightness discrimination (Reiner and Powers, 1983; Grisham and Powers, 1989, 1990; Prechtl, 1994; Prechtl *et al.*, 2000; Nenadic *et al.*, 2002). However, as in pigeons, other brain areas of reptiles, such as those involved in the tectothalamo-DVR pathway, play a more important role in brightness and pattern discrimination than the dorsal cortex (Morenkov and Pivovarov, 1975; Reiner and Powers, 1983).

Regarding color perception, the retina of birds and reptiles also supports color vision, but this appears to be more complex than in mammals. Thus, it appears that the retina of many diurnal birds and reptiles contains four types of cones, sentitive to red, green, blue, or UV or near-UV light (Ammermüller *et al.*, 1995; Bowmaker *et al.*, 1997; Kawamura *et al.*, 1999; Ventura *et al.*, 2001; Smith *et al.*, 2002). The cones of many diurnal birds and reptiles also contain colored oil droplets, which act as filters and apparently enhance color discrimination (Bowmaker *et al.*, 1997; Vorobyev, 2003). Parallel opponent retinal pathways have been shown in some species of reptiles, suggesting the existence of tetrachromatic color vision in these animals (Ammermüller *et al.*, 1995; Ventura *et al.*, 2001). In turtles, the opponent color systems described in the retina include a blue–yellow system, a red–green system, and a UV–blue system, among other possibilities (Ventura *et al.*, 2001). It is unclear whether all these systems are present in other reptiles or in birds. As noted above, the blue–yellow opponent system is apparently present in most mammals and may have been present in stem amniotes. However, the anatomical substrate of the red–green pathway of turtles is likely nonhomologous to that found in some primates. As noted above, birds and reptiles possess a retinotopically organized retinogeniculodorsal pallial pathway comparable (likely homologous) to the retinothalamo-V1 of mammals, suggesting that the avian and reptilian dorsal pallium may be involved in color vision processing. However, only a few aspects of color vision (if any) may be processed in the dorsal pallium of birds, and it appears that color vision in birds and possibly reptiles is mainly (if not only) processed by other brain areas and pathways, such as the tectothalamo (rotundal)-DVR pathway (Güntürkün, 1991; Chaves *et al.*, 1993; Wang *et al.*, 1993; Chaves and Hodos, 1997, 1998).

All of these data together indicate that, although the visual area of the reptilian dorsal cortex, avian hyperpallium, and mammalian V1 are involved in some similar basic aspects of visual perception, many complex functions shown by the visual hyperpallium of some birds and by V1 of highly visual mammals, such as depth perception (associated to binocularity) and subjective contour discrimination, among others, likely evolved independently. Consistent with this, the anatomical substrate for the binocularity is different in birds and mammals (Casini *et al.*, 1992; Medina and Reiner, 2000). Further, the role of V1 in color processing and the anatomical pathways related to it may have evolved only in mammals. Regarding motion, the dorsal pallial visual area of reptiles (at least turtles), birds, and mammals appears involved in its processing, and this may have characterized the dorsal pallial visual area of stem amniotes. All these data suggest that the retinogeniculodorsal pallial pathway found in birds and reptiles is mainly comparable to part of the magnocellular retinogeniculocortical pathway of mammals, but not to the parvocellular pathway (conveying mainly chromatic information of the red–green system) nor possibly the koniocellular pathway (conveying mainly chromatic information of the blue–yellow system).

In reptiles and many birds, the retinotectothalamo (rotundal)-DVR pathway is more developed than the retinogeniculodorsal pallial pathway, and appears to play an important role in some aspects of visual processing, such as motion, color, and pattern discrimination (perhaps important for knowing both what the stimulus is and where it is). This general pattern may have characterized stem amniotes. It appears that early mammals were nocturnal animals, which may explain why many extant mammals have dichromatic vision (instead of the tetrachromatic vision that characterizes many birds and reptiles). Perhaps this was accompanied by a regression in visual perception abilities and their anatomical substrate, and an improvement of other sensory systems, such as the somatosensory and the auditory systems. The evolution of new mammalian species living in diurnal niches was likely accompanied by the great development of the retinothalamodorsal pallial pathway, and by the development of more visual neocortical areas (Husband and Shimizu, 2001). An increase in size and complexity of the retinothalamodorsal pallial pathway also occurred in birds, but this was particularly important in some frontal-eyed birds (such as the owl). Did this involve the development of higher-order visual areas in the dorsal pallium of owls? As noted above, the visual hyperpallium of birds is involved in highly complex visual functions comparable to those carried out by higher-order

visual areas of the mammalian neocortex. However, physiological studies have not analyzed the existence of multiple visual areas in the hyperpallium of owls. A recent study has shown the existence of at least two somatosensory representations in the frontal hyperpallium of owls (Manger *et al.*, 2002), and it is likely that more than one visual representation exists in the large hyperpallium of owls.

Finally, regarding the question of whether mammals, birds, and reptiles see the same, it is clear that not all mammals have the same degree of depth, color, and/or form perception, and this is also true in birds. Regarding color vision, although many diurnal reptiles and birds appear to have tetrachromatic vision and most mammals have dichromatic vision, there are examples of color-blind or trichromatic animals within mammals. Further, a few mammals (such as mouse and rat) and many birds and reptiles detect UV light, whereas most mammals (including humans) do not. Thus, the question of whether mammals, birds, and reptiles see the same is nonsense since visual perception differs among mammals, among birds, and possibly among reptiles. Nevertheless, some basic aspects of visual perception appear to be similar between many amniotes. Of particular interest is the fact that some complex visual functions related to form and depth perception appear to be similar between frontal-eyed birds (such as owls) and some highly visual mammals such as cats and some primates. As noted above, the anatomical substrate for the complex visual processing by the dorsal pallium found in these animals likely evolved independently. Further, in birds and reptiles, many aspects of visual perception (including color perception) appear to be processed in the DVR (ventrolateral pallium), rather than the dorsal pallium.

2.07.5.2 Somatosensory Area: Somatotopy, Signal Types, Perception, and Multiple Maps

In mammals, S1 contains a somatotopically organized map of the whole body (contralateral side) (Tracey, 2004). The information received by S1 via the ventrobasal thalamic complex includes tactile (touch, pressure), vibration, and proprioceptive (postural) signals, as well as pain and temperature. The somatosensory information reaching the frontal hyperpallium in birds by way of DIVA is also somatotopically organized, and includes at least tactile (light touch and pressure signals) and vibration information, mostly from the contralateral body surface (Wild, 1987; Funke, 1989a). Based on the external cuneate (which receives proprioceptive information from extraocular and wing muscles; Wild, 1985; Hayman *et al.*, 1995) and spinal inputs to DIVA (Schneider and Necker, 1989; Wild, 1989), it is likely that the frontal hyperpallium also receives proprioceptive, pain, and temperature signals. However, in contrast to mammals, mainly the body (including the neck) appears to be represented in the frontal hyperpallium in several avian species (Wild, 1987, 1997), although some studies have also reported representation of the beak (Korzeniewska, 1987; discussed in Wild, 1989). In birds, it appears that the head somatosensory information is mostly represented in another pallial area, called nucleus basalis, located in the DVR (Berkhoudt *et al.*, 1981; Dubbeldam *et al.*, 1981; Wild *et al.*, 1997). The somatosensory information reaches this DVR nucleus by way of a direct, somatotopically organized projection from the principal sensory trigeminal nucleus (Dubbeldam *et al.*, 1981; Wild and Zeigler, 1996; Wild *et al.*, 2001). Further, in some birds, such as the budgerigar, the nucleus basalis of the DVR includes not only head but also body representation, and this appears to be more detailed than that in the hyperpallium (Wild *et al.*, 1997). Thus, it appears that birds possess two different systems for pallial somatosensory representation, which show different degrees of development depending on the species. As noted above, only the hyperpallial representation appears comparable to S1 of mammals. The frontal dorsal cortex of reptiles also appears to receive somatosensory information of the body (in lizards, turtles, and possibly crocodiles) and, at least in some lizards, also the head (Desfilis *et al.*, 1998). More studies are needed to know whether this pattern is common in other reptiles. It is unclear whether the somatosensory information reaching the frontal dorsal cortex in reptiles is or is not topographically organized. Although it seems likely that the primary somatosensory area observed in the dorsal pallium of extant birds, reptiles, and mammals evolved from a homologous area present in their common ancestor (stem amniotes), the scarcity of data in reptiles does not allow any suggestion on the specific features of this primitive area. In any case, this area was likely very small, and likely lacked many of the attributes (in terms of anatomical organization, connections, and functional complexity) found in S1 of mammals and in the frontal hyperpallium of birds. As noted above, the cytoarchitectural organization and intrinsic columnar circuitry shown by the neocortex and hyperpallium evolved independently. Since in birds there is a small overlap of the primary visual and somatosensory areas in the hyperpallium (Deng and Wang, 1992), it is possible that a partial

ovelap of sensory areas characterized the dorsal pallium of stem amniotes (Figure 3).

Of interest, the neocortex of extant mammals contains multiple somatosensory representations, many of which (including S1, a secondary somatosensory area or S2, and the parietal ventral area) appeared to be already present in the origin of mammals (Krubitzer, 1995; Kaas, 2004). This provides an idea of the importance and high quality of somatosensory perception in these animals, and this great development may be related to the fact that ancestral mammals were nocturnal animals, primarily relying on senses other than vision. Further, somatosensory representation is even more complex in some mammals, such as primates, in which S1 contains four subdivisions (areas 3a, 3b, 1, and 2), each one showing a complete body representation (Tracey, 2004). In other mammals, including rodents, S1 has a single body representation, possibly comparable to area 3b of primates (Northcutt and Kaas, 1995). In birds having a large hyperpallium (such as the owl), two separate somatosensory representations of the claw have been observed, each showing a detailed somatotopic organization (Manger *et al.*, 2002). Thus, it appears that at least some birds have a more complex somatosensory representation in the hyperpallium, which may mean that they have a more elaborated analysis of this information and a more sophisticated somatosensory perception. Since the somatosensory area of the dorsal cortex of reptiles is apparently very small, it seems unlikely that multiple somatosensory representations were present in the dorsal pallium of stem amniotes. This means that the additional somatosensory hyperpallial area found in owls likely evolved independently and cannot be compared to any of the multiple S1 areas found in primates, to S2, nor to other somatosensory areas of mammalian neocortex (Manger *et al.*, 2002). Another interesting aspect of somatosensory representation in the neocortex of mammals is its activity-dependent plasticity, which is important for behavior modification and adaptation as a result of sensory experience (Kaas, 1995; Tracey, 2004). It appears that plasticity also characterizes the somatosensory hyperpallial area of owls (Manger *et al.*, 2002).

Regarding the question of whether mammals, birds, and reptiles feel the same, based on the number of pallial representations and variety of somatosensory receptors found in mammals (Kaas, 2004; Tracey, 2004), it appears that in general mammals have a much better somatosensory perception than reptiles and most birds. But again, it appears that somatosensory perception differs among mammals, as well as among birds and maybe among reptiles. One of the reasons is that the number of somatosensory representations and higher-order areas varies between species (Kaas, 2004). Another reason may be the existence of differences in peripheral receptors (in terms of quality, quantity, and/or location). For example, the complex receptor type found in owl claws (Manger *et al.*, 2002) may not be present in the claws of other birds, or may be present at a low number/area ratio. Further, different parts of the body and head have a different representation (in terms of relative size) in the neocortex/dorsal pallium in different species, which depends on their specific behavior. For example, the S1 of humans has a very large (or relatively large) representation of digits (which is related to the great tactile discrimination and exploratory and manipulatory use of our fingers), whereas in S1 of mouse and rat, the digits are not so well represented but the area related to the whiskers (barrel field area) is relatively large (which relates to the great importance of vibrissae in exploratory behavior and texture discrimination in rodents; reviewed by Waite, 2004). This rule also appears to be true for somatosensory areas in pallial regions other than the dorsal pallium. An example of this is found in the nucleus basalis of the budgerigar, which shows a larger size and more extensive representation of areas such as the beak, highly used by these animals (Wild *et al.*, 1997). Similarly, the claw of barn owl, used for perching and grasping prey and containing an elaborated tactile sensory receptor, likely has a larger representation in the frontal hyperpallium of this animal (including two areas, as noted above; Manger *et al.*, 2002) than that of the pigeon or the canary.

2.07.6 Conclusions

The neocortex contains specific sensory, associative, and motor areas that allow mammals to obtain a detailed map of the world and to adapt their behavior to it. Available data suggest that at least two such areas, the primary visual area and the primary somatosensory area, are also present in the dorsal pallium of birds and reptiles, and likely evolved from similar areas found in stem amniotes. However, these dorsal pallial areas present in the common ancestor likely had a very simple cytoarchitecture (possibly including a rudimentary three-layered structure plus at least two mediolateral subdivisions), and possessed fewer cell types and connections than those found in the mammalian neocortex and avian hyperpallium. For example, the complex six-layered organization of neocortex and the four mediolateral subdivisions of hyperpallium evolved independently in mammals or

birds. Further, the columnar functional organization of neocortex and the columnar-like organization of hyperpallium also evolved independently. In addition, these primitive areas of stem amniotes were likely involved in few aspects of visual or somatosensory perception. The role of the visual area in complex aspects of form and pattern discrimination or in depth perception (associated to binocularity) likely evolved independently in mammals and some birds, and its role in color perception (and the anatomical substrate related to it) apparently evolved only in the mammalian radiation. Finally, available data suggest that the dorsal pallium of stem amniotes may have lacked a true somatomotor area, and this evolved independently in birds and mammals (see A History of Ideas in Evolutionary Neuroscience, Phylogenetic Character Reconstruction, Field Homologies, Evolution of the Nervous System in Reptiles, Visual Cortex of Turtles, The Evolution of Vertebrate Eyes, The Evolution of Ultraviolet Vision in Vertebrates, What Fossils Tell Us about the Evolution of the Neocortex, The Origin of Neocortex: Lessons from Comparative Embryology, Reconstructing the Organization of Neocortex of the First Mammals and Subsequent Modifications, The Evolution of Motor Cortex and Motor Systems, The Dual Elaboration Hypothesis of the Evolution of the Dorsal Thalamus).

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