CHAPTER

8

The Brains of Reptiles and Birds

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Abbreviations

AA Arcopallium anterior
Ac Nucleus accumbens
AD Arcopallium dorsale
ADVR Anterior dorsal ventricular ridge
AFP Anterior forebrain pathway
AI Arcopallium intermedium
AIvm Arcopallium intermedium pars ventromedialis
AM Arcopallium mediale
AOB Accessory olfactory bulb
APH Area parahippocampalis
AV Arcopallium ventrale
AVT Area ventralis tegmentalis
Bas Nucleus basorostralis palii
BO Bulbus olfactorius
BSTL Bed nucleus of the stria terminalis, lateral part
CDL Area corticoidea dorsolateralis
CG Nucleus cuneatus and gracilis
CM Caudomedial mesopallium
CPi Cortex piriformis
CPP Cortex prepiriformis
CTB Crossed tectobulbar pathway
D Nucleus of Darkschewitsch
DA Tractus dorsoarcopallialis
DCN Dorsal column nuclei
DIP Nucleus dorsointermedius posterior thalami
DLP Nucleus dorsolateralis posterior thalami
DLM Nucleus dorsolateralis medialis thalami
DM Dorsal medial nucleus of the midbrain
DVR Dorsal ventricular ridge
Ed Entopallium dorsale
Ee Entopallium externum
Ei Entopallium internum
EION Ectopic isthmooptic neurons
Ep Entopallial belt
Ev Entopallium ventrale
Field L1
Field L2
Field L2a
Field L3
GCt Substantia grisea centralis
GLd N. geniculatus lateralis pars dorsalis
GP Globus pallidus
HA Hyperpallium apicale
HD Hyperpallium densocellulare
HI Hyperpallium intercalatum
HL Hyperpallium laterale
HOM Tractus occipitomesencephalicus pars hypothalami
Hp Hippocampus
Hp-DM Dorsomedial nucleus of the hippocampus
Hp-VM Ventromedial nucleus of hippocampus
HVC Letter-based name
Hypoth Hypothalamus
IC Inferior colliculus
ICo Nucleus intercollicularis
IHA Nucleus interstitialis hyperpallii apicalis
INP Nucleus intrapeduncularis INP
Imc Nucleus isthmi pars magnocellularis
INL Inner nuclear layer
IPL Inner plexiform layer
ION N. isthmoopticus
Ipc N. isthmi pars parvocellularis
IS N. of interstitialis Cajal
ITP Ipsilateral tectopontine–tectoreticular pathway
L2/3, L4, L5 Cortical layer 2/3, 4, 5
LFS Lamina frontalis superior
LL Nucleus lemniscus laminaris
LMAN Lateral magnocellular nucleus of anterior nidopallium
LoC Locus coeruleus
MC Mesopallium caudale
MD Mesopallium dorsale
MFV Mesopallium frontoventrale
MLD Nucleus mesencephalicus lateralis pars dorsalis
MM Mesopallium mediale
MOB Main olfactory bulb
MSt Medial striatum
MVex Mesopallium ventrale externum
MVL Mesopallium ventrolaterale
NA N. angularis
NCL Nidopallium caudolaterale
NCM Nidopallium caudomediale
NCVl Nidopallium caudoventrale pars lateralis
NDB N. diagonalis Broca
NFL Nidopallium frontolaterale
NFT Nidopallium frontotrigeminale
NFM Nidopallium frontomediale
NI Nidopallium intermedium
NIf Nucleus interface
NIMl Nidopallium intermedium mediale pars lateralis
NL N. laminaris

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NM N. magnocellularis
NMm Nidopallium mediale pars medialis
NIL Nidopallium intermedium laterale
NSTL Nucleus of the stria terminalis
nXIIts Tracheosyringeal part of the nucleus hypoglossus
OS Nucleus olivaris superior
Ov Nucleus ovoidalis
Ov shell Shell of the nucleus ovoidalis
PMI Nucleus paramedianus internus thalami
PoA Nucleus posterioris amygdalopallii
PPC Nucleus principalis precommissuralis
Preopt Preoptic area
R Rhombencephalic tegmental field
RA Robust nucleus of the arcopallium
Re Nucleus reuniens
SNpc Substantia nigra pars parvocellularis
SL Septum laterale
Slu Nucleus isthmi pars semilunaris
SM Septum mediale
SMP Posterior song motor pathway
SPO Nucleus semilunaris parovoidalis
SQ Spinal quotient
SRt Nucleus subrotundus
StL Striatum laterale
StM Striatum mediale
TnA N. taeniae of the amygdala
TO Tectum opticum
TTD Nucleus of the tractus descendens nervi trigemini
TuO Tuberculum olfactorium
Uva Nucleus uvaeformis
VNO Vomeronasal organ
VP Ventral pallidum

Nothing in neuroscience makes sense, except in the light of behavior.

8.1 The Phylogeny of Reptiles and Birds

About 340 million years ago, a group of vertebrates developed the ability to reproduce on land. This evolutionary breakthrough became possible through major changes in the structure of the egg that evolved a fibrous shell membrane (the amnion) that permits sufficient gas exchange but still protects the embryo from drying out. At the same time, the adult forms of these animals started to have keratin-based dry skin with which they protected themselves against the absence of moisture in most areas of land. These changes granted them the ability to move away from coastal areas, even for reproduction. This group of animals would later be called reptile-like amphibians or reptiliomorphs, and we are their descendants.

Slowly, reptiliomorphs became more and more adapted to life on land and spread across the vast territories of our planet's continents. By 312 million years ago, in the late Carboniferous geological period, these changes had finally resulted in the emergence of the first true amniotes, defined as a group of animals characterized by the possession of an egg with sophisticated extra-embryonic membranes (Benton and Donoghue, 2006).

The word amnion in classic Greek described a dish in which the blood of sacrificed animals was caught. In Latin it means "membrane around a fetus"—a meaning that resonates better with the critical morphological feature of the amniote egg. Amniotes are a monophyletic group that consists of mammals, reptiles, and birds. Classically they were subdivided on the basis of the number of openings ("apses") on the sides of their skulls. In turtles these openings are missing, which is why they are called "anapsids"—a condition that was often understood as a signature of basal amniotes. Other amniote groups have one ("synapsids") or two ("diapsids") openings on each side (ten Donkelaar, 1998). Since synapsids have one opening more than anapsids, they were thought to represent the first group that diverged from the ancestral line. They constituted the protomammals and later became today's modern mammals. Their single opening is on the ventral part of each side of their skulls. Subsequently, a group of animals developed a second pair of openings at a more dorsal skull position. These animals are called diapsids and are constituted by crocodilians, birds, tuataras, lizards, and snakes.

This kind of evolutionary scenario frames mammals (synapsids) between turtles (anapsids) on the one

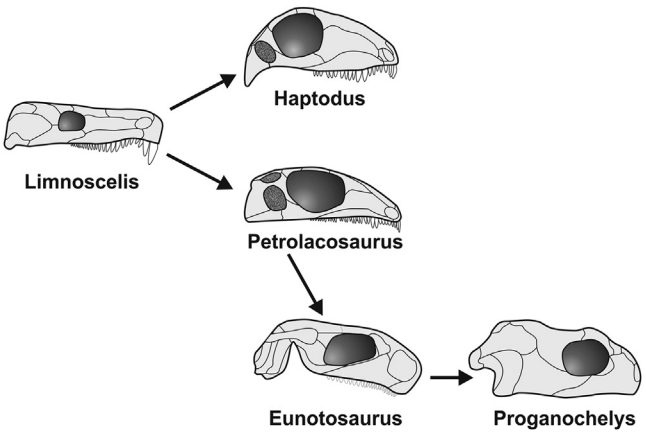

FIGURE 8.1 Generalized phylogeny of amniote skulls. *Arrows* do not imply biological descent but represent transformations in the fenestrae of skulls. *Limnoscelis* is a reptile-like amphibian from the early Permian that retained the anapsid condition of the amniote stem. *Haptodus* is a protomammal from the Carboniferous/Permian transition that shows the synapsid condition with lower temporal fenestrae (*gray/white* speckled area). *Petrolacosaurus* is a reptile from Carbon with a classic diapsid skull. *Eunotosaurus* represents a transitional form in turtle evolution from the late middle Permian with lower temporal fenestrae that are open ventrally and thus look like a prominent invagination. In the juvenile form an upper temporal fenestra is also present. *Proganochelys* is an uncontroversial stem turtle from the late Triassic that shows the classic anapsid condition. Based on the condition in *Eunotosaurus*, the anapsid state of turtles is not a basal but a derived condition. *Modified from Carroll, R.L., 1988. Vertebrate Paleontology and Evolution. W.H. Freeman, New York; Bever, G.S., Lyson, T.R., Field, D.J., Bhullar, B.A.S., 2015. Evolutionary origin of the turtle skull. Nature 525, 239–242.*

hand and diapsid reptiles on the other (ten Donkelaar, 1998). This view on the phylogenetic positioning of turtles seriously eroded in the beginning of the 2000s. Three novel hypotheses emerged. The first hypothesis saw turtles as the extant sister group to crocodiles and birds (Hugall et al., 2007); the second assumed that turtles are the sister group of the lizard–tuatara clade (Lyson et al., 2010), while the third hypothesis placed turtles inside diapsids (Shaffer et al., 2013). Major breakthroughs in gene sequence data (Wang et al., 2013), miRNA analyses (Field et al., 2014), and morphological discoveries (Bever et al., 2015) have largely clarified this issue. Careful analyses on *Eunotosaurus africanus*, a member of an extinct genus of close relatives of turtles from the Middle Permian, have shown that today's anapsid turtles are in fact previous diapsids that became anapsids secondarily (Bever et al., 2015). Thus, turtles started phylogenetically with two openings on each side of the skull and then lost them, giving the appearance of them as being a basal clade (Fig. 8.1).

These and further discoveries now enable a much more concise view on the phylogeny of reptiles and birds. These two groups comprise the sauropsids. In fact, as descendants from dinosaurs, birds could be called "flying reptiles" (Striedter, 2005). However, based on a cladistics analysis of shared derived traits, reptiles are not a monophyletic evolutionary group since it is impossible to define a single common ancestor that includes all reptiles but excludes all nonreptiles such as birds (Fig. 8.2). Aligators and crocodiles, for example, are actually more closely related to birds than to other reptilian lineages (Shine, 2013). Thus, it makes sense to combine sauropsids in one chapter when talking about their brains. Together, these two classes of vertebrates represent more than 18 000 species that live in all major ecosystems of our planet. If we aim to understand the deeper structure of our own brain, we have to study both mammalian and sauropsid brains. Only then can we identify the phylogenetic past and the variations and constancies among amniote brains of which we inherited the primate version.

8.2 Reptilian and Avian Brains in Numbers

8.2.1 Brain Size and Cognition: A Difficult Relation

It is often claimed that brain size is a predictor of an animal's cognitive abilities. This idea can be traced back to Aristotle, who wrote in his text peri zôôn moriôn

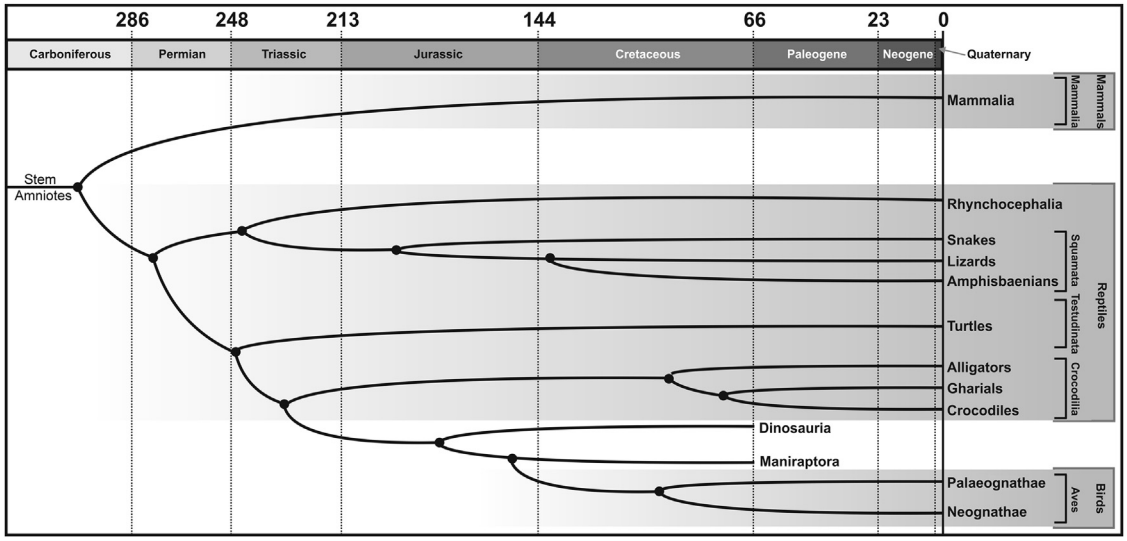

FIGURE 8.2 Genealogical tree of amniotes. The phylogeny shows the amniote radiation along with the time points of the last common ancestors for a given clade. Numbers across the top depict the time before present in millions of years. Geological eras are also shown along the top. Dinosaurs and Maniraptora are shown as extinct relatives of modern birds. *Based on information from Evans, S.E., 2003. At the feet of the dinosaurs: the early history and radiation of lizards. Biol. Rev. 78, 513–551; Green, R.E., Braun, E.L., Armstrong, J., Earl, D., Nguyen, N., Hickey, G., Vandewege, M.W., St John, J.A., Capella-Gutiérrez, S., Castoe, T.A., Kern, C., Fujita, M.K., Opazo, J.C., Jurka, J., Kojima, K.K., Caballero, J., Hubley, R.M., Smit, A.F., Platt, R.N., Lavoie, C.A., Ramakodi, M.P., Finger Jr. J.W., Suh, A., Isberg, S.R., Miles, L., Chong, A.Y., Jaratlerdsiri, W., Gongora, J., Moran, C., Iriarte, A., McCormack, J., Burgess, S.C., Edwards, S.V., Lyons, E., Williams, C., Breen, M., Howard, J.T., Gresham, C.R., Peterson, D.G., Schmitz, J., Pollock, D.D., Haussler, D., Triplett, E.W., Zhang, G., Irie, N., Jarvis, E.D., Brochu, C.A., Schmidt, C.J., McCarthy, F.M., Faircloth, B.C., Hoffmann, F.G., Glenn, T.C., Gabaldón, T., Paten, B., Ray, D.A., 2014. Three crocodilian genomes reveal ancestral patterns of evolution among archosaurs. Science 346, 1254449; Xu, X., Zhou, Z., Dudley, R., Mackem, S., Chuong, C.M., Erickson, G.M., Varricchio, D.J., 2014. An integrative approach to understand bird origins. Science 346, 1253293; Brusatte, S.L., O'Connor, J.K., Jarvis, E.D., 2015. The origin and diversification of birds. Curr. Biol. 25, R888–R898; Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M., Lemmon, A.R., 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature 526, 569–573.*

(Greek, "On the Parts of Animals"): "Of all animals, man has the largest brain in proportion to his size" (Jerison, 1977). Based on this statement and rightfully assuming that humans possess the highest cognitive abilities of all species, one could conclude that high cognitive abilities or "intelligence" is based purely on the size of the brain. What would that mean for reptiles and birds? In comparison to several mammalian species, reptiles and birds have very small brains, in many cases even in relation to their body mass. Crocodilians, which represent the largest living reptiles (with Nile and saltwater crocodiles sometimes weighing more than 700 kg; Northcutt, 2012), possess brains that weigh only 10–20 g (Northcutt, 2012; Ngwenya et al., 2013, 2016). Paleognathous birds, such as emus and ostriches, with body weights from 60 kg (in emus) to 200 kg (in ostriches) have the largest avian brains, weighing 20–27 g (Peng et al., 2010; Olkowicz et al., 2016). Compared to mammals with approximately the same body mass (eg, horses, sheep, or chimpanzees), these reptilian and avian brain sizes are relatively small, both in terms of absolute size and in relation to body size (from here on called relative brain size) (Roth and Dicke, 2005; Northcutt, 2012). Taking humans into account, with their average body mass of 70 kg and an average brain size of 1450 g (Roth and Dicke, 2005; Herculano-Houzel, 2012), the prospects for higher cognitive abilities in reptiles and birds would seem rather dire, if one assumes that those abilities depend solely on brain size.

Fortunately, the assumption that absolute or relative brain sizes have a causal relationship to complex cognition in vertebrates has come under fire. Sperm Whales and Killer Whales possess the highest absolute brain size in the vertebrate class, reaching up to 9000 g (Roth and Dicke, 2005; Ridgway and Hanson, 2014). But do we have reasons to assume that they surpass our human-typical cognitive abilities? Also for relative brain size, it is not the primate order that ranks on top, but the small, mole-like mammals of the order Eulipotyphla that have the highest brain/body ratios. The European pygmy shrew with a body weight of 4.7 g and a brain weight of 0.1 g has a brain/body ratio of 0.021, which is higher than the one found in humans (Jerison, 1977).

In line with these findings and despite their small brains, reptiles and especially some bird species possess highly complex cognitive abilities. Recent studies demonstrated that some reptilian species are capable of social learning (Wilkinson et al., 2010), problem solving behavior, and rapid associative and reversal learning (Leal and Powell, 2012). It has also been argued that modern reptiles might even have evolved a form of consciousness, possibly independently of consciousness in recent bird and mammalian species (Northcutt, 2012). For birds, a plethora of studies have shown that species from the corvid and parrot orders show cognitive abilities that are on par with those of nonhuman primates when it comes to tool and metatool use (Hunt, 1996; Taylor et al., 2007; Bird and Emery, 2009; Auersperg et al., 2011), mirror-self-recognition (Prior et al., 2008), causal reasoning (Emery and Clayton, 2004; Taylor et al., 2009; Mikolasch et al., 2011; Pepperberg et al., 2013), future planning (Clayton et al., 2003), and imagination (Emery and Clayton, 2001, 2004; for a review, see Güntürkün and Bugnyar, 2016).

Due to the discrepancies between absolute and relative brain mass measures on one side and cognitive abilities on the other, diverse measures were developed to come up with a satisfying correlation between body size, brain size, and cognitive abilities in vertebrates. Proposed measures were, for example, the encephalization quotient (Jerison and Barlow, 1985), brain region relative to total brain size (Krebs et al., 1989), or the use of brain surface instead of brain volume (Sultan, 2002). However, all these attempts were criticized as not being able to explain convincingly the distribution of higher cognitive abilities in vertebrates (Healy and Rowe, 2007).

A recent and more promising approach suggests that neuron numbers per telencephalic volume could explain cognitive skills of a species (Herculano-Houzel, 2011a). Along that line, a scaling analysis of how many neurons are gained as brain volume increases in a given order may also shed light on the cognitive abilities of corvid and parrot species (Olkowicz et al., 2016). This approach will be discussed more thoroughly in the next section.

8.2.2 Brain Sizes in Reptilian and Avian Species

Although brain size alone may not predict cognitive capabilities of a given vertebrate species or taxon, analysis of this rather simple measure allows valuable insights in the evolution of the nervous system. In general, brain mass correlates with body mass over all vertebrates (Martin, 1981), leading to the assumption that bigger bodies need bigger brains (but see below and Ngwenya et al., 2016). However, there are striking differences in relative brain size between vertebrate classes. On average, relative brain sizes are 10 times smaller in reptiles and ray-finned fishes than in birds and mammals, with the latter having rather similar relative brain sizes (Martin, 1981; van Dongen, 1998; Northcutt, 2012). This seems also to be the case for extinct dinosaur species which had, based on endocranial volume measures, relative brain sizes similar to those of modern crocodiles (Jerison, 1973; van Dongen, 1998). In recent reptiles, brain sizes range from 0.03 g in tiny lizard species, over 0.5 g in the tuatara and 1.1 g in varanid species, to 20 g in crocodiles (van Dongen, 1998; Northcutt, 2012). Crocodiles also represent a noteworthy special

case in terms of brain/body ratios. The body of Nile crocodiles (*Crocodylus niloticus*) shows a continuous growth over their lifetime. Ngwenya et al. analyzed brain size of Nile crocodiles at different ages with body weights ranging from 90 g to 90 kg. They found that this 10-fold increase in body weight was only accompanied by a 1.8-fold increase in brain size (Ngwenya et al., 2013). Thus, at least within this species, the correlation between body and brain size is not as fixed as had been assumed for vertebrate species in general. Snake species represent another interesting case when comparing relative brain sizes in reptiles, since they seem to have smaller brain/body ratios than the other analyzed reptilian clades and lie below the reptilian regression line (Northcutt, 2012). The reason for this is unclear but could be due to the elongation of their body, since elongated vertebrates tend to have on average smaller brains (van Dongen, 1998).

In contrast to reptiles, for which relatively few studies on brain allometry have been published, extensive research has been done on brain scaling in birds. Since it would be a futile attempt to cover all these findings within the boundaries of this book chapter, we will only cover a small fraction of the data here. However, the interested reader can find more information in Martin, 1981; Armstrong and Bergeron, 1985; Rehkämper et al., 1991a; Iwaniuk et al., 2004 and the Chapter 1.18, Functional Correlates of Brain and Brain Region Sizes in Nonmammalian Vertebrates by Andrew Iwaniuk within this volume.

In birds, brain sizes range from 0.22 g in hummingbirds, over 2 g in pigeons, to 14 g in Keas and ravens and 27 g in ostriches (Rehkämper et al., 1991b; Peng et al., 2010; Olkowicz et al., 2016). Especially noteworthy is that parrots and Passeriformes (perching birds) generally have higher relative brain sizes than *Palaeognathae* (eg, ostriches; but see Corfield et al., 2008; on kiwis) and *Galloanserae* species (eg, chicken, Rehkämper et al., 1991a; Olkowicz et al., 2016). Thus, birds of the Neoaves clade, which evolved approximately 90 million years ago (Prum et al., 2015), tend to have bigger relative brain sizes than their more basal relatives. These basal avians may represent a recent example for the transition from smaller brained reptiles to bigger brained modern bird species. Domestication of birds (eg, in chicken, ducks, and geese) leads to an opposite trend with a strong reduction in relative brain size in comparison to their wild relatives based on an increase in body size but also in a reduction in absolute brain volume which can reach up to a loss of up to 20% (Ebinger and Löhmer, 1987; Rehkämper et al., 1991a). Examples for brain to body ratios are depicted in Fig. 8.3 for reptiles (adapted from van Dongen, 1998; Northcutt, 2012). Note, however, that the data are restricted to few reptilian species with rather big brains of which many are lizards. This likely reflects a publication bias.

There is a rich literature on comparisons of individual species of vertebrate classes with respect to relative brain sizes (for review, see van Dongen, 1998; Northcutt, 2012). Although some overlap between classes exists, these analyses mostly suggest that during the transition from reptiles to birds and from reptiles to mammals, brain size increased massively. This increase in brain volume was, however, not uniform for all brain areas. When comparing the size of specific brain area in relation to the size of the whole brain, it is mainly the forebrain that increased dramatically. In frogs (*Rana catesbeiana*), the telencephalon constitutes only 22% of the total brain volume, while in reptiles, telencephalic values range from 29% in snakes (*Nerodia sipedon*) over

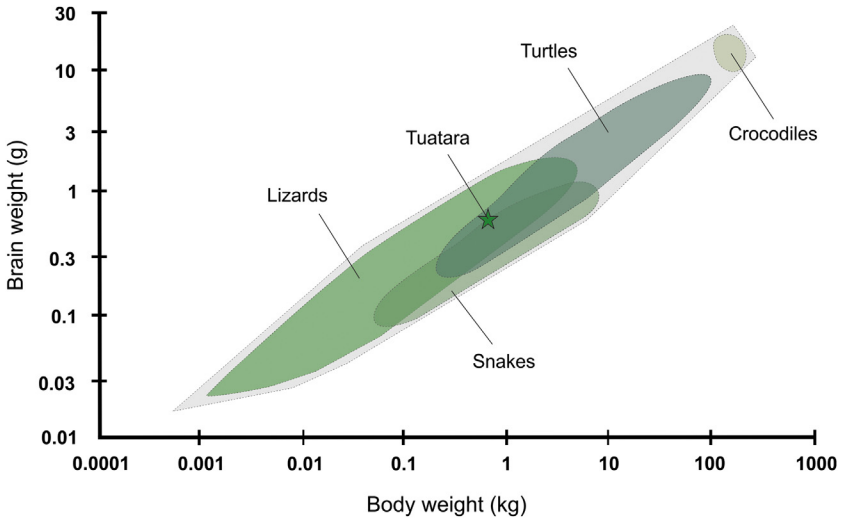

FIGURE 8.3 Brain weight in relation to body weight for the reptilian class. The *solid line* of the convex polygon encloses the data for all reptiles, while the *dotted lines* enclose the different reptilian clades. The tuatara, as the only recent member of the Sphenodontia, is indicated by a *star*. Note the lower brain-body ratios in snakes in comparison to the other reptilian taxa. *Figure modified from Northcutt, R.G., 2012. Variation in reptilian brains and cognition. Brain Behav. Evol. 82, 45–54.*

36% in the tuatara (*Sphenodon punctatus*) and 42% in warans (*Varanus bengalensis*) to 45% in crocodiles (*Caiman crocodilus*, Northcutt, 2012). In birds, the telencephalon constitutes an even bigger portion of the whole brain. The telencephalon takes up 43% of the whole brain in emus (Olkowicz et al., 2016; again, see Corfield et al., 2008 on kiwis, which seem to represent a special case within *Palaeognathae*) and 51% in chicken (Northcutt, 2012). In Neoaves, proportional telencephalon volume is even larger. Among parrots, the telencephalon comprises 68% of the total brain volume in budgerigars, 73% in African Grey parrots, and 77% in Indian ringed parrots (derived from Iwaniuk et al., 2004; see also Olkowicz et al., 2016 and below). Among Passeriformes, the telencephalon constitutes 67% of the entire brain in house sparrows, 68% in Eurasian jays, and 74% in hooded crows (derived from Rehkämper et al., 1991a).

Within the telencephalon, especially the pallium experienced a hypertrophy in both absolute size and in relation to the remaining telencephalon. A recent study showed that in birds, an increase in overall brain size is driven mainly by an increase in pallial volume (Sayol et al., 2016). These results even suggest that relative brain size can be used as a proxy for relative pallium size in comparative studies. In amphibians, the pallium takes only 52% of the total telencephalon volume, increasing to 70% in lizards and 85% in crocodiles and basal birds (Northcutt, 2012). Among Neoaves, the pallium of parrot species comprises 78% of the telencephalic volume in budgerigars, 86% in African Grey parrots, and 83% in Indian ringed parrots (data derived from Iwaniuk et al., 2004; Iwaniuk and Hurd, 2005). Within Passeriformes, the pallium constitutes 90% of the telencephalon in house sparrows, 86% in Eurasian jays, and 88% in hooded crows (data derived from Rehkämper et al., 1991a). This increase in proportional pallial volume probably enabled specific bird species to develop cognitive abilities that are beyond the capabilities of reptilians and bird species with smaller pallial structures. Indeed, several studies have shown that the sizes of certain pallial subdivisions, such as the meso- and nidopallium, correlate with some specific domains of higher cognition, such as innovation rate or tool use (Timmermanns et al., 2000; Lefebvre et al., 2002, 2013; Mehlhorn et al., 2010; Lefebvre et al., 2013).

8.2.3 Neuron Numbers and Scaling Rules

As mentioned above, pure allometric measures of brain sizes alone seem to be insufficient to explain cognitive capabilities of a species (Healy and Rowe, 2007). In response to this problem, a new approach was designed which is based on the number of neurons in a given brain or brain structure. The idea is quite simple: since neurons represent the smallest processing unit of a brain, a higher number of these units would increase information processing capacity (Roth and Dicke, 2005). Originally, it was assumed that neuron numbers scale with a common function of brain size across species (Haug, 1987), but studies during the last decade in mammals have shown that this is utterly wrong. These studies showed a great variety in the cellular composition of different mammalian brains (Herculano-Houzel et al., 2005, 2011b; Gabi et al., 2010; Sarko et al., 2009; Neves et al., 2014). For example, the cerebral cortex of the African elephant is twice as large as that of humans, but has only a third of the number of neurons (Herculano-Houzel et al., 2014a). These studies also revealed that brains of different mammalian orders gain neurons with different scaling rules as brain size increases (Herculano-Houzel et al., 2011b). Within the mammalian class, primates have the most favorable scaling rule of about 1:1 (Herculano-Houzel et al., 2007; Herculano-Houzel, 2009). Thus, their neurons numbers increase directly proportional to the increase of brain weight.

Data on neuron numbers in birds and especially reptiles are unfortunately scarce at the moment. In reptiles, only one study in Nile crocodiles has been conducted so far (Ngwenya et al., 2016). It found that the brains of these animals contain 80.5 million neurons. This corresponds to an overall neuron density of ~25 000 neurons/mg, but these neurons are not evenly distributed over the brain. As in mammals, a disproportionate number of neurons are allocated to the cerebellum (~40%), which shows a neuron density of ~168 000 neurons/mg. Roughly 27% of all neurons in Nile crocodiles are situated in the telencephalon which is similar to the percentage of neurons found in the mammalian cortex (Herculano-Houzel, 2009). Neuron density in the telencephalon (18 500 neurons/mg) is much lower than in the cerebellum, but on average still higher than in the brain stem and spinal cord. The remaining neurons are found in the brain stem and the olfactory bulb (which was analyzed separately from the telencephalon), with the biggest contributor being the mesencephalon, likely because of the cell dense optic tectum. Although the general distribution of neurons in the crocodile brain resembles that found in mammals, neuron density in the whole brain is much lower than in mammals (Herculano-Houzel, 2009). A further interesting finding of Ngwenya et al. (2016) was that these neuron numbers only change marginally during the growth of the animal. As mentioned above, Nile crocodiles grow constantly over their lifetime. However, while there was a 1000-fold increase in body size, neuron numbers increased by only 2.8-fold in the brain and 5.3-fold in the spinal cord. It was suggested that bigger bodies do not necessarily require more neurons to maintain

functionality but rather bigger neurons and axons to cope with the increasing distance to the innervation targets (Ngwenya et al., 2016).

Due to a recent publication, more data on neuron numbers are now available for birds. Olkowicz et al. (2016) analyzed the cellular composition of the brains in 28 avian species and found astonishing results. Although the brains of birds are rather small in comparison to mammals, neuron numbers are twice as high as in a primate with the same brain size and up to four times higher in comparison to rodents with a same sized brain (see Fig. 8.4A). Neuron numbers ranged from 136 million in zebra finches, over 310 million in pigeons and 697 million in monk parakeets, to 2.2 billion in ravens and 3.1 billion in macaws (see Fig. 8.4B). With the exception of the analyzed basal birds (chicken: 78 000 neurons/mg, emu; 61 000 neurons/mg), neuron densities are therefore higher in birds than in the analyzed mammalian species (eg, 275 000 neurons/mg in zebra finches, 148 000 neurons/mg in pigeons, 203 000 neurons/mg in monk parakeets, 154 000 neurons/mg in ravens, and 151 000 neurons/mg in macaws).

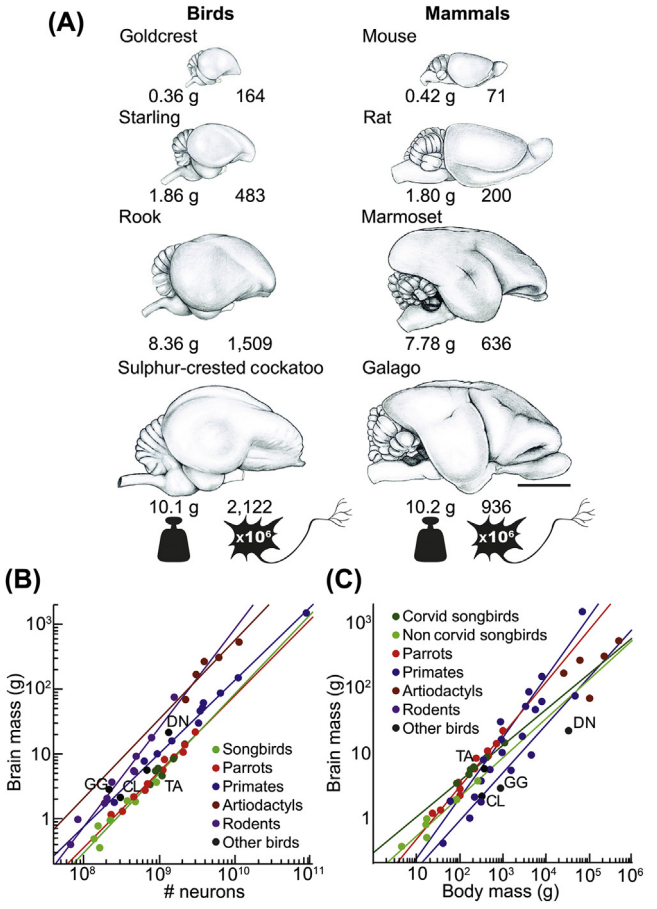

FIGURE 8.4 Neuron numbers and brain weights of selected avian species. (A) Comparison of absolute neuron numbers in four avian species with neuron numbers of four mammalian species with similarly large brains. Neuron numbers in birds are more than twice as high, even when the comparison is done with primate species (eg, rook vs marmoset or sulphur-crested cockatoo vs galago). In (B) neuron numbers in relation to brain mass is depicted for selected avian species in comparison to data from three mammalian orders. (C) shows brain mass in relation to body mass for the same species. *CL, Columba livia* (pigeon); *DN, Dromaius novaehollandiae* (emu); *GG, Gallus gallus* (chicken); *TA, Tyto alba* (barn owl). *Figure adapted from Olkowicz, S., Kocourek, M., Lučan, R.K., Porteš, M., Fitch, W.T., Herculano-Houzel, S., Němec, P., June 13, 2016. Birds have primate-like numbers of neurons in the forebrain. Proc. Natl. Acad. Sci. U.S.A. pii:201517131. [Epub], with permission of the authors.*

Although the overall distribution of brain mass across the major brain components is similar between mammals and birds (eg, the telencephalon occupies 72% of the brain in songbirds and 74% in primates), the distribution of neurons is vastly different. While in mammals the majority of neurons are found in the cerebellum (Herculano-Houzel, 2009), 38–62% of all neurons in songbirds and 53–78% of all neurons in parrot species are found in the telencephalon. If the striatum is excluded, to allow a better comparison to the mammalian cortex, 33–55% (songbirds) and 46–61% (parrots) of all neurons in the brain are found in the pallium. In the human brain, only 19% of all neurons are found in the cortex, although it takes up 82% of the brain mass. Thus, even though parrots and songbirds are already outnumbering mammalian species with comparable brain sizes regarding neuron numbers in the whole brain, this advantage gets even further pronounced when only comparing pallial neurons. For example, the cortex (dorsal pallium) of a macaque monkey weights 69.83 g and contains 1.7 billion neurons, whereas the pallium of the blue and yellow macaw weighs one-fifth of that but holds a whopping 1.9 billion neurons.

When comparing neuron numbers between avian species, it becomes apparent that neuron numbers in songbirds and parrots scale similarly with brain weight (see Fig. 8.4B). Thus, a parrot brain contains roughly the same number of neurons as the brain of a Passeriformes species with the same brain weight. Also, in both orders, brain mass gain is faster than neuron gain, leading to lower neuron densities in bigger brained species. In contrast, pigeons, chickens, and emus have relatively low neuronal densities. Given their proportionally lower brain and telencephalic size (see above), their telencephalon contains far fewer neurons than that of a similar sized parrot or songbird brain. As Olkowicz et al. (2016) noted, a chicken brain is 50 times bigger than that of a great tit, but both contain approximately the same number of neurons. Unfortunately, scaling rules for orders outside the Passera clade are currently unavailable, since data from the Columbiformes, Galliformes, and Casuariiformes orders come only from single species.

Still, the obtained data on neuron numbers in combination with the allometric data gathered over decades of research deliver some important evidence on how specific bird species were possibly able to develop cognitive

abilities which rival those of primate species (Güntürkün and Bugnyar, 2016), while other bird species could not. (1) Songbirds and parrots possess neuronal scaling rules which endow them with neuronal densities surpassing those of primates. (2) Songbirds and parrots developed a proportionately bigger telencephalon with a proportionately bigger pallium than other bird species. (3) Within songbirds, the corvid species possess the most developed cognitive abilities and also the biggest brains. Combining these points implies that corvid species have an absolutely larger number of neurons in their pallium than other bird species; they also have more pallial neurons than a five times bigger primate brain. Thus the processing capacity of the corvid pallium, based on the absolute neuron numbers, is likely to be higher than it is in other bird species and, for that matter, in many primates.

8.3 The Structures of the Reptilian and the Avian Brain

From an embryological point of view, the nervous system of vertebrates is divided into the spinal cord and the three primary brain vesicles, rhombencephalon, mesencephalon, and prosencephalon (Nieuwenhuys, 1998). In the adult form, the transition between the spinal cord and the rhombencephalon is the area between the first cervical spinal root and the exit of the vagal nerve. Despite this clear cut definition, no sharp morphological boundary is discernable; instead, spinal anatomy slowly transforms into the structural constituents of the rhombencephalon. Further anterior, the rhombencephalon borders with the mesencephalon and the cerebellar commissure, with the exit and decussation of the trochlear nerve serving as boundary landmarks. The rhombencephalon and mesencephalon jointly constitute the brain stem. Rostral to the mesencephalon is the prosencephalon with its diencephalic and more rostrally situated telencephalic components. These and further structures are components of the *bauplan* of the vertebrate brain and as such are obviously present both in reptiles and birds. To review all relevant anatomical details of these structures would be a futile attempt for the present treatise, especially since the three-volume book on the central nervous system of vertebrates serves as landmark publication for such a purpose (Nieuwenhuys et al., 1998). Instead, only those components and systems of brain entities will be presented for which specific and relevant adaptations were discovered in some reptile or bird taxa. They will be presented and discussed, moving from caudal to rostral entities.

8.3.1 The Sauropsid Spinal Cord

8.3.1.1 Reptilian and Avian Spinal Cords: Invariant Organization Despite Variances of Behavior

There are no standardized subdivisions of the reptilian spinal cord that are comparable to those of mammals or birds. In fact, there is no vertebrate class with such divergent spinal organization patterns as reptiles. In limbless forms like snakes, the number of spinal segments varies widely, reaching more than 400 in some species (ten Donkelaar, 1998). Snakes rely exclusively on their axial muscles for locomotion and move by large lateral undulations of the body. This is radically different from limbed amniotes like rats in which limbs are crucial for locomotion while axial muscles play only a secondary role. Despite these important differences, the motor neuron pools of rats and the limbless Florida water snake are astonishingly similar (Fetcho, 1986). Thus, even though the details of the arrangements of muscles differ, and the roles of the muscles in locomotion are likely to be very different, the arrangements of the motor pools in the two animals are located in comparable positions of the motor column. The same kind of observation was reported by Ryan et al. (1998) who labeled the motor neuron pools of seven homologous forelimb muscles in mice (*Mus musculus*) and iguanas (*Iguana iguana*) and discovered a similar topography despite dissimilar locomotion patterns. These data on reptiles and mammals suggest that species-typical differences in the locomotor mechanics are accomplished without any dramatic reorganization of the spinal motor column.

This conclusion is supported when studying birds—a group of animals that have developed flapping flight and thus undertook a major change in the concerted action of frontal limb muscles. Goslow et al. (2000) analyzed the spinal topography of motor neurons that innervate key muscles for flight in the European starling and found a pattern that is highly comparable to that seen in nonavian tetrapods. These data indicate that a massive evolutionary change of motor patterns can occur without a corresponding topological reorganization of the corresponding motor column. The evolutionary changes in motor patterns that accompanied the evolution of birds are probably involved alterations in synaptic input from supraspinal sources, not alterations in the topology of the motor columns. This similarity of the spinal motor pool organization among amniotes is in marked contrast to the spinal organization in anamniotes. The transition from anamniotes to

amniotes goes along with a breakup of the myomeres into discrete muscles and a subdivision of the spinal motor column into discrete, topographically arranged motor pools serving the individual muscles (Fetcho, 1987).

Dinosaurs were not only the largest reptiles but also the largest animals that ever roamed the land. Their spinal organization as revealed from fossil data provides some clues about their movement patterns. A simple predictor of limb size and extent of limb use is the spinal quotient (SQ), which expresses the enlargement of the spinal limb levels relative to interlimb levels. SQ is lowest in snakes and high in dinosaurs with manipulative forearms (Giffin, 1990). In some dinosaurs, the volume of the lumbar vertebral canal even exceeds the volume of their endocranial cavity (Romer, 1966). Some of this inflation could result from the glycogen body in the lumbosacral region that is sometimes wrongly associated with a "sacral brain"—a myth according to which dinosaurs had a second brain in the spinal cord that compensated for their tiny endocranial nervous system. Studies in birds may help to clarify the true function of the lumbosacral expansion, as outlined in the next section.

8.3.1.2 *The Mystery and the Sobering Reality of the Sacral Brain*

We associate birds with the ability to fly. But they can also walk and this kind of locomotion produces a special challenge: the legs of birds are inserted caudal to the center of gravity, and thus their bipedal walking pattern needs special control of balance. This is even more important when perching on swaying branches. Strikingly, as many farmers know, beheaded chickens can walk and fly for a short while keeping balance. Consequently, scientists had suggested since long that birds should have an extralabyrinthine sense of equilibrium in their abdomen (Mittelstaedt, 1964; Delius and Vollrath, 1973). Subsequent studies suggested that the peculiar glycogen body in the lumbosacral spinal cord might represent such a sense organ (Grimm et al., 1997; Fig. 8.5). The discovery of canals in the lumbosacral region which look similar to the semicircular canals in the inner ear led to the suggestion that some of the specializations in the lumbosacral region may function as a sense organ of equilibrium which is involved in the control of hind limbs (Necker, 1999).

In the avian lumbosacral cord the local vertebrae are fused and tightly connected to the pelvic girdle (Baumel and Witmer, 1993). In addition, the vertebral canal is enlarged considerably. Importantly, this enlargement is not due to an increase of neuronal tissue, but due to the presence of a glycogen body that is embedded in a dorsal groove of the spinal cord (Fig. 8.6). The cord itself is firmly attached by ligaments

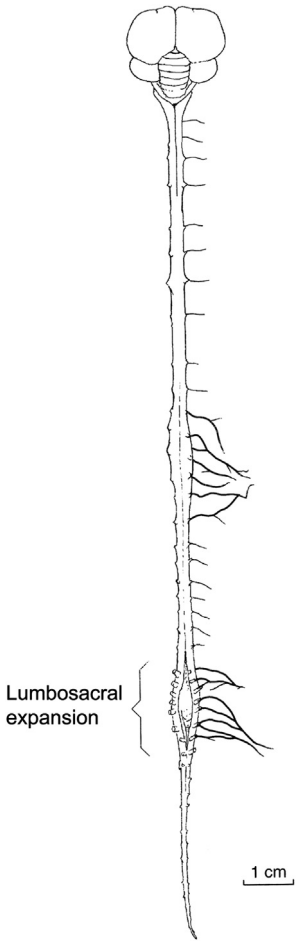

FIGURE 8.5 The spinal cord of the pigeon with the lumbosacral enlargement. *Reproduced from Dubbeldam, J.L., 1998. Birds. In: Nieuwenhuys, R., Ten Donkelaar, H.J., Nicholson, C. (Eds.), The Central Nervous System of Vertebrates. Springer, Berlin, pp. 1525–1636, with permission.*

to the vertebra. Necker (1999) discovered semicircular canal-like structures in the lumbosacral cord and proposed that these specializations could channel cerebrospinal fluid during body movements toward a specialized group of neurons (Necker, 1999). These neurons are equipped with mechanoreceptors (Necker, 2002) and are located in an accessory lobe at the ventrolateral end of the ventral horns (Schroeder and Murray, 1987). The activity of these neurons is transmitted to the cerebellum via paragriseal cells which are at the origin of a ventral spinocerebellar pathway (Necker, 2005a,b). Every time the bird takes a turn, the fluid near the lobes move by inertia to the opposite direction of the turn, thereby activating mechanoreceptors of neurons in the accessory lobe (Fig. 8.6A). Roll and pitch movements could thus be detected by an intraspinal sensory system involved in the control of posture and locomotion on the ground. Indeed, behavioral studies showed that these kinds of movements are less balanced during walking in animals where the

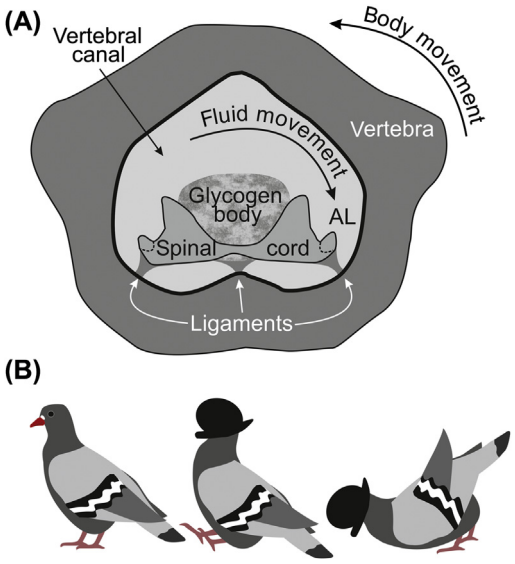

FIGURE 8.6 The lumbosacral spinal equilibrium system in birds. (A) is a section through the lumbosacral spinal cord, showing the glycogen body in the dorsal groove of the spinal cord. The ventrolateral extensions of the ventral horns constitute the accessory lobes (AL) that are able to detect movements of the cerebrospinal fluid. The cerebrospinal fluid moves in inverse direction to body turns, thereby activating mechanoreceptors in AL. (B) depicts the walking posture of pigeons with punctured lumbosacral cavities. When the birds can see, their gait is mostly normal (left); when blinded by a hood, they constantly tip over (middle and right). *Modified from Necker, R., 2006. Specializations in the lumbosacral vertebral canal and spinal cord of birds: evidence of a function as a sense organ which is involved in the control of walking. J. Comp. Physiol. A 192, 439–448.*

lumbosacral cavity was punctured, whereas flight was normal (Necker et al., 2000). Especially when these lesioned animals were blinded with a hood, they constantly tipped over while walking (Fig. 8.6B). Thus, two different sense organs are involved in the control of equilibrium: the vestibular organ during flight and the lumbosacral system during walking (Necker, 2006).

It seems likely that a similar lumbosacral system existed also in dinosaurs. Control of equilibrium in theropoda was probably at least as complex as in birds since they had often even longer necks than birds. This further decreases the usefulness of a cranial vestibular system for maintaining balance while walking. In addition, some theropoda could grow to enormous sizes. Thus, a vestibular-like system that is close to tail and hind legs is conceivably a faster sensory system—even outside the lineage of modern birds. Still, it is not a "second brain."

8.3.2 Mesencephalon

Moving from medial to lateral, the midbrain consists of the central gray, tegmentum, and tectum. The third ventricle is located in the center of the midbrain, but possesses laterally protruding extensions that are called tectal ventricles. In sauropsids, the "tectum acusticum" is located ventral to the tectal ventricle. In reptiles it is usually called torus semicircularis, and in birds it is nucleus mesencephalicus lateralis dorsalis. The tectum opticum has a position dorsal and lateral to the tectal ventricle. Especially in birds the optic tectum is so extraordinarily enlarged, that it bulges out laterally and is sometimes called the visual lobe (Butler and Hodos, 2005; Fig. 8.7).

In reptiles the optic tectum has six primary layers. Tectal lamination is much more complex in birds with at least 15 different tectal layers being easily identifiable. Despite these differences between reptiles and birds, the tectum possesses the same general organization and harbors highly similar input and output systems (Reiner, 1994). The major common

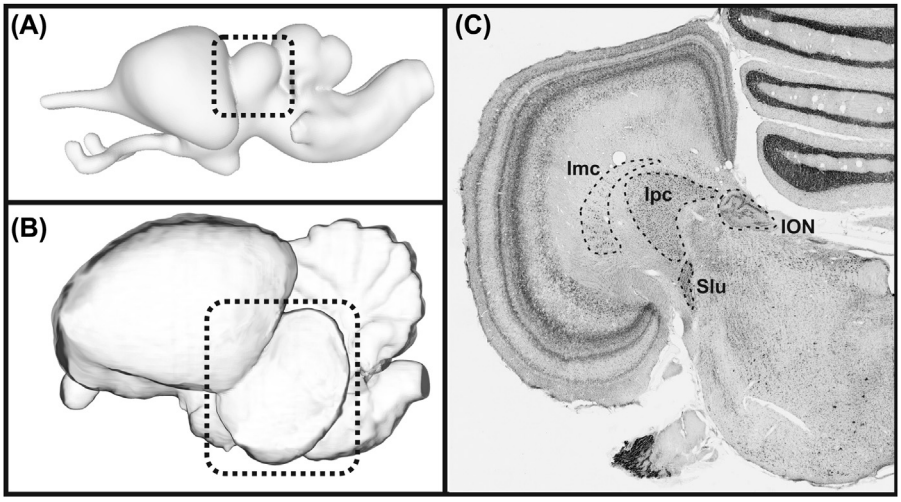

FIGURE 8.7 (A) Brain of a Nile crocodile. (B) Brain of a pigeon. The brains are not to scale, and the optic lobes are framed. (C) Frontal section through the midbrain of a pigeon. Note the highly laminated optic tectum. The isthmic nuclei are outlined. *Imc*, n. isthmi pars magnocellularis; *ION*, n. isthmoopticus; *Ipc*, n. isthmi pars parvocellularis; *SLu*, n. semilunaris. Crocodile brain. *Courtesy of Mehdi Behroozi.*

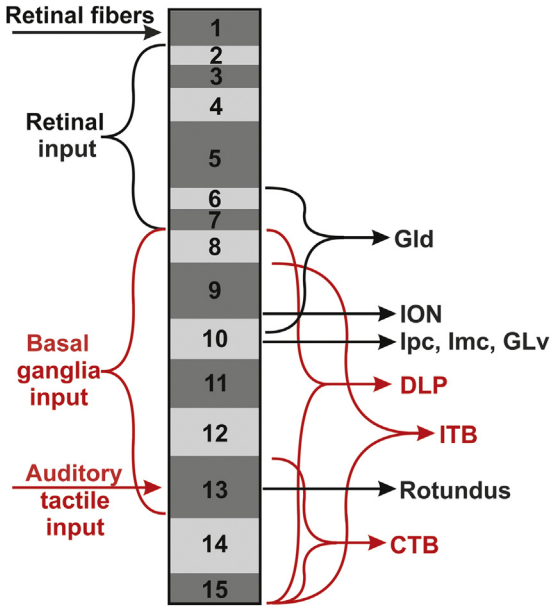

FIGURE 8.8 Major input (left) and output systems (right) of the avian optic tectum. Monomodal visual pathways are shown in *black*; multimodal nonvisual sensory and motor systems are shown in *red*. *CTB*, crossed tectobulbar pathway; *DLP*, n. dorsolateralis posterior thalami (multimodal ascending nucleus); *GLd*, n. geniculatus lateralis pars dorsalis (main ascending visual nucleus of the thalamofugal system); *Imc*, n. isthmi pars magnocellularis; *ION*, n. isthmoopticus; *Ipc*, n. isthmi pars parvocellularis (three isthmic nuclei); *ITP*, ipsilateral tectopontine-tectoreticular pathway. *Modified from Luksch, H., 2003. Cytoarchitecture of the avian optic tectum: neuronal substrate for cellular computation. Rev. Neurosci. 14, 85–106.*

organizational principles are (1) the retinal input from the contralateral eye enters via the most superficial input layer in a topographically organized manner; (2) ascending visual output arises from the intermediate and deeper layers; (3) descending projections to motor areas also arise from intermediate and deeper layers; (4) input from nonvisual sensory pathways terminates mostly in deeper layers (Reiner, 1994; Luksch, 2003; Hellmann et al., 2004; Fig. 8.8). In Section 8.3.2.3, we will take a more detailed look on this pattern when discussing the avian tectum.

8.3.2.1 The Infrared System of Snakes: Seeing the Heat

Being warm-blooded, mammals and birds have a lot of advantages in terms of mobility in the cold, but under certain circumstances, tables are turned: Even in total darkness, their higher body temperature can give their position away. To exploit this information, predators need infrared vision. Two groups of snakes, the Boidae (eg, the Boa constrictor) and the Viperidae (eg, common rattlesnakes and pythons) have evolved infrared vision and can use it to find prey, detect predators, and find warm places to rest.

In rattlesnakes the thermal sensor is a facial pit located on the lateral surface of the head between the external nose cavity and the eye (Fig. 8.9). This pit consists of an open anterior chamber that is closed at the back by a thin membrane that contains sensory receptors. The receptors consist of free nerve endings that are sensitive to radiant heat (Goris and Terashima, 1976; von Düring and Miller, 1979). The pit resembles a pinhole camera for thermal stimuli and, indeed, snakes display directional sensitivity in their thermal responses (Kohl et al., 2012). The thermal receptors can respond to changes as small as 0.001°C in thermal energy (Stanford and Hartline, 1984; Gracheva et al., 2010). The pit organs in rattlesnakes are innervated by fibers of the ophthalmic and the maxillary branches of the trigeminal nerve.

After entering the brain stem, the sensory trigeminal fibers divide into two projection streams. One serves the same purpose as the trigeminal input in all further vertebrates. The second branch, however, conveys thermal information and terminates in the n. descendens lateralis trigemini, which then projects to the n. reticularis caloris of the medulla (Stanford et al., 1981). From there, projections reach the deep layers of the contralateral optic tectum (Kardong and Berkhoudt, 1999). In the tectum, infrared information merges with visual information to create bimodal visual-thermal neurons (Hartline et al., 1978). Some of these neurons respond only to simultaneous bimodal stimulation while others respond to only one modality and are inhibited when simultaneously stimulated by the second modality. These cross-modality interactions could be relevant to disambiguate warm-blooded prey (simultaneous stimulation by visual and infrared input) from cold visual objects that represent nonliving objects (Newman and Hartline, 1981).

A further critical cue for identifying living objects is motion. Behavioral studies show that blindfolded rattlesnakes predominantly respond to moving infrared stimuli (Ebert and Westhoff, 2006). Indeed, slowly moving objects elicit only weak or no responses in tectal units that respond to infrared cues, while increasing object speed increases spike rate (Kaldenbach et al., 2016). This could imply that slow or even stationary objects may not be detected by the infrared system of snakes at all. Indeed, rattlesnakes are ambush predators that wait for prey. Immobile objects are mostly irrelevant as a food resource and do not stimulate the infrared receptors. Thus, the infrared sensory system as represented in the tectum can disambiguate infrared signals from thermal clutter. Rattlesnakes also use their infrared system to seek warm places for thermoregulation (Krochmal and Bakken, 2003). However, when doing so, snakes perform scanning head movements and thus create a

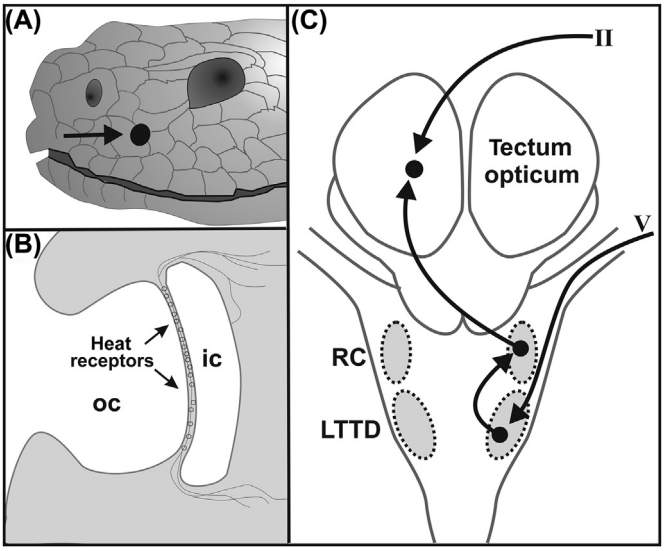

FIGURE 8.9 The infrared system in rattlesnakes. (A) The location of the facial pit containing thermal receptors is indicated by the *arrow*. (B) Cross section of the facial pit, showing the thermal receptors along the membrane suspended between the pit's outer and inner chambers (oc and ic, respectively). Fibers entering the membrane stem from the ophthalmic and maxillary branches of the trigeminal nerve. (C) Schematic dorsal view of the rhombencephalon and mesencephalon. The trigeminal nerve (V) innervates the n. descendens lateralis trigemini (LTTD), which then projects to the n. reticularis caloris of the medulla oblongata (RC). Neurons of the RC project to the optic tectum, where infrared information is merged with incoming visual input from the second cranial nerve (II).

relative movement between warm objects and the receptors (Ebert and Westhoff, 2006).

8.3.2.2 *The Centrifugal Visual System: What the Brain Tells the Eye*

The optic tectum has topographically organized reciprocal connections with the nucleus isthmi, a complex of several cytoarchitectonically distinguishable nuclei at the mesorhombencephalic border (Yan and Wang, 1986; Güntürkün and Remy, 1990; Wang et al., 2006; Faunes et al., 2013; Fig. 8.7). The isthmic complex is present in most vertebrates (eg, Künzle and Schnyder, 1984) but is most highly differentiated in birds (Wang, 2003), in which it comprises nucleus isthmi pars parvocellularis (Ipc), pars magnocellularis (Imc), pars semilunaris (SLu), and nucleus isthmoopticus (ION). All these structures receive ipsilateral tectal input (Güntürkün, 1987). It is the ION that gives rise to a conspicuous centrifugal projection to the contralateral retina that is present in practically all vertebrates, that is but extremely expanded and differentiated in granivorous birds.

Santiago Ramón y Cajal (1889), the founder of Neuroscience, was the first who discovered in birds axons that project from the central nervous system to the retina. A few years later, Adolf Wallenberg (1898) discovered the ION as the midbrain nucleus from which these fibers originate. Cajal (1889) suspected that such a system might modulate the retinal input according to expectations generated in the brain. It was long disputed whether such a system is a specialization of birds or is found also in other vertebrates, possibly including humans. Since these early studies, it has become well established that centrifugal visual fibers exist in all classes of vertebrates. Most likely, such a system has evolved multiple times within the vertebrate lineage, with at least eight distinct subsystems located in very different regions of the neuraxis (Repérant et al., 2006, 2007). And yes, centrifugal visual fibers also exist in humans, although they typically number no more than a few dozen (Repérant and Gallego, 1976). The diversity of centrifugal visual systems in vertebrates probably matches the diversity of their functions. In the following sections, the centrifugal system is outlined for reptiles and birds. The emphasis will be the avian centrifugal system since it is the most advanced retinopetal visual pathway of vertebrates and could serve as a model system on how and what the brain tells the eye.

8.3.2.2.1 The Centrifugal Visual System of Reptiles

After tracer injections into the retina of several turtle species, 10–60 retrogradely labeled neurons have been observed in the area of the isthmic region (Haverkamp and Eldred, 1998; Repérant et al., 2006). These centrifugal fibers make extensive collateral branches before penetrating and synapsing in the retina's inner plexiform layer (IPL) (Weiler, 1985). In lizards the situation is very similar (Repérant et al., 2006), although in some species a second source of centrifugal neurons is found in the ventral thalamus (El Hassni et al., 1997). Snakes possess several hundred centrifugal visual neurons, but their centrifugal neurons are found bilaterally in the basal telencephalon, the lateral preoptic area, and the ventral thalamus (Hoogland and Welker, 1981; Repérant et al., 2006). Crocodiles possess between 4000 and 6000 centrifugal visual neurons, depending on the species (Kruger and Maxwell, 1969; Médina et al., 2004). These neurons are mostly located in the isthmic region but can also be found in other tegmental areas. They may be part of a loop that starts with the retinotectal projection and then proceeds via the isthmic nucleus back to the retina (Ferguson et al., 1978).

8.3.2.2.2 The Centrifugal Visual System of Birds

The centrifugal visual system of birds originates in two different mesencephalic cell groups: the isthmooptic nucleus (ION), a folded bilaminate structure in the dorsolateral midbrain tegmentum, and the nucleus of the ectopic isthmooptic neurons (EION), a loosely scattered array of cells with reticular appearance surrounding the ION (Wolf-Oberhollenzer, 1987; Fig. 8.7). Both

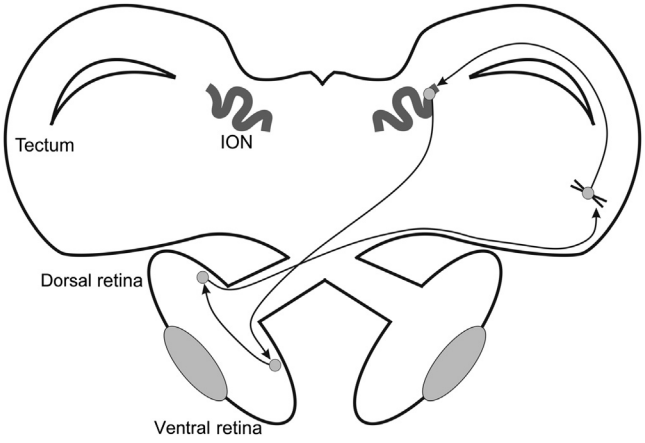

FIGURE 8.10 General organization of the avian centrifugal visual system. Ganglion cells of the dorsal retina (mostly) project to tectal neurons at the border of layer 9/10. These neurons project topographically to ION neurons that then project to association amacrine cells in the ventral retina. Association amacrine cells project to dorsal retina, thereby closing the loop.

structures are part of a closed loop consisting of a projection from the retinal ganglion cells to the contralateral tectum, the efferents of which project to both the ipsilateral ION and the EION, whence back projections lead to the contralateral retina (Güntürkün, 2000). All projections within this system seem to be topographically organized (Li et al., 1998; Fig. 8.10). Weidner et al. (1987) discovered important differences in this system between raptors and ground-feeding birds. In seed or fruit-eating birds, the ION is always large, well differentiated, and laminated. In raptors, the ION is small, poorly differentiated, and reticular in appearance. Thus, the centrifugal system seems to play a specific role in ground-feeding birds that are subject to predation by various animals, including birds of prey. As will be argued later, this condition is possibly relevant to understand the function of the centrifugal system.

In pigeons and chicks, cell bodies of tecto-ION neurons are located at the border of layers 9 and 10 of the tectum, reach up to layer 2 with their dendrites, and can thus pick up direct retinal input (Woodson et al., 1991). This input stems mostly, but not exclusively from the dorsal retina (lower visual field). The tecto-ION neurons project topographically onto the ipsilateral ION. The ION consists of a highly convoluted lamina in which two perikaryal layers are separated by a neuropil in which the dendrites from opposing layers ramify toward the middle of the two layers (Güntürkün, 1987). Afferent axons of tecto-ION neurons pass through this dendritic field and synapse topographically on small dendritic appendages and spines, providing virtually all excitatory synapses in the ION (Cowan, 1970; Angaut and Repérant, 1978). Additionally large numbers of inhibitory synapses on ION dendrites are found which partly originate from a small number of GABAergic neurons within the ION (Miceli et al., 1995). It is likely that these inhibitory neurons are key to ION function since, as pointed out by Uchiyama (Uchiyama et al., 1998; Uchiyama, 1999) the ION network shows a strong winner-take-all competition which possibly allows the selection of the most salient stimulus. Axons from ION cells proceed, together with those from the EION, to the contralateral retina. The number of efferent axons within the optic nerve is supposed to be about 12 000 in the pigeon, of which the ION contributes about 10 000 (Weidner et al., 1987). Since the tecto-ION and the tecto-EION pathway also consist of about 12 000 neurons, a 1:1 ratio of tectal and centrifugal neurons is likely (Woodson et al., 1991). The centrifugal axons terminate near the IPL, bordering the inner nuclear layer (INL) in the horizontal and ventral retina, barely penetrating the red field that serves frontal binocular vision (Lindstrom et al., 2009). They are composed of two distinct types, with divergent degrees of topographic localizations. Fibers from the ION are called "convergent" and give rise to a single restricted type of terminal fiber, which forms a dense pericellular nest covering the perikaryon of a single association amacrine cell (Uchijama and Ito, 1993; Uchiyama et al., 1995; Lindstrom et al., 2010). Association amacrines have long intraretinal axons, are mainly located in the horizontal plus ventral retina, and project dorsally (Catsicas et al., 1987; Uchiyama et al., 2004). Thus, ION fibers receive input from the dorsal retina (lower visual field), project back to the ventral retina (upper visual field), and are then connected via intraretinal association fibers to the dorsal retina (lower visual field). Axons originating from EION are called "divergent" and give rise to several terminal branches, each constituting an extensive and highly branched arbor (Fritzsch et al., 1990; Woodson et al., 1995).

Electrophysiological data are only available for the ION. Most ION cells have their receptive fields in the inferior anterior visual field and are thus related to the upper posterior parts of the retina (Hayes and Holden, 1983; Catsicas et al., 1987; Uchiyama et al., 2004). Miles (1972) and Holden and Powell (1972) demonstrated that a large number of ION units show a preference for moving shadowlike target movements in the anterior visual field and habituate rapidly to repetitive stimulations. This finding suggests a role in the analysis of transient and dynamic features of the visual environment. In a very sophisticated study, Li et al. (1998) demonstrated that retina, tectum, and ION form a closed loop of topographic excitations. In other words, the same ganglion cells in the dorsal retina that provide input to the ION via the tectum receive feedback from those same ION neurons.

Based on these data, several authors tried to establish the functional importance of the ION and EION in

behavioral studies (Rogers and Miles, 1972; Shortess and Klose, 1977; Knipling, 1978; Hahmann and Güntürkün, 1992). Usually, bilateral centrifugal lesions only caused mild or no deficits in visual discrimination experiments. However, Rogers and Miles (1972; but see Hahmann and Güntürkün, 1992) demonstrated profound deficits in the detection of suddenly occurring moving stimuli, suggesting that the centrifugal system may play a role in detecting moving objects under dim light conditions. Recently, Wilson and Lindstrom (2011) formulated a new functional hypothesis that rests on the assumption that the ION system can only be understood if the strange intraretinal projection from the ventral to the dorsal retina is taken into account. They propose that the ION acts as an early warning system that allows the presence of a moving shadow on the ground to trigger a rapid and parallel search of the regions of sky most likely to contain an aerial predator. This dual search could be the function of the intraretinal projection that links the ventral retina (looking into the sky) to the dorsal retina (scanning shadows on the ground). Once an association between shadow and object is established, the system could link these two stimuli via positive feedback and continue to track shadow and object together. This hypothesis could explain why the centrifugal system is so well developed in granivorous and ground-feeding birds. Bobwhite quail has an annual probability of mortality of 63% from aerial predators (Cox et al., 2004). Thus, any extremely fast neural system that tracks approaching birds of prey and their shadows in parallel could save lives.

8.3.2.3 *Projections of the Optic Tectum: From Retinotopy to Functionotopy*

Retinal projections to the tectum are retinotopically organized in most vertebrates (Remy and Güntürkün, 1991; Reiner et al., 1996; Dunlop et al., 2007). Retinal fibers and their tectal target cells are then segregated in different intratectal parallel streams, which project to diverse areas along the neuraxis (Reiner, 1994; Güntürkün, 2000; Marín et al., 2003; see also Section 8.2.2). In pigeons, about 90% of retinal ganglion cells project to the

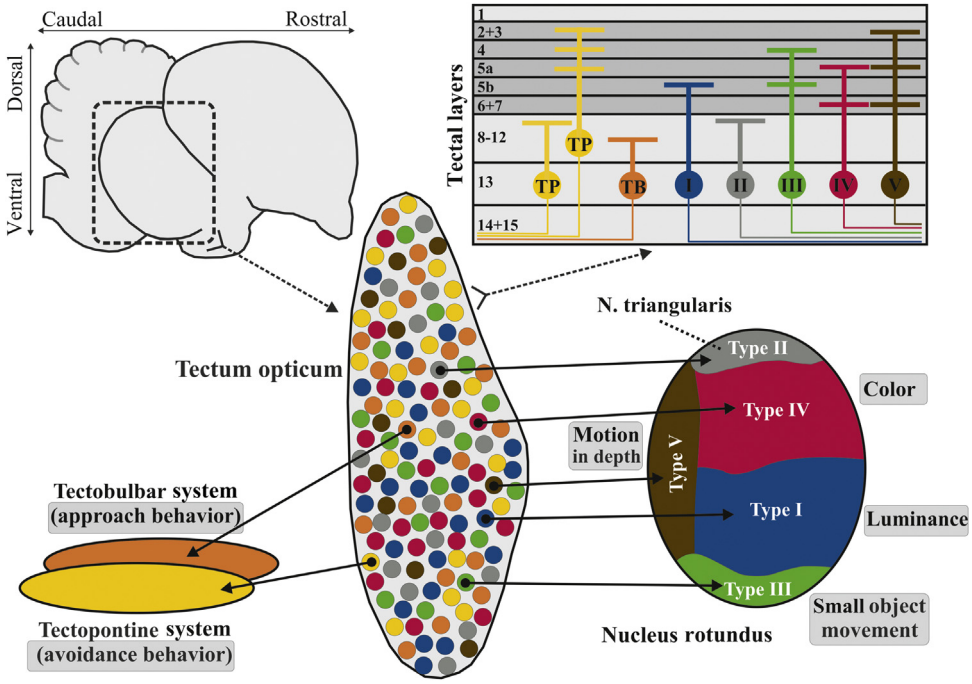

FIGURE 8.11 Schematic outline of the tectal mosaic hypothesis of Hellmann et al. (2014). It is proposed that multiple cell types with diverse visual inputs at about the same location of the tectal map projection onto diverse thalamic and rhombencephalic areas. These projections are both retinotopically organized and functionally specific. A pigeon brain with a highlighted optic tectum is represented at upper left. An "unfolded" tectum with a two-dimensional map of the tectal surface is shown in the center. Small circles in different colors represent cells on the tectal map that have descending projections within the tectopontine (TP, in *yellow*) and the tectobulbar systems (TB, in *orange*) or ascending ones within the tectorotundal projection (cell types I–V). Each of these cell types projects to an area with the same color code. It is yet unclear if retinotopy is preserved within such projections. At upper right, a schematic cross section of the optic tectum is shown, with retinorecipient layers 2–7 depicted in *dark gray*. Tectal neurons with descending projections to the brain stem and ascending projections to the rotundus are shown with their main dendritic bifurcations in the superficial tectal strata allowing a cell type–specific organization of visual input. The complete arrangement explains how functionally specific tectal projections arise from a retinotopically arranged organization. *Modified from Hellmann, B., Güntürkün, O., Manns, M., 2004. The tectal mosaic: organization of the descending tectal projections in comparison to the ascending tectofugal pathway in the pigeon. J. Comp. Neurol. 472, 395–410.*

tectum (Remy and Güntürkün, 1991). The outer retinorecipient layers of the tectum are characterized by a precise retinotopic representation with narrowly tuned receptive fields of less than 1 degree (Jassik-Gerschenfeld and Hardy, 1984; Luksch, 2003). However, receptive field widths gradually increase toward layer 13 (Jassik-Gerschenfeld and Guichard, 1972; Frost and DiFranco, 1976), which contains neurons with very large dendritic trees that have characteristic "bottlebrush endings" in specific upper tectal laminae (Luksch et al., 1998). These layer 13 cells are looming sensitive (Frost and Nakayama, 1983; Wu et al., 2005) and project to the diencephalic nucleus rotundus (Rt) (Luksch et al., 1998; Hellmann and Güntürkün, 2001; Marín et al., 2003; Hu et al., 2003). Retinotopic place coding seems to be absent within Rt, since each point of the tectum is connected to nearly the entire rotundus and its dorsal cap, the nucleus triangularis (Benowitz and Karten, 1976; Ngo et al., 1994; Hellmann and Güntürkün, 1999). Instead of retinotopy, a new function-based segregation seems to take place in the thalamus, as electrophysiological data could demonstrate separate rotundal domains in which mainly color, luminance, motion, or looming are processed (Wang and Frost, 1992; Wang et al., 1993). Behavioral data support this view since restricted rotundal lesions affect performance in only specific aspects of visual analysis (Laverghetta and Shimizu, 1999). In contrast to the tectorotundal connection, the rotundoentopallial projection (Benowitz and Karten, 1976; Fredes et al., 2010) and subsequent secondary and tertiary connections within the forebrain are again organized topographically (Benowitz and Karten, 1976; Husband and Shimizu, 1999), suggesting rotundal functional segregation to be carried onto the forebrain.

How is a retinotopically organized tectal system transformed into a functionotopically organized rotundal system (Karten et al., 1997)? According to Hellmann and Güntürkün (2001) and Marín et al. (2003), the transformation is achieved by five morphologically distinct types of tectal layer 13 cells (types I–V) that together establish the tectorotundal system. Each population is characterized by (1) its location on the tectal map, (2) the depth and size of its soma within layer 13, (3) its specific input from tectal laminae 3–11, and (4) its projection onto separate subregions of the rotundal system (Marín et al., 2003; Fig. 8.11).

1. Since the tectum is retinotopically organized, lamina 13 cells sample retinal input mainly from a specific retinotopic area (Gonzalez-Cabrera et al., 2016). However, there are different tectorotundal neuron types and they are differently distributed across the tectal map. For example, type I neurons are four times more common in ventral tectum (representing the frontal, binocular field of view) (Remy and Güntürkün, 1991; Hellmann and Güntürkün, 1999). In contrast, type V neurons are twice as common in the dorsal tectum and transmit information from the dorsal field of view (Hellmann and Güntürkün, 2001).
2. Each tectorotundal neuron type is characterized by a unique combination of soma size and position within the depth of layer 13 (Karten et al., 1997; Hellmann and Güntürkün, 2001; Marín et al., 2003). Thus, different projectional tectofugal streams have different morphologies and positions within the tectum.
3. Retinal ganglion cells can be subdivided according to morphological and physiological criteria into different classes, each of which subserves a different function (Ehrlich et al., 1987; Karten et al., 1990; Mpodozis et al., 1995). These different ganglion cell types terminate in a spatially segregated manner within tectal layers 2–7 (Yamagata and Sanes, 1995; Karten et al., 1997; Repérant and Angaut, 1977; Gonzalez-Cabrera et al., 2016). Therefore, retinorecipient laminae differ in their visual input. Since the tectorotundal neurons sample retinal input from different tectal laminae, they probably process different aspects of vision.
4. Tectorotundal cell type I projects to ventral and central rotundus and probably code for changes in luminance (Wang et al., 1993; Hellmann and Güntürkün, 2001). Fibers of type III neurons terminate in the most ventral rotundus, where the cells strongly respond to moving occlusion edges and very small moving objects, with either excitatory or inhibitory responses (Wang et al., 1993). Axonal projections of type IV neurons ramify within a relatively small area of the dorsal rotundus, which was shown to be highly sensitive for color and/or luminance variations of visual stimuli (Wang et al., 1993). Electrophysiological work revealed the caudal rotundus (termination of type V neurons) to be specialized to three dimensional motion analyses (Wang et al., 1993) with some of these neurons especially computing time to collision for looming stimuli (Wang and Frost, 1992; Sun and Frost, 1998).

Hellmann et al. (2004) showed that the mosaiclike architecture of the ascending tectal projections applies also to the descending fibers that target motor and premotor centers in the mes- and rhombencephalon. As for Rt, the descending motor systems are functionally segregated in pigeons: The crossed tectobulbar tract is involved in approach and orientation toward desired objects, whereas the ipsilateral tectopontine pathway guides movements away from aversive stimuli (Ingle, 1983; Ellard and Goodale, 1988; Dean et al., 1988). The ascending tectal projections to Rt originate mainly

from the ventral tectum, representing the frontal inferior field of view. In contrast, the descending tectal projections overrepresent the upper field of view (Hellmann et al., 2004). Thus, the principle of a retinotopic-to-functionotopic transformation seems to apply also for the descending tectal projections. Interestingly, some looming-sensitive layer 13 neurons that project to the Rt also have descending projections to the pons (Wu et al., 2005). Therefore, looming information can directly initiate avoidance behaviors in an animal facing an impending collision. These data support the concept that the tectum is arranged as a mosaic of multiple cell types with diverse input functions at the same location on the tectal map. By a transformation from retinotopic to functionotopic coding, tectal projections onto diverse areas become both retinotopically organized and functionally specific (Fig. 8.11). It is not yet known if retinotopy is preserved in the different functionotopic zones.

8.3.3 Telencephalon

Most reptilian brains only partly fill the cranial cavity. As a result, the shape of reptilian skulls is only slightly influenced by the form and structure of the brain (Starck, 1979). This is especially true for marine turtles, tuataras, and most lizards (ten Donkelaar, 1998). Brains that are much smaller than their skull are also found in many theropod dinosaurs (Witmer and Ridgely, 2009). Exceptions among reptiles are the snakes, in which the space between the brain and the cranial wall is quite narrow. In birds, the brain completely fills the cranial cavity and shapes the skull—a condition already observed in the extinct ancestors of modern birds (Balanoff et al., 2013).

The sauropsid telencephalon consists of paired evaginated hemispheres. Astonishingly, this seemingly inconspicuous brain structure has ignited many heated discussions among comparative neuroanatomists and was subject to major conceptual changes. Based on classic anatomical studies at the turn of the 19th to the 20th century, several leading scholars, including Ludwig Edinger in Germany and Cornelius Ubbo Ariëns Kappers in the Netherlands, decided that the telencephalon of amniotes had gradually expanded by the successive addition of new parts. Comparative neuroanatomists of this time thus followed the ancient concept of *scala naturae* according to which organisms are organized in stepwise increases of complexity and "souls." This conception, as translated into vertebrate comparative neuroanatomy, assumed that the telencephalon of ancestral jawless vertebrates was the starting point and as such related entirely to olfaction. With the advent of jawed fishes, the globus pallidus was added, followed by the addition of the striatum in amphibians. Reptiles added a three-layered cortex while birds dramatically expanded the volume of their telencephalon by increasing the size of their striatum. With the emergence of mammals, a novel brain entity started to dominate the outer rind of the telencephalon: a six-layered cortex. Since the cortex was seen as the newest addition to the vertebrate telencephalon, it was called "neocortex." As outlined below, the neocortex derives from just one of the four pallial components of the telencephalon. Ventral to these four pallial components are the subpallial basal ganglia. Taken together, reptiles were seen as having developed at least a primitive forerunner of the cortex, while birds had nothing comparable but expanded their basal ganglia instead (Edinger et al., 1903; Ariëns-Kappers et al., 1936).

It was the Swedish neuroanatomist and embryologist Bengt Källén (1962) who departed from this view and proposed that parts of the avian telencephalon are of pallial nature. The strongest shift in general understanding, however, came with the seminal work of the American neuroanatomist Harvey Karten (2015) in pigeons that started in the 1960s and sparked new insights into the organization of the avian forebrain. These and many further studies finally resulted in the Duke Avian Nomenclature Forum of 2002 (Reiner et al., 2004a; Jarvis et al., 2005). Based on an overwhelming body of data from genetics, neurochemistry, anatomy, and physiology, a consortium of neuroscientists at the conference concluded that most of the large dorsal territory of the avian cerebrum is pallial. This pallial territory was seen as homologous to regions of the mammalian brain that includes neocortex, hippocampus, claustrum, and pallial amygdala. The smaller ventral part of the avian cerebrum was identified as subpallial and highly comparable with its mammalian counterpart in all developmental and anatomical details. Thus, bird brains are not dominated by striatum. But how much of the avian pallium is homologous to neocortex? These and further questions are hotly debated (Puelles et al., 2000, 2016; Pfenning et al., 2014; Montiel et al., 2016) and will be discussed by Luis Puelles in this book. We will leave homology questions mostly out of our scope but will concentrate instead on the functional anatomy of the sauropsid forebrain. We begin by briefly charting the overall territory of the telencephalon.

The telencephalon of tetrapods can be divided into a pallial and a subpallial sector. The pallial entity has been subdivided into medial, dorsal, lateral, and ventral components based on cellular migratory patterns, cytoarchitecture, gene expression, and connectivity (Holmgren, 1922; Puelles et al., 2000; Nomura et al., 2008; Montiel et al., 2016). The lateral pallium comprises the olfactory cortex, the medial pallium the hippocampal complex, and the dorsal pallium the neocortex. In reptiles, some parts of the ventral pallium possibly constitute the

dorsal ventricular ridge (DVR) along with diverse nuclei of the amygdaloid complex (Northcutt, 2013). Birds do not have a three-layered cortex as seen in reptiles. However, they have a component called "wulst" that is typical for the avian class and is located in the dorsal or dorsofrontal part of the pallium (Striedter, 2005).

When taking a histological frontal section, the division between a pallial and a subpallial component is easily discernable using markers for acetylcholinesterase or dopamine (Reiner et al., 1998). In all vertebrates the basal ganglia play a prominent role in the control of movement patterns. However, neuropsychological studies increasingly make it likely that the selection of future actions is possibly a much more important role (Graybiel and Grafton, 2015). It is likely that this is true not only for humans but also for all sauropsids.

8.3.3.1 *The Sauropsid Basal Ganglia*

Before reviewing the organization of the avian and reptilian basal ganglia, some more general comments on the functions of these ancient structures of the vertebrate brain seem to be in order. From the earliest days of neurological analyses on, the basal ganglia were seen as a central entity of action generation (Ferrier, 1876). Indeed, neurological disorders that affect the basal ganglia always also affect behavioral output in terms of either a lack of movement (hypokinesia) or a production of undesired movements (hyperkinesia) (Mink, 2003). These observations substantiated the view that the role of the basal ganglia is to produce and control movements. In the last decades this view eroded and gave way to the opinion that the main function of the basal ganglia is to select contextually appropriate actions among many alternatives (Yin, 2016). Indeed, this idea fits with the network structure of corticostriatopallidal-thalamic loops in which the bandwidth of cortically selected behavioral options is successively reduced until only one planned action survives the competition and is then successively produced (Humphries and Prescott, 2010). Parallel to this conceptual shift, the learning of habits and skills at the level of the striatum moved into the focus of scientific attention (Graybiel and Grafton, 2015). While learning such actions requires reward in the beginning, they become increasingly automaticed and are produced without any further reinforcement. Learning psychologists were the first to point out that new behavioral sequences are sensitive to omission of reward in the beginning of acquisition, but become increasingly independent of reward later on, when they are established as habits (Dickinson, 1985). In humans, fMRI studies demonstrate that those subjects who reduce activity patterns in the prefrontal cortex (PFC) sooner are the ones who learn sequential actions faster (Bassett et al., 2015). Concomitantly, striatal units seem to "bracket" an action, thus firing in the beginning and the end of a habit, as if encapsulating a behavioral unit (Barnes et al., 2005). It is conceivable that the basal ganglia help to store and subsequently select sequences of habit units, depending on the ensuing situation (Graybiel and Grafton, 2015). This short prologema to the basal ganglia will be important toward the end of this section when discussing how the basal ganglia changed during the phylogeny of vertebrates. Now let us turn to the anatomy of the subpallium in general and the basal ganglia in particular.

The subpallium can be subdivided anatomically and developmentally into five entities: (1) the dorsal somatomotor basal ganglia; (2) the ventral viscerolimbic basal ganglia; (3) the extended amygdala; (4) the basal telencephalic cholinergic and noncholinergic corticopetal systems; (5) the septum and septum-associated neuroendocrine systems. In the following we will review the basal ganglia only. Unfortunately, our current knowledge of this system in birds far outweighs what we know from reptiles. A succinct overview of the avian subpallium is provided by Kuenzel et al. (2011).

The sauropsid striatum is considered to be homologous to the mammalian caudate/putamen (Reiner et al., 2004a; Kuenzel et al., 2011). It consists of lateral and medial somatomotor as well as viscerolimbic components. The principal wiring pattern of these components is similar but differs with respect to some connections so that some striatal territories receive more somatic or more viscerolimbic input than others. The vast majority of striatal neurons are GABAergic projection neurons with spiny dendrites. About half of these neurons show a colocalization of GABA with enkephalin (ENK). The other half has a colocalization of substance P (SP) with dynorphin. Both cell types project outside of the striatum. The striatum is rich with cholinergic fibers due to the abundance of local projections of cholinergic interneurons. A further characteristic of the striatum is the dense dopaminergic innervation from the tegmental dopaminergic cell groups.

The striatum shows a winner-take-all dynamic, resulting in a narrowing of many diverse activity fields into a few, or even into just one (Ponzi, 2008). Activity patterns mostly arise from glutamatergic pallial input (Csillag et al., 1997). Indeed, most of the pallium projects onto the striatum. This is true for reptilian cortex/wulst, DVR and for amygdala and hippocampus (Reiner et al., 1998). Descending fibers from the pallium can arise as axon collaterals from cells that project mainly to other pallial areas or from neurons with long projections to subtelencephalic targets (Veenman et al., 1995). The bottom line is that most pallial activity patterns reach the striatum and are then subject to competition with other striatal activity foci elicited by other pallial inputs. A second source of striatal afferents are the dorsomedial group of thalamic nuclei (Reiner, 2002). If the pallial

input is blocked or entirely abolished, the tested mammals and birds are able to move and feed and even learn operant tasks, albeit after quite some recovery time (Bjursten et al., 1976; Cerutti and Ferrari, 1995). This is an important insight: the thalamic input into the basal ganglia is sufficient to generate largely normal behavior in amniotes.

The third major input to the striatum consists of the dopaminergic axons from several clusters of tegmental dopamine neurons: the area ventralis tegmentalis (AVT), the substantia nigra pars compacta (SNc), and the retrorubral field. While the AVT input dominates in the ventral striatum, the main source of dopaminergic input to the avian striatum arises from the SNc (Durstewitz et al., 1999b). Autoradiographic D1 receptor binding studies demonstrated that D1 receptors are most abundant in the bird striatum (Schnabel et al., 1997; Stewart et al., 1996). Consequently, the striatal parts of the basal ganglia also exhibit very dense labeling for DARPP-32 (Durstewitz et al., 1998; Schnabel et al., 1997), which is a dopamine- and cAMP-regulated phosphoprotein that acts as a "third messenger" in the D1 receptor stimulation cascade (Berger et al., 1990; Hemmings et al., 1995). The density of D2 receptors in the striatum seems also to be high in birds (Dietl and Palacios, 1988; Stewart et al., 1996).

SP- and ENK-positive GABAergic striatal neurons project densely to the pallidum, which contains sparsely packed large GABAergic neurons; dopaminergic inputs are less abundant. This pattern is seen in both birds and reptiles (Anderson and Reiner, 1990; Brauth, 1984). The second major descending projection from the striatum leads to the GABAergic neurons of the substantia nigra pars reticulata (SNr). Again, both in reptiles and birds, these seem to arise mainly from the SP+ GABAergic neurons. A smaller ENK+ input to dopaminergic tegmental neurons also exists, especially in snakes (Reiner et al., 1998).

Both the pallidum and the SNr project to a small nucleus in the avian dorsal thalamus – the ventrointermediate thalamic area (VIA) (Medina et al., 1997). VIA projects to the most rostral part of the wulst, which serves motor functions and is the source of the avian "corticospinal tract" (see Section 8.3.3.3.1). Through this pathway the striatum is able to modulate the wulst. The organization of this circuit strongly suggests a homology to the mammalian loop from the globus pallidus interna to the thalamus and thence back to the cortex.

A further pallidal projection leads to the thalamic nucleus of the ansa lenticularis (ALa) which projects back by a glutamatergic pathway to the pallidum and the SNr (Jiao et al., 2000). The ALa is homologous to the subthalamic nucleus of mammals that receives input from the external pallidal segment [globus pallidus pars externus (GPe)] and constitutes a component of the indirect pathway of the basal ganglia. It is presumed that this circuit promotes suppression of unwanted movement patterns (Jiao et al., 2000).

The pallidum of birds also projects to a small number of dorsomedial thalamic nuclei that project back to the striatum as well as several pallial areas (Medina and Reiner, 1997; Veenman et al., 1997). Through this pathway the basal ganglia can modulate processes of the DVR and contribute to aspects of action selection. An important pallidal projection of birds, turtles, crocodiles, and lacertid lizards leads to the pretectum. In birds this GABAergic nucleus is called the nucleus spiriformis lateralis (SpL); in reptiles it is called the dorsal nucleus of the posterior commissure (nDCP) (Reiner et al., 1982a,b, 1998; Medina and Smeets, 1991). SpL and nDCP project to the deeper layers of the tectum, including those that project to premotor cell groups of the hindbrain (see Section 8.3.2.3) (Reiner et al., 1982a). Given the importance of the motor output pathway via the tectum in sauropsids, this projection could provide a major route by which the basal ganglia can influence movements in birds and reptiles (Fig. 8.12). A comparable basal ganglia-pretectotectal pathway seems to be absent in some lizard groups and snakes (Russchen and Jonker, 1988).

The general pattern of this system seems to be ancient and can be traced back to the earliest anamniotes (Grillner and Robertson, 2015), although the loop back to the cortex/pallium seems to be lacking in these animals (Wullimann, 2014). However, the relative contributions of the components can differ between taxa. In anamniotes, the pallium and subpallium are quite small and possibly have less influence on the overall behavior of the animals (Reiner, 2002).

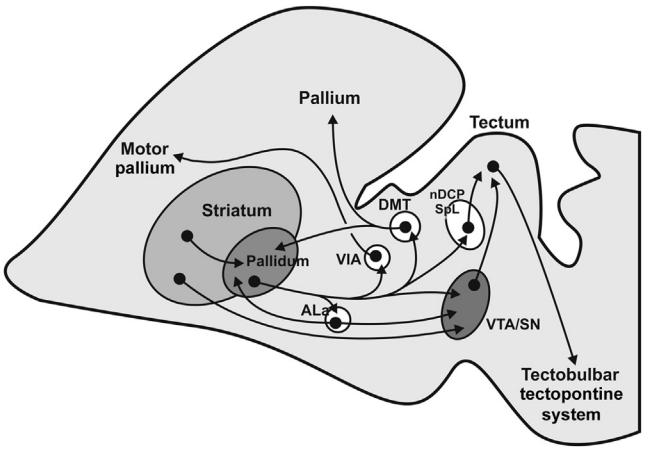

FIGURE 8.12 Highly simplified schema of the sauropsid basal ganglia system. Only a subset of the connections is shown. Abbreviations are given in the list of abbreviations. *Modified from Reiner A., Medina L., Veenman C., 1998. Structural and functional evolution of the basal ganglia in vertebrates. Brain Res. Rev. 28, 235–285.*

8.3.3.2 *The Reptilian Pallium*

The reptilian pallium can be easily discerned from the septum and other subpallial structures by several major anatomical landmarks that are already visible from the outside. Medially, a longitudinal sulcus that is easily visible on the telencephalon marks the border between the medial cortex and the septum. Laterally, a groove divides the pallium from the subpallium. Frontally, the olfactory bulbs are distinctly visible. In most reptiles the bulbs assume a position quite distant from the rest of the telencephalon and are connected by long and slender olfactory tracts; these can be very long in adult crocodiles. In turtles, however, the olfactory bulbs are sessile and frontally abut the more caudal telencephalon. In reptiles the pallium is constituted by the cerebral cortex dorsal to the lateral ventricle and the DVR. We present these two entities separately.

8.3.3.2.1 The Reptilian Dorsal Cortex

Different from birds, reptiles and mammals possess a true multilayered cortex (Ulinski, 1990). The word "cortex" stems from the Latin word "bark" or "skin" but within the neurosciences, it defines a laminated gray matter that harbors multiple layers. To our knowledge, this definition goes back to the 19th century. Leuret and Gratiolet already use it in their famous two-volume book on comparative neuroanatomy (1839, 1857) but possibly, the meaning of "cortex" as referring to a laminated gray matter mantle is even older, given that cortical lamination was first described in 1776 by Francesco Gennari in the human visual cortex. Although cortex is by definition always laminated, there are different numbers of layers that can comprise a cortex. Only the mammalian neocortex that covers the bulk of the cerebral hemispheres has six layers. The human hippocampus (archicortex) has three or four laminae (depending on hippocampal area) while the piriform cortex (CPi) (paleocortex) has three layers.

The reptilian cortex also has three layers. The outer layer 1 is called the superficial plexiform or molecular layer and contains only few scattered interneurons. Afferent axons from the lateral forebrain bundle travel through this layer and fan out in a seemingly nontopographic manner (Naumann et al., 2015). These axons make numerous en-passant synapses on both layer 1 interneurons and distal dendrites of layer 2 principal neurons (Smith et al., 1980). The intermediate layer 2 is called cellular layer and forms a continuous and densely packed sheet of principal neurons, a much smaller number of interneurons as well as afferent and local axons. Layer 3 is the deep plexiform or subcellular layer and is only loosely packed with interneurons; it contains a large number of basal dendrites of principal neurons as well as corticofugal and local axons. A distinct bundle of unmyelinated fibers called alveus is situated deep to layer 3 in most cortical areas (Ulinski, 1990; ten Donkelaar, 1998). These cortical areas show distinct cytoarchitectonic differences that could point to computational specializations.

According to Fournier et al. (2015) and Naumann et al. (2015), the reptilian dorsal cortex strongly resembles the three-layered mammalian CPi. Based on this comparison, and substantiated by some studies in reptiles, they propose a couple of highly interesting functional interpretations of the local dynamics of the turtle dorsal cortex (Fig. 8.13). The starting point of these local dynamics is the system of afferent fibers that reach the dorsal cortex via the dorsal forebrain bundle from sensory thalamus. These axons run across layer 1 and synapse both on inhibitory interneurons of layer 1 as well as on distal dendrites of principal neurons of layer 2 (Kriegstein and Connors, 1986). Interneurons receive more afferent input than the principal cells and thus provide a massive feed-forward inhibition to principal neurons (Fournier et al., 2015). In addition, principal cells activate layer 2 interneurons and receive feedback inhibition. Principal neurons also provide recurrent excitation to other pyramidal neurons via the associational intracortical connections (Fournier et al., 2015). As a result, sensory stimulation evokes strong inhibition, combined with sparse coding properties of principal neurons (Mancilla et al., 1998).

What kinds of computational properties would such a network have? Based on the similarity to the CPi, it is

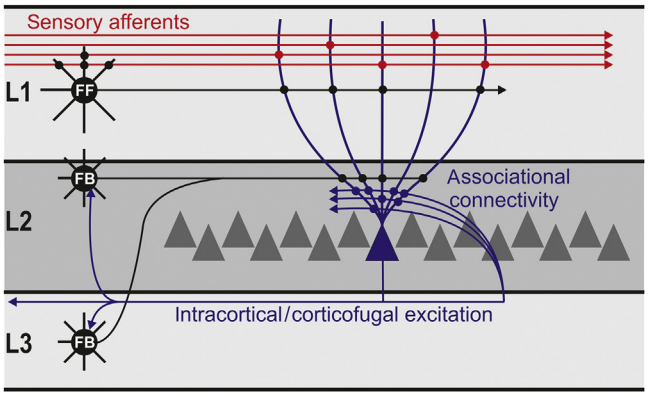

FIGURE 8.13 A schematic overview of the principal wiring pattern of the turtle cortex. Sensory afferents enter layer 1 (L1) and loosely contact apical dendrites of principal neurons that have their somata in layer 2. Inhibitory interneurons of the feedforward type (FF) also receive massive input from sensory afferents and synapse onto the dendrites of principal neurons. These principal neurons receive recurrent excitation from other principal neurons (associational connectivity) and feedback inhibition (FB) from interneurons of layers 2 and 3 that are excited by principal neuron output along the intracortical/corticofugal path. *Modified from Fournier, J., Müller, C.M., Laurent, G., 2015. Looking for the roots of cortical sensory computation in three-layered cortices. Curr. Opin. Neurobiol. 31, 119–126.*

conceivable that coding should not occur by means of topographic maps but by nontopographically organized ensembles of neurons (Fournier et al., 2015; Naumann et al., 2015). Indeed, attempts to discover topography of the visual field in the visual aspects of the turtle cortex were not successful (Mazurskaya, 1973). If this holds, the implication would be both important and unexpected. First, it would be important since it would speak against a functional similarity in the coding properties of mammalian isocortex and reptilian dorsal cortex. Second, it would be unexpected since a nontopographical coding is conceivable for a stimulus-like odor but would be surprising for vision, in which an inherent topographic order is physically provided. In any case, the described attempts to use the architectural similarities between the mammalian CPi and the turtle dorsal cortex as point of explorative departure provides a novel and rich approach to understand the functional properties of the reptilian pallium.

8.3.3.2.2 The Reptilian Dorsal Ventricular Ridge

The DVR is a massive nuclear brain structure that is positioned below and lateral to the lateral ventricle. It is usually divided into a much larger anterior (ADVR) and a smaller posterior (PDVR) component. The ADVR receives thalamic sensory input via the lateral forebrain bundle and can be further subdivided into three longitudinal slabs that receive different types of sensory input (ten Donkelaar, 1998). From lateral to medial, these slabs represent the termination areas of visual, somatosensory, and auditory pathways. They will be discussed in greater detail in Sections 8.4.1–8.4.3.

As outlined in Section 8.3.2.1, rattlesnakes and some other snake species possess a thermal pit below their nasal cavity with which they can detect the heat landscape in front of them. This information is fed into the deep layers of the optic tectum via a branch of the ascending trigeminal system. Some of the deep tectal neurons respond to both infrared and visual input. These bimodal tectal neurons project to the thalamic Rt which projects to the lateral sector of the ADVR (Berson and Hartline, 1988). Single units in this area also evince visual/infrared response properties (Berson and Hartline, 1988). These findings demonstrate two interesting principles. First, despite a large variability in body structures and ecological specializations, sauropsids share a common basic neural bauplan that is evident even in pathways that transport idiosyncratic and highly specialized "unusual" sensory information. In the case of rattlesnakes, infrared sensing is processed along a pathway that exists from snakes to birds across all sauropsids. Second, this commonality is achieved by the incorporation of these special sensory senses into pathways of the "classic" senses. For infrared vision, the trigeminal system merges with the tectofugal visual pathway to transport vision from deep blue to infrared.

The ADVR projects massively to the ipsilateral striatum and to the PDVR (Ulinski, 1978). In addition, ADVR projects via the hippocampal and/or anterior commissures (Bruce and Butler, 1984) to the contralateral hemisphere. Although pallial commissural systems in reptiles are rather small, most of the reptilian pallium is interhemispherically connected (Northcutt, 1981). The PDVR does not receive sensory thalamopallial afferents and resembles the mammalian amygdaloid complex in several respects.

The DVR shows, especially in its anterior component, several specializations that differentiate snakes, lizards, and turtles from crocodiles and birds. In the first group of animals, the ADVR shows a lamination-like pattern in the vicinity of the lateral ventricle. This "first pattern" (ten Donkolaar, 1998) includes a cell-poor zone immediately under the ventricular surface; the second zone consists of clusters of neuronal somata that create a ribbonlike structure along the ventricular border; and the third zone consists of scattered individual neurons. In contrast, the "second pattern" of the DVR in crocodiles and birds lacks the first and second zones, such that the third zone (scattered individual neurons) directly abuts the ventricle.

The first pattern of snakes, lizards, and turtles resembles to some extent a laminar pattern. And indeed, it is conceivable, that is, the remainder of a lamination also encompasses the DVR. This possibility becomes likely when studying the organization of the DVR of the tuatara *S. punctatus*, which is endemic to New Zealand and is the sole survivor of a distinct order, the Rhynchocephalia. Their closest living relatives are the squamates (lizards and snakes). Reiner and Northcutt (2000) demonstrated that in tuatara the distinction between a cortex and the DVR does not exist. Instead, the trilaminar cortex seems to extend into the entire DVR and harbors the termination areas of the ascending visual tectofugal and the ascending auditory pathway. This finding has potentially important implications. If the trilaminar DVR of tuatara is the primitive condition for reptiles, then major aspects of pallial organization in ancestral sauropsids might have been similar to the dorsal cortex of today's reptiles. With the exception of the tuatara, the various sauropsid lineages then must have changed their laminated ancestral DVR into a nuclear arrangement during evolution. A nuclear arrangement, rather than lamination, would then be the derived architecture.

8.3.3.3 The Small World of the Avian Pallium

Bird brains are large, and most of their volume consists of the pallium. As nicely outlined by Striedter (2005), the brain of a 1 kg macaw weighs 20 g more than that of a 200 kg alligator and about as much as that of 1000 kg megamouth shark. As outlined in Section

8.2.3, these and further novel insights allow a fresh look at the question of why corvids and parrots are able to master complex cognitive tasks similar to primates. But even if avian brains are large, what is their internal organization? Overall, avian brains have a very large DVR that hardly leaves space for the lateral ventricle. However, bird brains lack an obvious homolog of the reptilian cortex. Instead, birds have a structure that was named "wulst" (ie, "bulge") by German neuroanatomists of the 19th century. The wulst assumes the same position within the telencephalon as the reptilian cortex and resembles mammalian neocortex and reptilian cortex in embryology, genetics, and topology (Puelles et al., 2000; Reiner et al., 2004a; Jarvis et al., 2005). Despite these similarities, the fact remains that the wulst in its architecture is unique to birds. One might assume that brains with so many unique anatomical features produce unique behaviors but, astoundingly, this is not the case. Instead of major differences in behavior and cognition, we find important similarities, at least for cognition in birds and mammals.

Recent years has a surge of comparative studies on "higher" cognitive abilities such as aspects of impulsive control, inferential reasoning, planning ahead, perspective taking, and role understanding. It has been argued that these skills, often subsummed under the term "complex" cognition, form a cognitive tool kit comparable to that of mammals (Emery and Clayton, 2004). Although also reptilian cognition should not be underestimated, nothing at the level and scope of bird cognition has been reported for this animal group so far (Burghardt, 2013). Critiques have pointed out that most studies on bird cognition have tested these animals in narrowly defined domains with few paradigms that are mostly related to food hoarding (Penn and Povinelli, 2007; Shettleworth, 2010). Using such paradigms, food-caching scrub jays and ravens could show a cognitive prowess that can be interpreted as an indication for corvids having mental capacities that are on par with those of great apes (Clayton and Dickinson, 1998; Bugnyar and Heinrich, 2005; Raby et al., 2007; Prior et al., 2008). On the other hand, the corvid results may be seen as a special adaptation to the very context of food caching. The birds' mental capacities are thus thought to be highly domain specific and not directly comparable with the flexibly used skills of primates (Seed et al., 2009). There are, however, a large number of recent studies that indicate that such a criticism is too restrictive: corvids show various primate-typical behaviors such as alliance formation, third-party intervention, postconflict reconciliation, and consolation (Bugnyar, 2013), and they excel in a variety of experimental tasks and contexts other than caching (Prior et al., 2008; Güntürkün and Bugnyar, 2016). This interpretation becomes even more convincing when parrots are included in the analysis (Pepperberg, 1999; Mikolasch et al., 2011). Even the lowly pigeon can perform noteworthy feats of cognition, such as long-term recollection (Fagot and Cook, 2006), transitive inference reasoning (von Fersen et al., 1990), complex pattern recognition (Yamazaki et al., 2007),

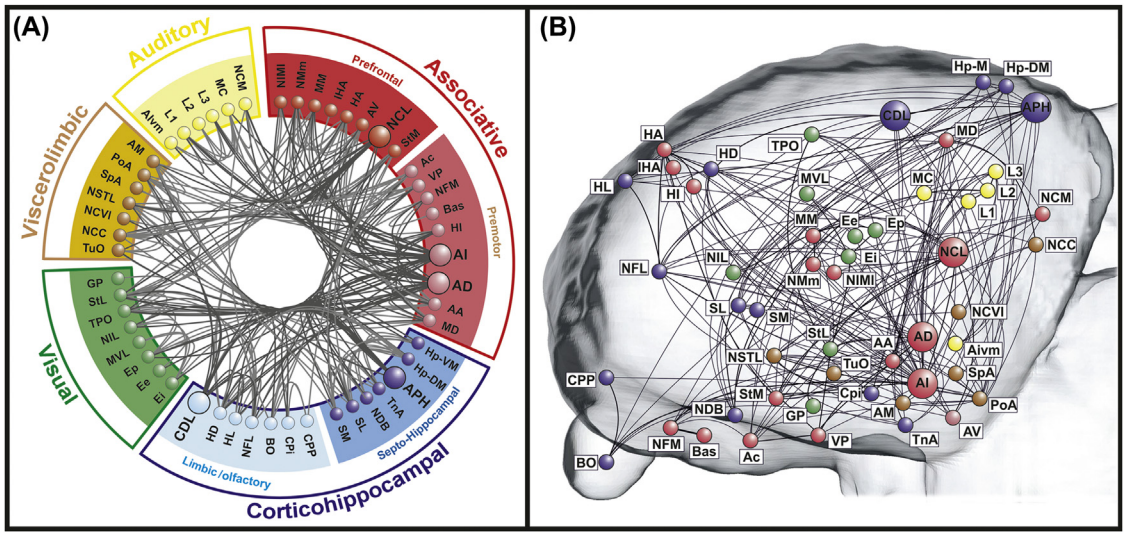

FIGURE 8.14 The connectome of the pigeon telencephalon. (A) Network analysis of the matrix of connections revealed five top-level modules; the associative and the corticohippocampal modules each consist of two lower level modules. Connections to and from hub nodes are shown in a slightly darker color. (B) Sagittal view of the pigeon forebrain with all nodes and their connections. Nodes are colored according to module level membership. Note that the modules are spatially distributed rather than restricted. Color codes: *red*, associative; *blue*, corticohippocampal; *green*, visual; *brown*, viscerolimbic; *yellow*, auditory. Abbreviations are given in the list of abbreviations. *From Shanahan, M., Bingman, V., Shimizu, T., Wild, M., Güntürkün, O., 2013. The large-scale network organization of the avian forebrain: a connectivity matrix and theoretical analysis. Front. Comput. Neurosci. 7, 89, with permission.*

and optimal choice (Herbranson and Schroeder, 2010). But some birds not only reach the same levels of cognitive capacity as mammals but also display identical details of their cognitive architecture as visible in fine-grained analyses of the way they represent objects, categories, or relations (magpies: Pollok et al., 2000; pigeons: Scarf et al., 2011). These similarities of cognitive organization are astounding given that the telencephalon of birds and mammals exhibits a very different anatomical organization.

Looking carefully, it is obvious that the differences apply to the overall organization of the telencephalon but are quite small when it comes to the connectivity of the ascending sensory pathways, associative forebrain areas, and subpallial structures (Reiner et al., 2005; Güntürkün and Bugnyar, 2016]. Thus, avian and mammalian forebrains might have similar connectivities despite a radically different overall organization. These similarities in connectivity might drive similarities in behavior. Indeed, it is a futile enterprise to try to understand cognitive functions of a brain without analyzing information flow within its neural network. To analyze the overall connectivity and possible information flow of the avian telencephalon, Shanahan et al. (2013) compiled a large-scale "wiring diagram" for the pigeon and analyzed it with the mathematical tools of graph theory. Combining more than four decades of tracer studies, they constructed a structural "connectome" of the pigeon telencephalon.

This work revealed, first, that the pigeon pallium is a small-world network. In such a network, neighboring nodes have tight links with each other, but most nodes can be reached from every other node by a small number of steps (Watts and Strogatz, 1998). These properties are achieved by a dense local connectivity (high level of clustering) that is combined with a much smaller number of connections that randomly reach out to far-distant nodes (random graph that creates a short path between two distant nodes). In social networks, this effect is known from the finding that people may live in close-knit societies, but still everybody is linked to any stranger in the world by an astonishingly short chain of acquaintances (Fig. 8.14).

Second, the connectome analysis revealed that the pigeon telencephalon comprises a number of distinct modules, defined as clusters of nodes with dense connections between each other but sparse connections with the nodes of other modules. Remarkably, the pigeon modules were found to be functionally analogous to those of humans. The largest pigeon module is the associative module, which consists of prefrontal and premotor submodules that likely mediate higher cognition. The second largest module is the corticohippocampal module, which includes septohippocampal and limbic/olfactory submodules. They integrate multimodal information that is used, for example, in hippocampus-based spatial orientation and navigation. The visual module represents the tectofugal forebrain areas, including their primary, associative, and descending (motor) components. The tectofugal pathway constitutes the dominant visual system in pigeons, while the auditory module represents subdivisions of the primary auditory fields along with their secondary, associative, and premotor structures. Thus, most of the modules of the pigeon's telencephalon are functionally and/or anatomically comparable to modules that are revealed when network analysis is carried out on human or nonhuman mammalian brains (van den Heuvel et al., 2016). Interestingly, while the top-level modules of mammalian brains are anatomically localized, those of the pigeon brain are more anatomically distributed. So, similar connectome patterns do not necessarily resemble each other in spatial organization.

Third, the pigeon telencephalon has a central connective core, and the hub nodes that comprise this core are functionally analogous to hub nodes in the primate brain's connectome core. What does that mean? Hubs are nodes with a large number of connections to other nodes. They serve functions similar to major international airports: if one flies from a small local airport to another small local airport far away, flights are always routed via connection flights through major airports (hubs). A collection of such hubs within the brain constitutes the functional "backbone" of neural information flow. This neural backbone in pigeon and primate brains consists of very similar hubs. So, if the topologically central connective core of the primate brain plays an important role in high-level cognition (Shanahan, 2012), the required connectional infrastructure seems also to be present in birds. This finding is even more exciting when we realize that the prefrontal-like area of birds and the PFC of primates are not homologues but functionally analogues. Thus, these two structures do not derive from a common ancestral structure but represent the outcomes of two completely independent and convergent evolutionary trajectories. The fact that these two structures constitute such highly similar topological centralities of their respective connectomes suggests the following: if two neural structures of different animals share the same function, they may also share the same connectivity blueprint.

8.3.3.3.1 The Avian Wulst

As outlined above, the avian wulst is a likely candidate for homology with mammalian neocortex and reptilian dorsal cortex, although its internal structure is different (Reiner et al., 2004a; Jarvis et al., 2005). The wulst has three functional zones. Starting from anterior, a very small portion of the most anterior tip of the wulst is motoric. From here, the tractus septomencephalicus

descends, like the mammalian tractus corticospinalis, to the cervical spinal cord and terminates predominantly contralaterally in the medial part of the base of the dorsal horn of the upper six to seven cervical segments (Wild and Williams, 2000). More posterior is a slightly larger zone that is somatosensory. In barn owls, this area contains a small protuberance that contains the representation of the contralateral claw (Wild et al., 2008). Even more posterior is the wulst's largest zone, which is visual.

This visual wulst bears some resemblance to the mammalian primary visual cortex. This could be due to a one-to-one homology of the visual wulst to the visual cortex as backed by similarities of chemoarchitecture, afferent inputs from the thalamic n. geniculatus pars dorsolateralis (GLd), output pathways to thalamic and midbrain structures, genetic markers, as well as topological position (Karten et al., 1973; Reiner et al., 2004a; Güntürkün and Karten, 1991). However, the four layerlike areas of the wulst are not truly comparable to laminae of the reptilian dorsal cortex or the mammalian neocortex. Instead, they are called "pseudolayers" by Medina and Reiner (2000), since they have some of the properties of cortical layers; however, they lack pyramidal neurons with translaminar dendritic trees. Thus, the avian visual (and nonvisual) wulst shares many similarities with neocortex but also displays some unique derived features.

8.3.3.3.2 The Avian Dorsal Ventricular Ridge

The avian dorsal ventricular ridge is organized into four major subdivisions that are distinct from each other in terms of gene expression, connectivity, and physiology. The nomenclature conference (Reiner et al., 2004a) renamed them as nidopallium, mesopallium, arcopallium, and pallial amygdala. The nidopallium contains zones that are the termination fields of the ascending auditory, visual tectofugal, and trigeminal thalamopallial pathways. We will discuss the internal connectivity of this area in Section 8.3.3.3.2.3. The mesopallium is an associative pallial field that receives neither ascending sensory input nor harbors descending extratelencephalic output systems. The arcopallium and the amygdala are topologically closely intertwined. While the arcopallium is a premotor area, pallial amygdalar nuclei are limbic in nature. Various one-to-one homologies have been proposed before and after the nomenclature conference for these four subdivisions and various parts of the mammalian pallium, including cerebral cortex (Bruce and Neary, 1995; Puelles et al., 2000, 2016; Dugas-Ford et al., 2012; Belgard et al., 2013; Jarvis et al., 2013; Pfenning et al., 2014). This is an active area of research and debate, and it is far from settled. Güntürkün and Bugnyar (2016) reviewed the different standpoints on this matter and Luis Puelles is providing a comprehensive account on possible homologies in this volume. We will only discuss two specific aspects of the avian dorsal ventricular ridge; the arcopallium/amygdala dichotomy and the laminar organization of the thalamopallial termination zone in the nidopallium.

8.3.3.3.2.1 The Avian Premotor Arcopallium and the Pallial Amygdala According to the nomenclature used in the atlas of the pigeon brain (Karten and Hodos, 1967), the highly complex region in the ventral part of the posterolateral telencephalon was called archistriatum. The complexity of this area results from its histological and connectional heterogeneity that includes both premotor and limbic features (Zeier and Karten, 1971). In the new nomenclature, the premotor components are called arcopallium while the remaining portions are assumed to constitute the avian pallial amygdala (Reiner et al., 2004a). We first talk about the arcopallium as a central premotor constituent of the avian brain in which sensory input patterns are translated into action signals.

8.3.3.3.2.2 The Arcopallium as a Premotor Center of the Avian Dorsal Ventricular Ridge The arcopallium consists of the arcopallium anterius (AA), the arcopallium dorsale (AD), the arcopallium intermedium (AI), and the arcopallium mediale (AM) (Reiner et al., 2004a). The connections and functions of the first three components deviate clearly from an amygdaloid pattern. The situation is far less settled for the AM, and this structure could be more comparable to the anterior part of the medial amygdala of mammals, where olfactory and vomeronasal inputs overlap (Abellán et al., 2013). We therefore discuss only the roles of AA, AD, and AI in sensorimotor transfer. The term "arcopallium" is used as an umbrella name for these three substructures.

The arcopallium receives different sensory information from other pallial entities and projects to brain stem motor systems. A good example for the role of the arcopallium in sensorimotor transformation is the trigeminal system and its role in ingestive behavior. Tactile input from the beak is conveyed to the arcopallium from the frontal trigeminal nidopallium (NFT) which receives input from the n. basorostralis pallii (Bas) (Wild et al., 1985; Schall et al., 1986; Letzner et al., 2016). A second trigeminal pathway runs through the mesopallium frontoventrale (MFV), which is reciprocally connected to Bas and NFT (Atoji and Wild, 2012). As demonstrated by Letzner et al. (2016), both NFT and MFV are interhemispherically connected via arcopallial projections. From the arcopallium, descending fibers reach the medial and the lateral components of the striatum (MSt and LSt), as well as the ventral pallidum (VP) (Veenman et al., 1995; Dubbeldam et al.,

1997; Cohen et al., 1998; Kröner and Güntürkün, 1999). In addition, the arcopallium projects to the deep layers of the optic tectum, from where descending axons reach the rhombencephalic motor fields (Zeier and Karten, 1971; Dubbeldam et al., 1997; Cohen et al., 1998; Hellmann et al., 2004). More medially, OM fibers terminate in the substantia grisea centralis (GCt) and fan out into the medial and lateral aspects of the mesencephalic and medullary reticular formation, as well as to the n. reticularis pontis caudalis and n. reticularis parvocellularis (Zeier and Karten, 1971; Dubbeldam et al., 1997). The picture emerging from this overview is that of a classic sensorimotor pathway. Indeed, perturbations along this pathway affect both sensory and motor aspects of pecking, grasping, and feeding in the pigeon (Wild et al., 1985; Jäger, 1993).

Another example of the arcopallium's sensorimotor role is the ability of birds (especially owls) to respond with a fast gaze shift to novel stimuli. The most important sensory cues for gaze shifts are provided by the visual and the auditory senses. In birds, visual information is conveyed from the retina to the telencephalon via two main visual pathways; the tectofugal and the thalamofugal system (see Sections 8.4.1.1 and 8.4.1.2). Tectofugal projections terminate in the entopallial core of the DVR, which then projects to a penumbra of associative visual areas (Husband and Shimizu, 1999; Krützfeldt and Wild, 2005; Stacho et al., 2016). Nearly all of these areas project to the arcopallium (Husband and Shimizu, 1999; Kröner and Güntürkün, 1999; Letzner et al., 2016) via the tractus dorsoarcopallialis (DA). Thalamofugal visual projections terminate in the avian wulst and then also project to the arcopallium via associative visual areas (Bagnoli and Burkhalter, 1983; Shimizu and Karten, 1990; Shimizu et al., 1995; Kröner and Güntürkün, 1999). The same pattern is observed for the avian auditory pathway (Wild et al., 1993; Cohen et al., 1998; Kröner and Güntürkün, 1999; Letzner et al., 2016). Thus, the arcopallium integrates associative visual and auditory information via associative and modality-specific areas of the avian pallium. As outlined later, some of this input is used to orient toward new targets in the surrounding.

Knudsen et al. (1995) reported that microstimulations of the anterior and intermediate arcopallium of the barn owl evoke orienting movements of the eyes and head. The saccade directions were place-coded in the arcopallium; implying that single arcopallial neurons evinced a receptive field in 2D space. Anatomical studies show that subfields of the arcopallium have downsweeping projections to the brain stem (summarized above for the trigeminal system). Spatial attention guided by the arcopallium incorporates auditory and visual input and is translated into gaze shifts via the projections to the deep layers of the optic tectum (Knudsen and Knudsen, 1996; Cohen et al., 1998). Indeed, Winkowski and Knudsen (2006) demonstrated that electrical microstimulation in critical areas of the owl's arcopallium can regulate the gain of tectal auditory responses in an attention-like manner. When the arcopallial circuit was stimulated, tectal responses to the place code of the auditory stimuli (the point in space from where the sound emanates) were enhanced, and spatial selectivity was sharpened. At the same time, auditory inputs from other locations were suppressed in the midbrain map.

Taken together, these and many more studies demonstrate that the arcopallial subfields receive associative sensory input and generate premotor outputs to subpallial areas. The studies in barn owls make it clear that the arcopallium's role in this pathway is not that of a simple relay, but that of an integrator of various sensory signals that are associated, based on past experience, with a certain response. According to Shanahan et al. (2013), the AI is among the most important hubs of the avian telencephalon that controls information flow of a large number of forebrain structures. Fig. 8.15 schematically summarizes what we know about the projections of the three arcopallial subfields AA, AI, and AD. It is visible from this schema that the importance of the arcopallium as a hub may have been underestimated by Shanahan et al. (2013) because they limited their analysis to the telencephalon.

8.3.3.3.2.2.1 The Avian Pallial Amygdala The avian pallial amygdala consists of the posterior pallial amygdala (PoA), the nucleus taeniae of the amygdala (TnA), and a component that is usually called the AM but may be a component of the avian pallial amygdala (Reiner et al., 2004a; Atoji et al., 2006; Abellán et al., 2013). According to Letzner et al. (2016), only the ventral part of the PoA, which projects to the hypothalamus, has homotopic interhemispheric connections with the contralateral PoA. Birds also have a subpallial amygdala that was reviewed by Kuenzel et al. (2011) but will not be discussed here.

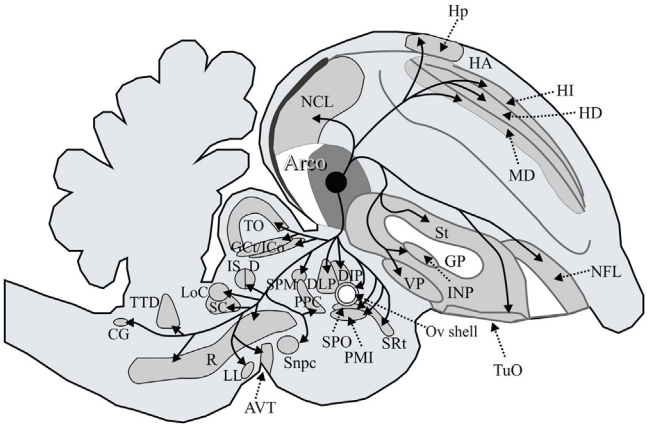

FIGURE 8.15 Projections of the avian arcopallium. The arcopallium as defined here includes the subareas AA, AD, and AI. Abbreviations are listed in the list of abbreviations.

Within the telencephalon, projections of the avian pallial amygdala reach major aspects of the basal ganglia. Both PoA and TnA project to tuberculum olfactorium (TuO), VP, nucleus of the stria terminalis (NSTL), and preoptic nuclei (Veenman et al., 1995; Kröner and Güntürkün, 1999; Cheng et al., 1999). Additionally, PoA projects to the n. accumbens (Ac) and the MSt (Veenman et al., 1995). Within the pallium, axons of the amygdala reach the hippocampal complex (Casini et al., 1986; Cheng et al., 1999; Atoji et al., 2002; Shanahan et al., 2013). Further intratelencephalic projections of TnA target the septum mediale and the nidopallium caudolaterale (NCL) (Cheng et al., 1999). Telencephalic projections to the nuclei of the avian pallial amygdala originate mainly from the hippocampal complex (Casini et al., 1986; Cheng et al., 1999; Atoji et al., 2002), septum laterale, accumbens, NSTL, and bulbus olfactorius (Reiner and Karten, 1985; Cheng et al., 1999; Patzke et al., 2011). Projections descend from the avian pallial amygdala via the tractus occipitomesencephalicus pars hypothalami (HOM) and terminate in hypothalamic subfields (Zeier and Karten, 1971; Dubbeldam et al., 1997; Kröner and Güntürkün, 1999; Cheng et al., 1999), the locus coeruleus (LoC), substantia nigra pars parvocellularis (SNpc), and AVT (Kröner and Güntürkün, 1999; Cheng et al., 1999).

This network resembles that of the mammalian amygdala and places the avian pallial amygdala into the core of a system of various limbic, multimodal, and memory-related structures with which actions can be modulated according to emotional processes. Accordingly, Kingsbury et al. (2015) demonstrated that vasoactive intestinal peptide (VIP) peptide−containing neurons in the AM showed increased transcriptional activity in response to and correlated with nest building activity in zebra finches. Schubloom and Woolley (2016) found that immediate early gene expression in the TnA of female zebra finches was related to the degree of individual preferences for their mate's courtship song. Testosterone levels in TnA also differ relative to breeding or nonbreeding seasons in swamp sparrows (Heimovics et al., 2016). In crows, dominance relationships develop in dyadic encounters. During such social interactions, neural activity levels in TnA correlate with aggressive and submissive behaviors (Nishizawa et al., 2011). Accordingly, lesions of TnA in zebra finches alter the interaction of lesioned males with sexually accessible females only when another male is present (Ikebuchi et al., 2009). These and many more studies demonstrate that the nuclei of the avian pallial amygdala are part of a limbic network that controls emotional behavior during social interactions that include sexual and agonistic components. Fig. 8.16 schematically summarizes the projections of subnuclei of the avian pallial amygdala.

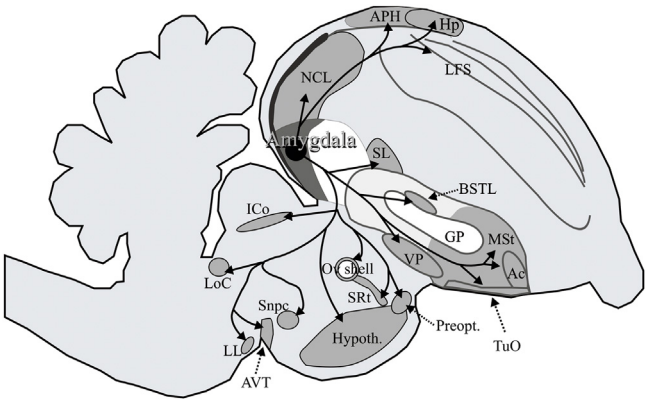

FIGURE 8.16 Projections of the avian pallial amygdala. Efferents of the n. taeniae of the pallial amygdala (TnA) and the n. of the posterior pallial amygdala (PoA) are shown. Abbreviations are given in the list of abbreviations.

8.3.3.3.2.3 Layers in a Nonlaminated Forebrain At the turn of the 19th to the 20th century, comparative neuroanatomists were sure that they had discovered the core feature that distinguishes mammalian from nonmammalian brains: the six-layered cerebral cortex. Reptiles with their three-layered cortex seemed to possess at least a forerunner of the mammalian cerebral cortex, but birds seemed to possess only the CDL (area corticoidea dorsolateralis), a small and paper-thin three-layered structure in the dorsolateral pallium. The situation changed after the turn to the 21st century. Dugas-Ford et al. (2012) discovered that gene expression patterns of mammalian cortical neurons from granular (layer IV) and infragranular (layer V) laminae corresponded to those of avian pallial clusters that receive sensory thalamic input ("granular") or have descending projections to subpallial targets ("infragranular"). Interestingly, these results spanned both DVR and wulst and incorporated them into a common pattern. Subsequent studies even suggested that most of the avian pallial clusters may be homologous to certain cortical layers, such that most of the avian pallium would have a hidden laminated architecture (Chen et al., 2013; Jarvis et al., 2013; but see Montiel et al., 2016).

Genetic expression patterns are a great tool, but when it comes to the demonstration of a layered organization, local connectivity data are needed. This is what Wang et al. (2010) and Ahumada-Galleguillos et al. (2015) demonstrated in the auditory and the visual tectofugal thalamopallial termination zones of the nidopallium. Using in vitro tracing, they demonstrated three main layerlike entities that can be further subdivided into several sublayers. In this arrangement, neuronal clusters and axonal columns are oriented orthogonally to the layers. The neurons in the sensory recipient laminae are reciprocally connected with the cells in the

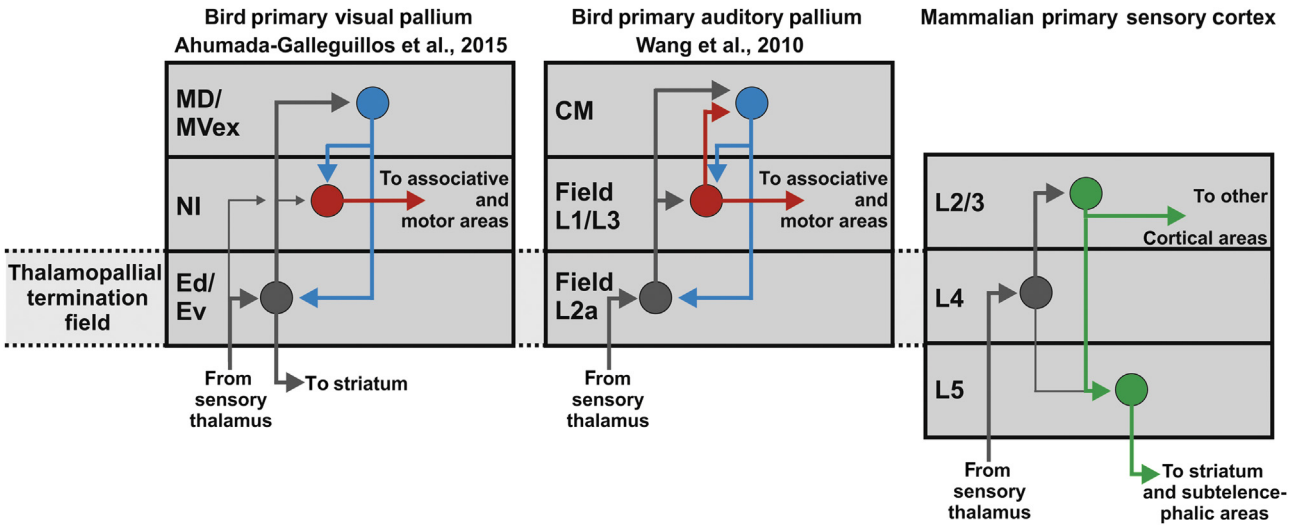

FIGURE 8.17 Overview of the connectivity patterns in the "layered" primary tectofugal visual and primary auditory bird pallium as well as the mammalian primary sensory cortex. For the bird data, some layers were collapsed into one. The cortex schema is shifted vertically so that the thalamopallial projections are aligned; only the main connections are shown. *Thin lines* represent weaker connections. The left two panels represent results from in vitro tracing experiments. The *horizontal arrow* that leads to associative and motor areas depicts connections that are known from the literature (Shanahan et al., 2013) but for which we do not know if they originate from the depicted cell types.

topographically overlaying nidopallial and mesopallial columns. In addition, columns have horizontal projections to associative and motor structures (Fig. 8.17). The entry point to this system is the thalamorecipient layer, which shares genetic expression profiles and morphological features with the cortical granular layer IV (Dugas-Ford et al., 2012; Chen et al., 2013; Belgard et al., 2013). To some extent, this avian circuitry resembles the cortical canonical circuit that is defined by repetitive topographic interlaminar circuits (Douglas and Martin, 2007). These neocortical circuits are the heart of the computational properties that characterize cortical dynamics. Looking carefully at Fig. 8.17, it becomes obvious that mammalian and avian pallial layers are similar, but not identical. If their similarity is due to evolutionary convergence, a laminated forebrain based on repetitive columnar interlaminar circuits could represent a computational necessity for flexible sensorimotor integration. In principle, however, a more mundane interpretation is possible: cascades of interconnected pallial territories around a primary sensory cortical field are also found in cerebral cortex, where diverse associative cortical areas are arranged around a primary sensory cortical field. Thus, the avian pattern could simply reflect sequences of sensory integration along adjacent fields. However, the precise orthogonal arrangement of the cellular columns, combined with the cortical lamina-specific genetic expression patterns, makes the hypothesis of the "invisibly layered" bird pallium attractive. Still, whether birds indeed possess a cortical layerlike organization in the DVR remains an open question.

8.3.3.3.2.4 The Avian "Prefrontal Cortex" In Section 8.3.3.3 we had outlined that avian cognition is not inferior to mammalian cognition. Corvids and parrots even reach the same achievements in complex cognitive tasks as primates, despite having much smaller forebrains (see Section 8.2.2). However, birds are on par with mammals not only with respect to the level of cognitive abilities, but also with respect to the functional details of the cognitive mechanisms (Pollock et al., 2000; Scarf et al., 2011). This is especially true for a cluster of cognitive abilities that are subsumed under the umbrella term "executive functions"—a circumscribed cluster of cognitive functions (working memory, behavioral inhibition of an imminent action, timing, goal shifting, etc.) that reflect the ability to spontaneously generate efficient strategies and schedule future behavior when relying on self-directed task-specific planning. Birds show similar executive functions as mammals (Laude et al., 2016; Castro and Wasserman, 2016). But since birds do not have a cortex, how do they generate their executive functions? The PFC of primates is a large part of the frontal portion of the neocortex. Neither the avian DVR nor the wulst has any entity that even remotely resembles the PFC. Comparative neuroanatomists are happy to accept that common function can emerge in different taxa as a result of convergent evolution, but they then often expect that this process is accompanied by the convergent evolution of similarities in brain architecture. This is, at least at the first glance, not the case for NCL and PFC. The view that similarities of function require similarities of anatomy is the classic trap in which neuroanatomists often step: they know that a certain structure generates a certain

function (structure → function). Erroneously they then conclude that a certain function can only be generated by one kind of structure (function → structure). The analysis of the avian "prefrontal cortex" demonstrates the fallacy of this logic.

Classic neuropsychological studies had demonstrated that lesions of the PFC in humans result in prominent deficits in all aspects of executive functions (Taylor et al., 1986). Subsequent neurobiological advances provided means for mechanism-driven instead of phenomena-driven explanations. For example, a detailed analysis on the biophysical effects of dopamine release within the PFC showed that some of the observed deficits, ranging from working memory to planning, may be the result of a single system failure (Seamans and Yang, 2004; Durstewitz and Seamans, 2008). This is exemplified by working memory tasks, in which the subject has to hold information online until using it for some future actions. The problem in a working memory task is twofold: first, a neuronal/mental trace of a stimulus has to be held over time although the physical representation (the perceived stimulus) is no longer present; second, the neuronal trace has to be shielded against other neuronal processes that result from currently interfering stimuli. Delay activity in the PFC of human and nonhuman primates indeed persists during working memory tasks even if interfering stimuli intervene between the presentation of the sample and the target stimulus (Puig et al., 2014). Durstewitz et al. (1999a) proposed in a biophysically realistic model that dopamine can, via D1 receptor stimulation, selectively increase the firing rate of prefrontal neurons that hold information during a delay period. It thereby also increases inhibitory feedback and thus reduces activity of the "background" neurons. In this manner, dopaminergic effects may act to stabilize current delay activity in a PFC network. Thus, the model offered a mechanistic explanation for the cellular firing properties of PFC neurons or the behavioral deficits observed after blockade or after supranormal stimulation of dopamine receptors in the PFC. Armed with such a mechanistic explanation of a core feature of executive functions in PFC, we now can turn our attention to birds to look if their working memory capacity is realized by similar mechanisms.

In 1982, Mogensen and Divac lesioned an area in the caudolateral aspect of the pigeon's nidopallium and tested the animals in a delayed alternation task. In this task, the animal has to choose one of two keys to obtain reward. After a delay period, it has to select the other key and so forth. The problem is the delay: the subject has to keep in working memory its last choice to be able to select in the subsequent task the next key. Mogensen and Divac (1982) demonstrated

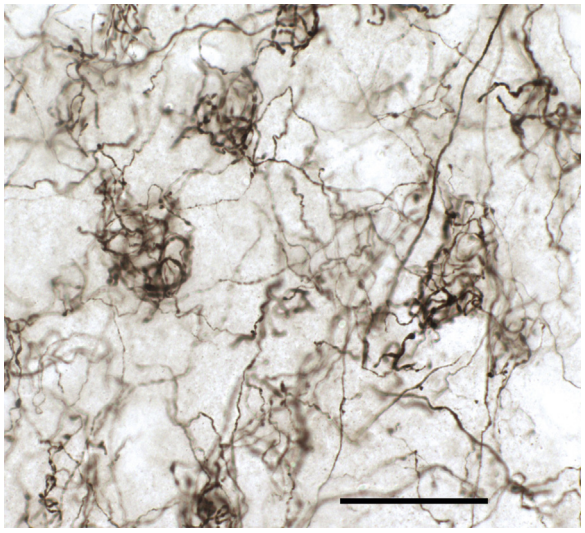

FIGURE 8.18 Tyrosine hydroxylase-positive, presumably dopaminergic, fibers in the pigeon NCL. Note occasional swelling on axons that are probably synapses en-passant. Baskets that tightly wrap around singe neurons are clearly visible. Bar = 50 μm.

that birds with lesions in the NCL displayed deficits in this classic test for executive functions. In subsequent studies, the team also showed that the NCL is densely innervated by catecholaminergic fibers of possibly dopaminergic nature (Divac et al., 1985; Divac and Mogenson, 1985). They concluded that the NCL could be a functional equivalent to the mammalian PFC. Later on, Waldmann and Güntürkün (1993) showed that the NCL is innervated by dopaminergic axons from the SNc and the AVT. Interestingly, these axons either innervate NCL neurons by boutons-en-passant or create dense baskets with which they coil around a soma and possibly bring this neuron under tight dopaminergic control (Wynne and Güntürkün, 1995; Fig. 8.18). NCL neurons within these baskets are never GABAergic interneurons but principal cells that are activated by a D1 receptor cascade (Durstewitz et al., 1998). Some of the principal cells in these baskets are readily elicited by weak excitatory inputs, yet produce a sustained response to a prolonged input—a pattern that favors the function to retain information of their input for a short time (Kröner et al., 2002). Indeed, neurons in the mammalian PFC show enhancement in their firing rate during the delay component of working memory tasks, often also accompanied by brief gamma bursts that possibly gate access to, and prevent sensory interference with, working memory (Lundqvist et al., 2016). Neurons with similar delay activities to those recorded from primate PFC have been observed in the pigeon's NCL during delay tasks (Kalt et al., 1999; Diekamp et al., 2002; Veit et al., 2014). Karakuyu et al. (2007) could show that dopamine in NCL is specifically released during the delay period of working memory

tasks and could thus stabilize sustained activity patterns of delay neurons against interference. Since dopamine release in NCL follows (like in PFC) a volume transmission mode, it can affect extended aspects of the network that is currently involved in executing the delay task (Bast et al., 2002). Consequently, locally antagonizing or agonizing D1 receptors in NCL decreases or increases working memory performance, respectively (Herold et al., 2008). These receptors are also massively expressed in NCL when pigeons are subject to cognitive training with working memory tasks (Herold et al., 2012).

Thus, both mammals and birds seem to realize the working memory aspect of their executive functions within their PFC/NCL using mechanisms that are highly similar (Güntürkün, 2005). Astonishingly, these similarities range from the molecular up to the behavioral level. What about executive functions beyond working memory? NCL lesions or local pharmacological alterations of NCL activity patterns do not affect perceptual or motor processes (Gagliardo et al., 1996; Güntürkün, 1997), but they interfere with behavioral inhibition (Güntürkün, 1997; Hartmann and Güntürkün, 1998), self-scheduling along time domains (Kalenscher et al., 2003), response selection (Lissek and Güntürkün, 2004), context integration (Lissek and Güntürkün, 2005), goal shifting (Diekamp et al., 2000), and control of extinction learning (Lissek and Güntürkün, 2003; Lengersdorf et al., 2014). Furthermore, NCL neurons encode cognitive operations like decision-making (Lengersdorf et al., 2014; Veit et al., 2015), rule tracking (Veit and Nieder, 2013), encoding of subjective values (Kalenscher et al., 2005), and the association of outcomes to actions (Starosta et al., 2013). Thus, the full extent of executive functions is encoded at the level of both PFC and NCL.

Thus far, we have not discussed the neuroanatomy of the NCL. In mammals, the PFC is recognized as a hub that connects various sensory, motor, and associative systems (van den Heuvel et al., 2016). Like the PFC, the NCL is also a center of multimodal integration and connects the higher-order sensory input from trigeminal, somatosensory, visual (tecto- and thalamofugal), and olfactory systems and links them to limbic and premotor structures (Leutgeb et al., 1996; Kröner and Güntürkün, 1999; Güntürkün, 2012; Fig. 8.19). Consequently, NCL neurons can integrate and process relevant cues, irrespective of their modality (Moll and Nieder, 2015). Thus, identical to the PFC, the avian NCL is a convergence zone between the ascending sensory and the descending motor systems (Kirsch et al., 2008). Here, all sensory modalities overlap and connect to premotor areas of the arcopallium. However, NCL and PFC are not in all aspects identical to each other. The most important difference is the lack of a thalamic input from the mediodorsal thalamic nucleus in birds (Kröner and Güntürkün, 1999). Instead, the n. dorsolateralis posterior thalami (DLP) innervates the NCL (Güntürkün and Kröner, 1999). The DLP integrates multimodal input and is probably homologous either to the intralaminar or the posterior thalamic nuclei in mammals (Korzeniewska and Güntürkün, 1990; Veenman et al., 1997). However, DLP lesions cause deficits that are comparable to lesions of the mammalian nucleus mediodorsalis (Güntürkün, 1997). A second difference to the mammalian prefrontal system is the fact that NCL neurons exhibit high firing rates and are selective for highly familiar stimuli (Veit et al., 2015). This is dissimilar to the PFC but resembles primate association cortices posterior to PFC. Thus, NCL and PFC are highly similar but not identical in all aspects. Despite these similarities, NCL and PFC are certainly not homologous. While NCL is located in the most posterior end of the telencephalon, PFC is at the cortical rostral pole. Thus, it is difficult to conceive how this topological transformation should occur during evolution from a common homologous structure. Also some genetic expression patterns contradict the idea of a homology of NCL and PFC (Puelles et al., 2016). Thus, nonhomologous brain areas converged over the course of 300 million years into mammalian and avian prefrontal structures that serve highly similar functions. In doing so, both areas gained the ability to generate the same cognitive functions using similar cellular properties.

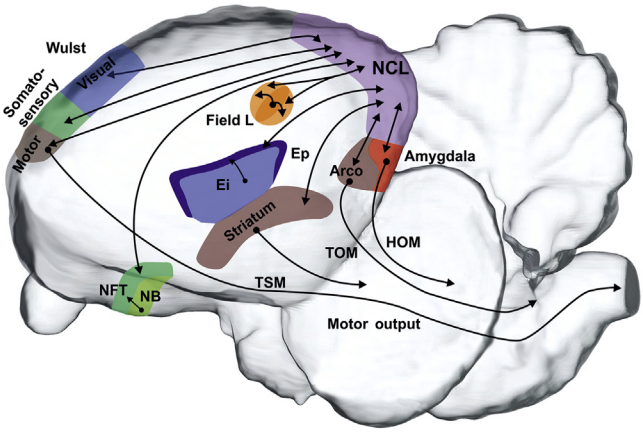

FIGURE 8.19 The NCL is a hub that integrates diverse sensory pathways and links them to limbic and motor structures. Auditory (*orange*), visual (*blue*; thalamofugal, tectofugal), and somatosensory (*green*; somatosensory, trigeminal) regions have reciprocal connections with NCL via their association fields. *Pigeon brain modified from Güntürkün, O., Verhoye, M., De Groof, G., Van der Linden, A., 2013. A 3-dimensional digital atlas of the ascending sensory and the descending motor systems in the pigeon brain. Brain Struct. Funct. 281, 269–281. For abbreviations see list of abbreviations.*

8.4 Functional Systems

8.4.1 Ascending Visual Systems

As pointed out by Butler and Hodos (2005), the dorsal thalamus of anamniotes can be divided into (1) a rostral lemnothalamic component that receives direct retinal and, in some cases, other sensory lemniscal projections; and (2) a caudal collothalamic component that receives its input mostly from the midbrain roof. The lemnothalamus receives its sensory input without an extra synapse in the midbrain roof. Accordingly, the collothalamus receives sensory afferents via a tectal relay. The visual system of sauropsids is characterized by two parallel ascending systems, a lemnothalamic and a collothalamic visual pathway. Especially in avian neuroscience, the terms "lemnothalamic" and "collothalamic" never gained broad acceptance. Instead, scientists generally use the terms "thalamofugal" and "tectofugal visual pathway," respectively. Since avian neuroscience is often used as a reference benchmark for studies on reptiles, most scientists working on the reptilian visual system also refer to thalamofugal and tectofugal systems. To avoid any confusion, we therefore also use these terms.

8.4.1.1 The Thalamofugal Visual Pathway in Reptiles and Birds

As true for practically all aspects of the central nervous system, we know much more about birds than about reptiles. We therefore will first discuss birds before turning our attention to reptiles.

The thalamofugal pathway in birds consists of the retinal projection onto the n. geniculatus lateralis pars dorsalis (GLd) and the bilateral projection of the GLd onto the wulst in the anterodorsal forebrain (Güntürkün, 2000). Due to its anatomical, physiological, and functional properties, the avian thalamofugal pathway probably corresponds to the mammalian geniculostriate system (Shimizu and Karten, 1993).

While the tectofugal pathway receives afferents from the complete extent of the retina, the retinal location of ganglion cells projecting onto the GLd differs in various species. In birds of prey, ganglion cells in the temporal retina subserving frontal vision project primarily onto the GLd (Bravo and Pettigrew, 1981). Consequently, many neurons in the visual wulst of owls, kestrels, and vultures possess binocular visual fields and detect retinal disparity (Pettigrew, 1979; Porciatti et al., 1990). In pigeons, however, efferents to the GLd originate mainly from ganglion cells outside the superiotemporal retina (Remy and Güntürkün, 1991). The paucity of afferents from this retinal field should render the pigeons' thalamofugal pathway largely "laterally oriented," an assumption supported by electrophysiological (Miceli et al., 1979) and imaging results (De Groof et al., 2013). Rotundus- and GLd lesions in pigeons also selectively interfere with acuity in the frontal and lateral visual field, respectively (Güntürkün and Hahmann, 1999). Similarly, wulst lesions result in the lateral but not frontal visual far-field deficits (Buszynski and Bingman, 2004). This "lateral orientation" of the pigeon's thalamofugal system is very likely the reason for the virtual absence of behavioral deficits in a variety of discrimination tasks after GLd or wulst lesions in which frontally placed pecking keys were used (Güntürkün, 1991). Thus, in pigeons, frontal and lateral visual acuity performances seem to depend on tecto- and thalamofugal mechanisms, respectively.

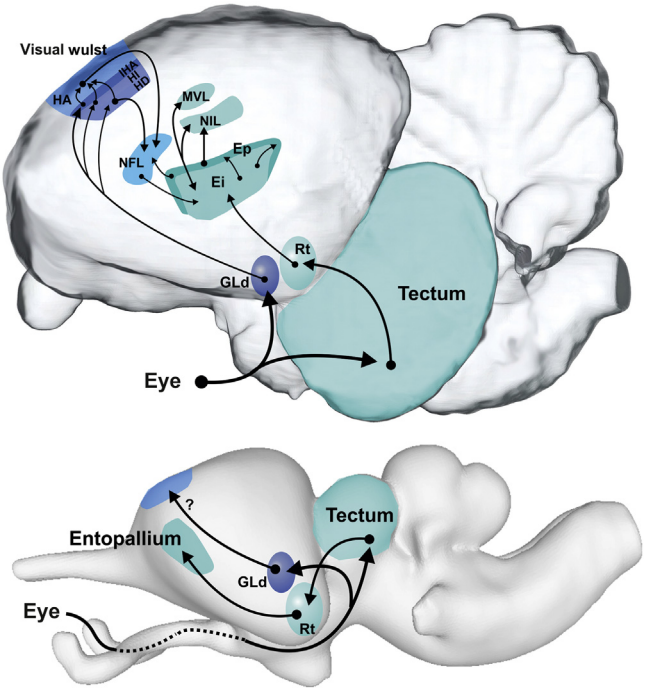

FIGURE 8.20 Ascending visual pathways of the tectofugal (turquoise) and the thalamofugal pathways (*blue*) in the pigeon (above) and the Nile crocodile (below). The projection area of the GLd has been studied in turtles but not yet in crocodiles. The two brains are not drawn to scale. For abbreviations see list of abbreviations. *Pigeon brain modified from Güntürkün, O., Verhoye, M., De Groof, G., Van der Linden, A., 2013. A 3-dimensional digital atlas of the ascending sensory and the descending motor systems in the pigeon brain. Brain Struct. Funct. 281, 269–281.*

The GLd consists of six components, of which four are retinorecipient and project onto the visual wulst (Güntürkün and Karten, 1991; Heyers et al., 2007). Liu et al. (2008) found "distance-to-collision" neurons in the pigeon's GLd that fire briskly at a certain distance when a large surface moves toward the animal. These GLd neurons nicely complement the "time-to-collision" neurons found within the tectofugal system (Xiao et al., 2006).

The projection of the GLd to the wulst is bilateral and topographically organized (Miceli et al., 1990; Fig. 8.20).

In owls with their more frontally oriented eyes, the proportion of ipsi- and contralateral GLd → wulst is about equal (Bagnoli et al., 1990). The visual wulst is organized from dorsal to ventral in four laminae: hyperpallium apicale (HA), interstitial nucleus of HA (IHA), hyperpallium intercalatum (HI), and hyperpallium densocellulare (HD). These subdivisions are based on the cytoarchitectonics of the wulst and do not reflect the full complexity of the structure, since Shimizu and Karten. (1990) were able to distinguish at least eight subdivisions using immunocytochemical techniques. The granular IHA and to some extent also lateral HD and HI are the major recipients of the cholinergic and colecystokinergic GLd input (Watanabe et al., 1983; Güntürkün and Karten, 1991).

Electrophysiological studies demonstrate similarities between the visual wulst of birds of prey and the striate cortex of mammals. The visual wulst of owls is retinotopically organized and contains both simple and complex cells tuned to basic visual parameters such as orientation, direction, and end-stopping (Pettigrew, 1979; Nieder and Wagner, 1999). As in the mammalian primary visual cortex, visual wulst neurons of owls signal the local orientation of features within moving object (Baron et al., 2007). In the visual wulst of further birds of prey, most neurons are primarily concerned with binocular visual processing, are selectively tuned to stereoscopic depth cues, and have small receptive fields that subtend about 1 degree of visual space (Pettigrew and Konishi, 1976; Pettigrew, 1979; Wagner and Frost, 1993). Wulst cells are also clustered into functional domains with orientation pinwheels analogous to those found in cat and monkey V1 (Liu and Pettigrew, 2003). The owl visual wulst also shows cellular correlates of binocular interaction (Pettigrew and Konishi, 1976; Pettigrew, 1979; Nieder and Wagner, 2001) and of illusory contours (Nieder and Wagner, 1999). Thus, in many aspects, the wulst of the barn owl is equivalent to mammalian primary visual cortex. But is the similarity a result of homology or of convergent evolution? It is currently impossible to decide this question, but studies in pigeons make it likely that at least some of these physiological characteristics result from convergence. A study on the neuronal population dynamics of the pigeons' visual wulst captured with voltage-sensitive dye imaging revealed a different kind of dynamic than what was observed in owls. In pigeons, analysis of the imaged spatiotemporal activation patterns revealed no clustered orientation or maplike arrangements as typically found in the wulst of owls and in the primary visual cortices of many mammalian species (Ng et al., 2010). A similar conclusion was also drawn by Bischof et al. (2016): using optical imaging of intrinsic signals, electrophysiological recordings, and retrograde tracers, they discovered that the visual wulst of zebra finches consists of three visual field representations, each receiving input from distinct subdivisions of the GLd in both hemispheres. No foveal magnification was evident in any of the subdivisions. Bischof et al. (2016) did discover some similarities to the mammalian design but also several features that seem unique to birds.

Astonishingly, the avian thalamofugal system serves two parallel functions. On the one hand, it is a classic visual pathway that transmits object vision from the eyes to the forebrain. On the other, it also has a key role in magnetic compass perception (Mouritsen et al., 2016).

Some avian species migrate over thousands of kilometers, while other just home over a lengthy valley back to their loft. Especially during long flights, but to some extent also during smaller voyages, global cues like those from a compass are very important. Indeed, many bird species have a magnetic compass that was first discovered in European Robins (Wiltschko and Wiltschko, 1972). The avian magnetic compass is an inclination compass, which detects the angle between the magnetic field lines and the Earth's gravity but not their polarity. Consequently, birds do not discriminate North from South, but poleward from equatorward (Wiltschko and Wiltschko, 1995).

How do birds sense the Earth's magnetic field, and where in the brain is magnetic compass information processed? Sensing magnetic fields as weak as that of the Earth is a tall task. Presently, a magnetic compass that is based on a light-dependent, radical-pair-based, chemical compass mechanism is the best candidate (Ritz et al., 2000). The primary sensory molecules appear to be cryptochrome proteins (Mouritsen et al., 2004). Indeed, retinal neurons contain at least four different cryptochromes (Liedvogel and Mouritsen, 2010).

If the avian magnetic compass is light dependent, covering the eyes should abolish compass perception. Indeed, magnetic compass sensing is lost especially when the right eye is covered (Witschko et al., 2002). Although the lateralization of magnetic compass vision is a matter of heated disputes (Hein et al., 2011; Wiltschko et al., 2011), it is clear that vision is required to sense the Earth's magnetic field orientation. This vision is also in need of high-frequency visual input, possibly because the low frequency compass input cannot be disambiguated from ordinary object vision (Stapput et al., 2010). Which parts of the avian brain process magnetic compass information? A forebrain area named "Cluster N" in the visual hyperpallium is by far the most active part of the brain when night-migratory songbirds use magnetic compass information for orientation behavior (Mouritsen et al., 2005). Activation of Cluster N disappears when the eyes are covered (Liedvogel et al., 2007), and neuronal tracing showed that Cluster N is a small part of the visual wulst, which receives its input from the eyes via the thalamofugal

visual pathway (Heyers et al., 2007). When Cluster N is inactivated, night-migratory songbirds cannot use their magnetic compass anymore, whereas their sun and star compasses remain functional (Zapka et al., 2009). Since Cluster N is part of the thalamofugal visual pathway, this is very strong evidence that the magnetic compass is light dependent that the primary sensors are in the eyes and that birds perceive magnetic compass information as a visual impression.

To some extent, magnetic compass perception resembles infrared vision in snakes. In both cases, a "classic" sensory pathway is used to transmit a different kind of signal. The result is a change at the sensory input level but not an alteration in the pathway. The tectofugal visual pathway of snakes stays the same, at least from the tectum on, but now incorporates thermal information superimposed on object vision. In birds, magnetic compass information is also superimposed on object vision (Ritz et al., 2000). The thalamofugal pathway stays the same, but now includes a special field, Cluster N, within the visual wulst.

Now let us discuss the thalamofugal system in reptiles. Retinal ganglion cells of all reptilian species project contra- or bilaterally onto the GLd (Ulinski and Nautiyal, 1988; Derobert et al., 1999). The GLd in turtles subsequently projects onto the ipsilateral visual cortex (Mulligan and Ulinski, 1990). In addition, visual cortex has projections back onto both GLd and the optic tectum, as also is the case in birds (Hall et al., 1977; Güntürkün, 2000; Fig. 8.20). This pattern does not apply to all reptiles, however. In lizards, Lohman and van Woerden-Werkley (1978) demonstrated that GLd projects to striatum but not to cortex.

The functional organization of thalamocortical projections in turtles is not resolved. According to Mazurskaya (1973), visual cortical neurons respond to small visual stimuli from everywhere in the visual field. This would imply an absence of retinotopy. In contrast, Mulligan and Ulinski (1990) describe a topological projection from GLd to visual cortex, albeit with multiple boutons-en-passant. They conclude that there is an orderly representation of the rostral–caudal axis of the ipsilateral dorsal lateral geniculate complex within the visual cortex of turtles that is combined with a convergence of inputs from neurons located along a given dorsal–ventral dimension. This would result in topography along one dimension, but not along the other. As outlined in Section 8.3.3.2.1, it is conceivable that place coding in the visual cortex of turtles does not occur by means of topographic maps but by nontopographically organized ensembles of neurons (Fournier et al., 2015; Naumann et al., 2015).

Extensive lesions of the forebrain pathway severely impair the ability of turtles to relearn visual discrimination that they had acquired before surgery (Reiner and Powers, 1980). This is different, when only the visual cortex has been damaged. In this case, deficits are very subtle (Bass et al., 1973).

8.4.1.2 The Tectofugal Visual Pathway in Birds and Reptiles

In all sauropsids, optic nerve axons decussate virtually completely in the optic chiasma and then terminate in diverse areas of the midbrain and thalamus. In birds, the largest contingent of optic axons synapses in the optic tectum. The exact proportion is difficult to estimate but according to the data of Bravo and Pettigrew (1981) in barn owls and Remy and Güntürkün (1991) in pigeons, 75–95% of ganglion cells have axons leading to the tectum in these bird species. With regard to these numbers, the burrowing owl, *Speotyto cunicularia*, is an exception. This bird relies heavily on its thalamofugal pathway and consequently has less than 50% tectally projecting ganglion cells (Bravo and Pettigrew, 1981).

In Section 8.3.2.3 we briefly outlined the organization of the visual input to the optic tectum in birds. Only few things should be added here: in birds, retinal axons only innervate the superficial layers 2–7 and reach their highest synaptic density in layer 5 (Hayes and Webster, 1985). The retinal projection onto the tectum is strictly topographically organized in all species studied, with the inferior retina projecting to the dorsal tectum while the posterior tectum is reached by the nasal retina (Clarke and Whitteridge, 1976; Frost et al., 1990a; Remy and Güntürkün, 1991). The tectal representation of the foveae or the areas of enhanced vision are considerably expanded (Clarke and Whitteridge, 1976; Frost et al., 1990a). Single-unit recordings in the optic tectum demonstrate that the visual receptive fields of neurons in the superficial layers are small (0.5–4 degrees) but increase to up to 150 degrees in deeper laminae (Jassik-Gerschenfeld et al., 1975; Frost et al., 1981). It is possible that these numbers have to be downsized a bit when more objective measures of determining receptive field borders are used (Verhaal and Luksch, 2013). However, the principal pattern of an increasing receptive field size in deeper layers is valid across studies spanning four decades. According to Verhaal and Luksch (2013), about 10% of tectal neurons are luminance sensitive.

Tectal cells also respond selectively to the spatial frequency of drifting sine-wave gratings, with most neurons having their optima between 0.45 and 0.6 c/degree (Jassik-Gerschenfeld and Hardy, 1979). Most of these cells are more selective to spatial frequencies than they are to single bar stimuli (Jassik-Gerschenfeld and Hardy, 1980). Birds therefore appear to be able to perform Fourier analysis of patterns in visual space at the level of the tectum. Indeed, Neuenschwander and Varela (1993) demonstrate visually triggered gamma oscillations in the pigeon's tectum. This oscillatory activity

has characteristics similar to those reported in the mammalian neocortex in the context of synchronization of unit responses as a putative physiological basis of perceptual binding (Yu et al., 2008).

In all birds (and possibly in all amniotes), the dominant brain structure for shifting visual attention of the animal toward relevant stimuli is the optic tectum (Luksch, 2003). The tectum works like a saliency map where the relative salience of stimuli is processed and compared with other objects (Dutta and Gutfreund, 2014). Novel or moving objects are potentially important. Consequently, most tectal cells are movement sensitive and play an important role in figure–ground segregation through discontinuities in velocity (Jassik-Gerschenfeld and Guichard, 1972; Frost et al., 1990b; Verhaal and Luksch, 2016).

One type of layer 13 neuron with projections to the Rt has very large, circular dendritic fields that span up to 2 mm and extend into retinorecipient tectal layer 5b. These retinorecipient "bottlebrush" ending-neurons respond with rhythmic bursts (chattering) to depolarizing current injections (Luksch et al., 2001). Such high-frequency bursts have been observed in response to small moving spots in deep tectal neurons of pigeons with burst frequency linearly increasing with stimulus speed (Troje and Frost, 1998). These neurons respond best to fast motion and also show strong directional selectivity. They may be ideal for detecting movement and novelty and subsequently initiating an orienting response (Verhaal and Luksch, 2016).

Indeed, Marín et al. (2007) demonstrated that tectal responses that are triggered by a salient moving stimulus are swiftly transmitted to the layer 13 neurons that then project to Rt (Güntürkün et al., 1998). Marín et al. (2012) showed that tectally initiated visual responses from the isthmic nucleus Ipc send phase-locked feedback signals to the tectum and thus select which afferent activity propagates to the different subdivisions of the Rt and entopallium. The entopallium further projects to multiple visual associative areas including the nidopallium frontolaterale (NFL), mesopallium ventrolaterale (MVL), and nidopallium intermediale pars lateralis (NIL) (Husband and Shimizu, 1999; Krützfeld and Wild, 2005). Stacho et al. (2016) demonstrated that visual stimulus repetition in pigeons results in a reduction of cellular responses in these associative visual regions, just as single-unit recordings revealed reduced activity after repeated or prolonged visual stimulation throughout the primate visual system (Müller et al., 1999). It is likely that this effect reflects a learning-related buildup of stimulus familiarity and represents selective stimulus memory with subsequent response sharpening (Tartaglia et al., 2015). If this interpretation holds, these associative visual telencephalic areas would be part of a distributed visual memory system of birds (Fig. 8.20).

The situation in reptiles is highly similar to that in birds, although far less is known. Since the majority of studies were conducted in crocodilian species, we will first review these experiments. As in birds, retinal fibers in crocodile's project massively to the contralateral tectum end terminate in the upper six layers (Derobert et al., 1999). The pattern is extremely similar to birds with the exception that the first two plexiform tectal layers in crocodiles are practically fused and narrow. Neurons from deep tectal layer (corresponding to the avian tectal layer 13) project bilaterally onto the thalamic Rt (Pritz, 1980). Like in birds, also the Rt of crocodiles can be subdivided anatomically, although no functional data on different cellular properties of these thalamic constituents exist (Pritz, 1997; Pritz and Siadati, 1999). Telencephalic projections of Rt assemble ventromedially and ascend within the dorsal peduncle of the lateral forebrain bundle. At more anterior levels of the telencephalon, these axons turn dorsally and terminate massively in the dorsolateral part of anterior DVR (Pritz, 1975). The termination area corresponds to area G of Rose (1923), is rich in succinate dehydrogenase (Pritz and Northcutt, 1977), and is probably homologous to the avian entopallium (Fig. 8.20).

The situation in other reptiles is comparable. In turtles, a tectofugal pathway very similar to the one described in crocodiles has been discovered (Balaban and Ulinski, 1981). In lizards, large multipolar neurons of the deep tectal layer stratum griseum centrale project toward the Rt (Dávila et al., 2002). The ascending projections of the Rt make synaptic contacts in the striatum and synapse in dorsolateral and ventromedial region of ADVR and the amygdaloid complex (Guirado et al., 2000).

8.4.2 Ascending Somatosensory Systems

Both in reptiles and birds, an important part of the spinal projections terminates in the dorsal column nuclei (DCN) of the caudal rhombencephalon and transmit non-facial tactile information from the limbs and the trunk. The DCN refers to the gracile and the cuneate nucleus. Both in reptiles (Pritz and Stritzel, 1994b) and birds (Necker, 1991), the spinal input is constituted by direct projections of the dorsal root ganglia to the DCN and a further pathway that involves at least one synapse in the spinal cord before terminating in the DCN. Previously, these nuclei were seen to be a derived system that only exists in amniotes (Hayle, 1973). However, more recent studies could clearly demonstrate a comparable system in frogs (Muñoz et al., 1997; Hiramoto and Cline, 2009).

In birds, the upper cervical spinal segments and the DCN project via the medial lemniscus to the inferior olive, then to the deep tectal layers and finally to the n. intercollicularis (ICo) (Wild, 1989, 1995; Luksch, 2003).

In budgerigars, spinal efferents also reach a small rhombencephalic nucleus which projects directly to the n. basalis prosencephali (Bas) in the telencephalon. Thus, in budgerigars, the Bas has both a head (from the trigeminal input; see below) and a body representation (Wild et al., 1997). In pigeons, no such projection has been demonstrated. Although the situation in reptiles is less clear, spinal and DCN projections to the central nucleus of the torus semicircularis of the midbrain were observed in various species (crocodiles: Ebbesson and Goodman, 1981; Pritz and Stritzel, 1989; turtles: Künzle and Woodson, 1982).

Spinal segments and the DCN of birds project to two main thalamic targets, the DLP and the n. dorsalis intermedius ventralis anterior (DIVA) (Funke, 1989; Korzeniewska and Güntürkün, 1990; Wild et al., 2008). No projection from the ICo to these thalamic targets is reported in this species (Wild, 1987; Korzeniewska and Güntürkün, 1990). In *Caiman*, spinal projections also terminate in a thalamic target, the medialis complex (Pritz and Nortcutt, 1980). Different from pigeons, also the crocodilian torus semicircularis projects to this thalamic nucleus (Pritz and Stritzel, 1990).

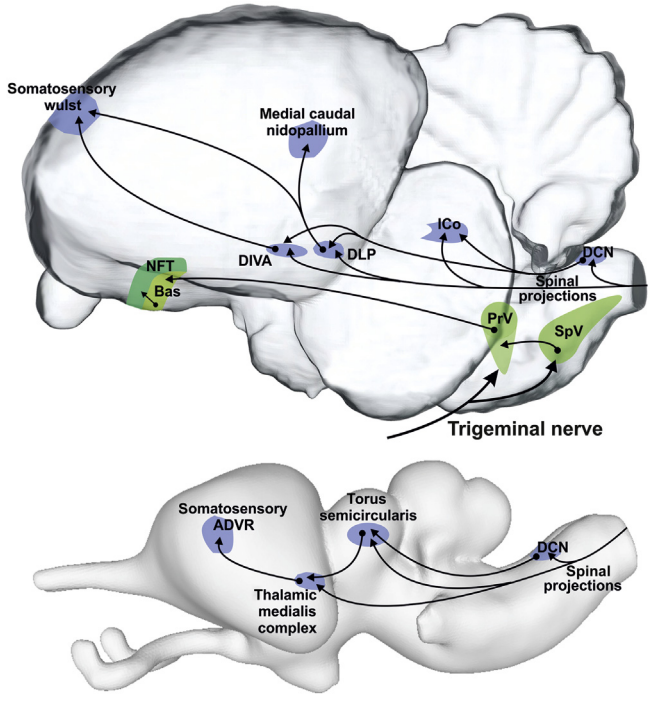

FIGURE 8.21 Ascending somesthetic pathways in birds (above) and crocodiles (below). In budgerigars also a spinal projection via a rhombencephali link to the n. basalis prosencephali (Bas) was demonstrated (not shown here for the pigeon brain). Central trigeminal projections in crocodiles are unknown. For abbreviations, see list of abbreviations. *Pigeon brain modified from Güntürkün, O., Verhoye, M., De Groof, G., Van der Linden, A., 2013. A 3-dimensional digital atlas of the ascending sensory and the descending motor systems in the pigeon brain. Brain Struct. Funct. 281, 269–281. For abbreviations, see list of abbreviations.*

In pigeons, the thalamic somatosensory nuclei DLP and DIVA have different ipsilateral projections to the telencephalon. DLP projects to a somatosensory area in the medial caudal nidopallium and to the somatosensory wulst (Wild, 1987). The main thalamic projection, however, ascends from DIVA and terminates in the rostral somatosensory part of the wulst (Wild et al., 2008). In crocodiles and turtles, the main thalamic somatosensory nuclei (medialis complex in crocodiles, n. caudalis in turtles) project to the central part of the ADVR (Balaban and Ulinski, 1981; Pritz and Stritzel, 1994a; Fig. 8.21). The reptilian medialis complex and n. caudalis are probably comparable to the avian DLP. This accords with their thalamic topography and their projection pattern that is restricted to the DVR. This would imply that the DIVA-wulst projection could be a derived feature of avian evolution, although it resembles the mammalian somatosensory projection in almost all aspects of its features.

A second major source of somatosensory information stems from the head area and is transmitted via the trigeminal system as well as the sensory components of the facial and the glossopharyngeal nerves (Necker et al., 2000). Although crocodiles seem to be extremely sensitive to even slightest touches on their heavily armored jaws (Leitch and Catania, 2012), our knowledge on the trigeminal system in reptiles is extremely limited. The following account is therefore centered on birds.

The somata of the trigeminal nerve in pigeons are located in the trigeminal ganglion gasseri of which the central root enters the brain stem and terminates in the n. principalis nervi trigemini (PrV) and the spinal sensory nucleus of the trigeminal nerve (SpV) (Wild and Zeigler, 1996). In the mallard duck, SpV shows bilateral intratrigeminal projections to the ventral component of PrV as well as ipsilateral projections into various cerebellar lobes (Arends et al., 1984). In addition, a descending part of the trigeminal tract extends caudally to the upper spinal cervical segments and terminates in the n. cuneatus externus (Dubbeldam and Karten, 1978). The only known projection of PrV to higher brain centers is a direct connection via the quintofrontal tract to the n. basalis prosencephali (Bas) in the rostrocaudal telencephalon (Wild et al., 1985; Schall et al., 1986). Bas projects via the nidopallium frontotrigeminale (NFT) to arcopallial substructures and the NCL (Mouritsen et al., 2016). This pathway was outlined in Section 8.3.3.3.2.1 (Fig. 8.21).

The ophthalmic branch of the trigeminal nerve in birds (representing the upper beak) possibly also mediates magnetoreception. Surgical ablation of the ophthalmic branch results in deficits in the detection of magnetic field changes (Mora et al., 2004) or decreases of magnetically induced neural responses of SpV and PrV (Heyers et al., 2010). It is conceivable that the

trigeminal system of birds carries positional magnetic information because migratory birds can only compensate for a 1000 km displacement if the ophthalmic nerve remains intact (Kishkinev et al., 2013).

8.4.3 The Olfactory System

Olfaction is among the most ancient sensory systems and still plays a key role in a variety of behaviors that range from feeding to mating. Broadly speaking, the olfactory system comprises two distinct components: the main olfactory system, which is responsible for the sense of smell, and the vomeronasal system, which guides pheromone-based communications. Both systems are extremely sensitive and are, in some species, capable of discriminating between distinct odors of extremely low concentrations. Once chemical molecules bind to receptors cells in the olfactory epithelium, this information is transmitted via the olfactory nerves to the main olfactory bulb (MOB) and, in some species, to the accessory olfactory bulb (AOB) of the vomeronasal system. The MOB exists in nearly all vertebrates, but the AOB first appears in amphibians and is present in reptiles and mammals; it is absent in birds (Hayden and Teeling, 2014).

8.4.3.1 The Olfactory System of Birds

Birds possibly do not have a vomeronasal system. Their MOB projects via the lateral olfactory tract to the CPi, the prepiriform cortex (CPP), the HD, the anterior olfactory nucleus, the TnA, and some perihippocampal structures. Via the intermediate olfactory tract, the olfactory bulb also reaches the medial septum (SM), the TuO and, by crossing the midline, the contralateral bulb (Reiner and Karten, 1985; Patzke et al., 2001; Atoji and Wild, 2014). CPi and CPP are interacted with the visual system and limbic structures (Atoji and Wild, 2014).

Birds were historically considered microsmatic or even anosmic, but their behavior and their neuroanatomy tell a different story (Caro et al., 2015). When pigeons home over previously unexplored areas, they rely on an olfactory map (Wallraff, 2005). The critical role of olfaction in pigeon navigation was first discovered by Papi et al. (1971), who observed that anosmic pigeons were unable to home. He proposed that pigeons acquire an olfactory map by associating the odors carried by the winds at the home area with the directions from which they blow. Once at the release site, they recognize the local odors and determine the direction of displacement. Since then, a large number of studies could firmly establish the role of olfaction in avian navigation (Gagliardo, 2013). The relevance of smell for navigation is also reflected in the neuroanatomy of birds. Olfactory bulbs are spectacularly enlarged in birds known to use olfactory cues for navigation and foraging such as seabirds (Wallraff, 2005). Manipulation of the olfactory system such as plugging the nostrils (Gagliardo et al., 2007), anaesthetizing the olfactory mucosa (Wallraff, 1988), transecting the olfactory nerve (Papi et al., 1971; Gagliardo et al., 2009), or ablating the CPi (Papi and Casini, 1990) generates remarkable and lateralized disruptions of initial orientation and homing performance in pigeons (Gagliardo, 2013). In addition, when homing pigeons are released at an unfamiliar location, their CPi is much more active, compared to a release at a familiar site. These results implicate the CPi of pigeons in the processing of olfactory map cues over uncharted territories when lying home (Patzke et al., 2010).

8.4.3.2 The Olfactory System of Reptiles

In reptiles, the main olfactory pathway and the vomeronasal system were investigated in quite a number of species, although the majority of the studied species focus on lizards and snakes (Reiner and Karten, 1985; Lanuza and Halpern, 1998; Martinez-Marcos et al., 2002). These studies suggest that snakes especially live in an olfactory world. As outlined later, the olfactory system constitutes a major part of their brain.

The main olfactory system is an open-ended detector of airborne odorants since it is able to represent endless combinations of compounds. The vomeronasal system is different. It evolved for detection of biologically relevant chemical cues (pheromones) that are mostly related to ingestive, sexual, or agonistic interactions. The vomeronasal organs (VNOs) are paired chemosensory organs in the anterior roof of the mouth that reach their highest development in squamate reptiles, and especially in snakes (Burghardt, 1993). Since vomeronasal olfaction serves a different behavioral role than the main olfactory system, their neural substrates differ as well (Martinez-Marcos et al., 2002). While olfaction can be mainly achieved during normal respiration, the vomeronasal system is activated by specific sequences of behavior. In snakes, chemical compounds are gathered in the environment by the tongue and are delivered to the VNOs and the main olfactory system with tongue-flicks. But tongue-flicks are not only about smell; a second kind of newly discovered tongue-flick is optimized for tasting objects on the ground (Daghfous et al., 2012).

The MOBs in snakes project through the lateral, the intermediate, and the medial olfactory tracts to the full extent of the lateral cortex as well as to the external and the ventral anterior amygdala. In addition, olfactory fibers reach the olfactory tubercle, the olfactory gray, and the dorsomedial retrobulbar formation (Lanuza and Halpern, 1998). Interestingly, these structures project back to the bulb, creating a closed loop within the main olfactory system.

The vomeronasal epithelium relays chemosensory information to the AOB, which in turn projects through the accessory olfactory tract to secondary vomeronasal-

recipient areas such as the medial amygdala and, especially, to the nucleus sphericus (Lanuza and Halpern, 1998; Martinez-Marcos et al., 2002). The latter structure occupies a very large fraction of the telencephalon, thus testifying to the relevance of vomeronasal input for snakes. N. sphericus projects to the rostral dorsal cortex, the rostral lateral cortex, the olfactostriatum of the rostral basal telencephalon, the ventromedial hypothalamic nucleus, and several amygdaloid nuclei olfactostriatum in the basal telencephalon (Halpern, 1992; Lohman and Smeets, 1993; Lanuza and Halpern, 1997). Minor projections of the AOB also lead to the nucleus of the accessory olfactory tract.

As for the main olfactory system, the vomeronasal pathway features reciprocal projections between the olfactory and its target structures. However, the structures that receive vomeronasal input also have projections to the hypoglossal nucleus which controls the tongue-flicks (Martinez-Marcos et al., 2005). Especially the medial amygdala, which receives both olfactory and vomeronasal afferents, has projections to the hypoglossus via the lateral hypothalamic nucleus. Thus, the olfactory brain of snakes directly feeds back to the recipient sensory areas and controls the tongue with which odorant molecules are gathered (Martinez-Marcos et al., 2001).

8.4.4 Ascending Auditory Systems

The subtelencephalic auditory pathways were outlined in great detail in Chapter 1.14, Evolutionary Trends in Hearing in Nonmammalian Vertebrates by Catherine Carr in this volume. We therefore will only shortly summarize the main auditory brain stem components in birds and will contrast them with those of reptiles. Subsequently, we will review the telencephalic components of the auditory system in birds in some detail, thereby emphasizing both anatomy and function.

In birds, the fibers of the nervus octavus enter the medulla oblongata and split into two branches that terminate in the n. magnocellularis (NM) and the n. angularis (NA). Neurons of NM project bilaterally to n. laminaris (NL), which thus is the first neural entity that integrates input from both ears and is involved in processing interaural time differences (Young and Rubel, 1983; Necker et al., 2000). It seems that NM afferents to NL constitute delay lines, such that NL neurons can act as coincidence detectors, thereby creating an ordered map of interaural time differences (Vergne et al., 2009). Both NA and NL project bilaterally to the n. olivaris superior (OS) which projects back in inhibitory manner to NM and NL to increase the acuity of temporal integration (Burger et al., 2005). Besides these descending projections, OS, NA, and NL project in ascending direction to the n. mesencephalicus lateralis pars dorsalis (MLD) of the midbrain as well as to diverse subnuclei of the lateral lemniscus (LL; Arends and Zeigler, 1986). Since MLD is believed to be homologous to the mammalian inferior colliculus (IC), especially scientists working on the owl auditory system prefer to use the term IC when referring to the avian MLD (Wagner et al., 2003). The subnuclei of the lateral lemniscus have differential projections, with one component projecting to the forebrain Bas, thereby bypassing the thalamus, while other branches terminate in MLD (Wild, 1987). The ventral component of LL projects to MLD as well as the thalamic relay nuclei n. ovoidalis (Ov) and n. uvaeformis (Uva) (Wild et al., 2010). Uva projects via the pallial n. interface (NIf) to the HVC in songbirds and thus plays a key role in the auditory input into the song system (Mooney, 2014). The midbrain MLD projects ipsilaterally to Ov from where projections ascend ipsilaterally to field L of the telencephalon (Wild et al., 1993). Field L has been divided into three laminae (Ll, L2, L3), and it is L2 where the fibers from the Ov mainly terminate (Carr, 1992; Fig. 8.22).

In reptiles, the auditory nerve also projects topographically to the reptilian version of NM and NA (Burger et al., 2005; Vergne et al., 2009). The functional organization of these cochlear nuclei seems to be very

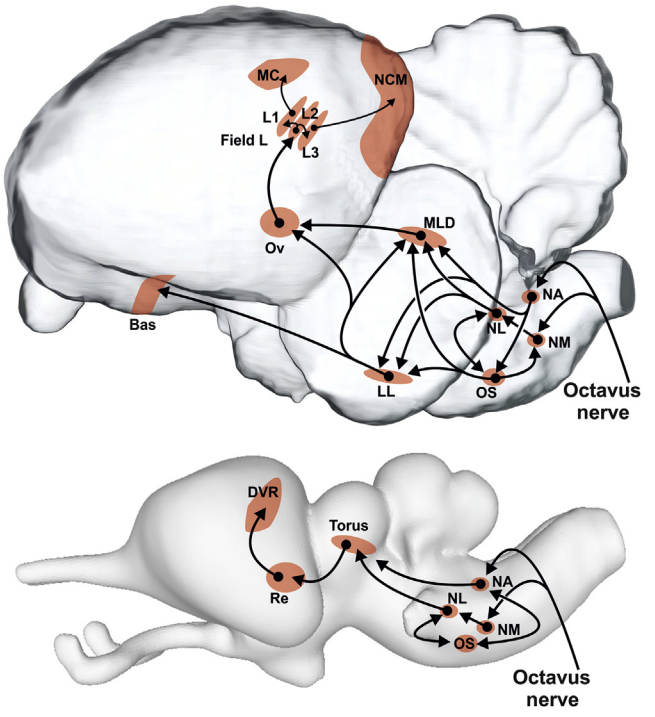

FIGURE 8.22 Ascending auditory pathways in birds (above) and crocodiles (below). The avian auditory pathways are depicted in pigeons, which is not a song bird. Therefore song system–specific structures were omitted. *Pigeon brain modified from Güntürkün, O., Verhoye, M., De Groof, G., Van der Linden, A., 2013. A 3-dimensional digital atlas of the ascending sensory and the descending motor systems in the pigeon brain. Brain Struct. Funct. 281, 269–281.*

similar to that of birds (Manley, 1970). As in birds, the reptilian NL receives afferents from NM and possibly also plays a role in sound localization (Vergne et al., 2009). In caiman, NA and NL project to OS, which then backprojects (Strutz, 1981). Again, this connectivity pattern resembles that of birds and thus could imply that also in reptiles OS projections sharpen auditory temporal integration.

In crocodilians, NA and NL project bilaterally to the torus semicircularis (ten Donkelaar, 1998). This structure shows a clear tonotopic frequency organization (Manley, 1971). According to Pritz (1974a), the central nucleus of the torus semicircularis projects to the core of the thalamic n. reuniens (Re) in caiman. It is likely that the reptilian reuniens and the avian ovoidalis are homologous thalamic auditory relay nuclei. Both structures show a clear tonotopy. Pritz (1974b) also demonstrated that the central core of Re projects to a caudomedial region of the ipsilateral DVR. This is highly similar both in terms of connectivity as well as in terms of topography to the projection of Ov to field L in birds. The auditory caudomedial area in the crocodile DVR shows a similar tonotopic organization as found in the torus semicircularis and in the cochlear nuclei (Weisbach and Schwartzkopff, 1967). Thus, the frequency-specific projections from the auditory medulla to the dorsal thalamus and thence to the forebrain are well conserved in birds and reptiles (Vergne et al., 2009; Fig. 8.22).

Auditory processes beyond the termination area in the caudomedial DVR were not studied yet in reptiles, but were extensively analyzed for field L in birds. Projections of the Ov mostly terminate in field 2, but only sparsely terminate in the adjacent L1 and L3 (Wild et al., 1993). L2 projects upon L1 and L3, while L1 projects to the caudal mesopallium. Efferents of L3 terminate in the nidopallium caudomediale (NCM) and HVC in songbirds (Reiner et al., 2004) (see Section 8.4.5). It is possible that the HVC of songbirds represents an auditory specialization that derives from the NCL (Feenders et al., 2008). Consequently, in pigeons, L3 projects to NCM and NCL. Axons from NCL terminate in the arcopallium (Kröner and Güntürkün, 1999).

Single-unit recordings in L2 reveal rather simple V-shaped tuning curves with inhibitory side bands (Leppelsack, 1974). Other cells in the entire field L-complex show broad responsiveness to stimuli such as bird calls, pure tones, or white noise (Prather, 2013). Recordings or immediate early gene studies from NCM already evince a high auditory selectivity, with some cells in songbirds being specialized for song of the bird's own species or songs of other species (Phan et al., 2006; Stripling et al., 2001). Most importantly, NCM seems to serve as an acoustic memory (Moorman et al., 2011). This is visible in the ability of NCM neurons to progressively reduce their activity to repeated presentation of the same song, but to then immediately be very active when being presented with presentation of a new song (Prather, 2013). NCM is one of the critical gateways between the ascending auditory pathways and the song system that is outlined in Section 8.4.5.

In birds, a subcomponent of the n. lemniscus lateralis (LL) of the midbrain has a direct projection to the n. basalis prosencephali (Bas) in the frontoventral telencephalon (Schall et al., 1986). The Bas is also the termination area of the trigeminal system (see Section 8.4.2). Why should a trigeminal area receive auditory input? Imagine that you chew a nut. You will sense the haptic component of the nut via your trigeminal system. But you will also hear the cracking sound of the nut via bone-conducted hearing. Thus, auditory input always accompanies eating as a vital fast feedback pathway. This is true for both biting and pecking. Accordingly, Schall and Delius (1986) could show that the characteristics of evoked potentials from Bas make a bone as well as a cochlea-mediated sound input likely. Schall et al. (1986) demonstrated that Bas receives also direct input from the medullary nucleus vestibularis superior. Thus, Bas has a trigeminal, an auditory, and a vestibular input which all bypass the thalamus. As shown by Schall (1987) in pigeons with multiunit recordings, Bas neurons evince a specific directional sensitivity to rotatory vestibular stimulation that results from pitch motions of the head in the downward direction. This is exactly the head motion that occurs during pecking! Taken together, the auditory projection to Bas is possibly part of a sensory system that is highly specialized to represent the relevant sensory properties to guide pecking in birds (Fig. 8.22).

8.4.5 The Avian Song System

All birds vocalize, but only some birds sing. The trick about birdsong is that it has to be learned during early ontogeny (or during each season in some species). Vocal learning is a rare trait that only few animal groups possess, among them humans (Wilbrecht and Nottebohm, 2003). Possibly, vocal learning evolved independently multiple times in different vertebrate species (see Petkov and Jarvis, 2012 for various evolutionary scenarios). Among primates, vocal learning is well developed only in humans but not in nonhuman primates (Egnor and Hauser, 2004; Fischer et al., 2015). There are only a handful of other mammals that are vocal learners. These include marine mammals such as cetaceans (King et al., 2013; Janik, 2014) and pinnipeds (Reichmuth and Casey, 2014) and some terrestrial mammals including bats (Boughman, 1998; Knörnschild, 2014) and elephants (Poole et al., 2005). However, the most numerous vocal learners are three groups of birds—songbirds (Nottebohm and Liu, 2010), hummingbirds (Gaunt et al., 1994; Araya-Salas

and Wright, 2013), and parrots (Berg et al., 2012). Learned vocalization can be used to address and label individuals, attract females, repel rivals, and define territory (Nottebohm and Liu, 2010; Berg et al., 2012; King and Janik, 2013; Janik, 2014; Knörnschild, 2014). It should be noted that there is no simple dichotomy between vocal learners and nonlearners, as some vocal nonlearners possess at least a limited form of vocal learning (Saranathan et al., 2007; Arriaga et al., 2012; Petkov and Jarvis, 2012).

The learning of song in songbirds has many parallels with the human speech acquisition (Doupe and Kuhl, 1999). Both have a critical phase in early life during which they can acquire new vocalizations much easier. Song learning and speech acquisition start with a purely sensory phase followed by a motor (sensory-motor) phase during which vocalizations are produced. In both species, auditory feedback is essential for proper learning. It is interesting to note that although mammals and birds possess different, nonhomologous vocal organs, the underlying physical mechanisms of vocalizations produced by these vocal organs might be largely the same in both species (Elemans et al., 2015).

Juvenile songbirds memorize the song of a tutor bird during a sensory period and form an internal representation of its song (Brainard and Doupe, 2002; Konishi, 2010). The learning process is facilitated by an auditory predisposition for conspecific sounds which is likely genetically determined (Wheatcroft and Qvarnström, 2015). Later in the sensorimotor phase, birds start to produce their own vocalizations. The auditory feedback of these developing vocalizations that the individual bird produces is compared to the tutor song template. These early initial vocalizations are called subsong and resemble babbling in humans. The subsong gradually develops into plastic song which already incorporates some recognizable elements from the tutor's song. This song is further refined until it reaches its final, crystallized form (Brainard and Doupe, 2002; Bolhuis et al., 2010).

There are several hypotheses on the evolution of vocal learning (Nottebohm and Liu, 2010; Nowicki and Searcy, 2014). One interesting possibility is that vocal learning evolved due to a preexisting sensory bias of females for complex sounds which can be explained by stimulus-specific habituation mechanisms (Searcy, 1992). Since it may be easier to produce more complex songs through learning rather than innate motor programs (Nowicki and Searcy, 2014), sexual selection based on the preference of females for complex songs might have promoted the emergence of vocal learning in males, at least in some species (Soma and Garamszegi, 2011; Woodgate et al., 2011, 2012). In turn, the complexity of male's song seems to have become an indicator for the bird's fitness (Nowicki et al., 1998, 2002; Woodgate et al., 2012). According to one hypothesis, a well-developed song repertoire in males indicates quality of the individual because of the temporal coincidence of song learning and developmental stress (Nowicki et al., 1998, 2000, 2002). Thus, if an individual manages to acquire complex songs despite stressful factors during the developmental period, such as limited nutrition, it probably possesses a stress-resistant genotype and more robust phenotype. Accordingly, song repertoire size was shown to correlate with survival of offspring (Woodgate et al., 2012) and learning performance in a foraging task (Boogert et al., 2008). The latter indicates that song complexity may signal to the female, a male's cognitive capacities, which in turn correlates with parental, foraging, and predator-avoidance skills, as well as with territory quality (Searcy, 1992; Nottebohm and Liu, 2010). Therefore, it is likely that one of the main advantages of vocal learning in songbirds was the expansion of the vocal repertoire which then increased mating success (Nowicki and Searcy, 2014).

The neurobiology of vocalization has been extensively studied in songbirds. Because they have a specialized "song system" of cell groups that are easily identifiable, songbirds represent a suitable animal model to investigate neurobiology of language, learning, and memory as well as neuronal plasticity and neurogenesis (Jarvis, 2004; Doupe et al., 2005; Bolhuis et al., 2010; Barnea and Pravosudov, 2011; Moorman et al., 2011).

Two specialized neuronal pathways within the song system have been implicated in vocalization (for reviews, see Brainard and Doupe, 2002; Jarvis, 2004; Bolhuis and Gahr, 2006; Bolhuis et al., 2010; Moorman et al., 2011; Fig. 8.23). These pathways are the posterior song motor pathway (SMP) and the anterior forebrain pathway (AFP). Both originate in the HVC, a song system nucleus in the dorsal aspect of the caudal nidopallium (HVC is its full, letter-based name). However, the two pathways originate from distinct neuronal populations. The HVC neurons that give rise to the SMP project to the robust nucleus of the arcopallium (RA), which in turn projects to the dorsal medial nucleus of the midbrain (DM), to the tracheosyringeal part of the nucleus hypoglossus (nXIIts), and to some respiratory brain stem nuclei (Wild, 1997). The nXIIts innervates the muscles of the syrinx, the vocal organ of songbirds. The HVC neurons of the AFP project to the AreaX in the medial striatum. The striatal medium spiny neurons in AreaX project to pallidal-like neurons of the AreaX which in turn project to the dorsal lateral nucleus of the medial thalamus (DLM; Carrillo and Doupe, 2004; Kuenzel et al., 2011). DLM projects back to the telencephalic lateral magnocellular nucleus of anterior nidopallium (LMAN). Finally, LMAN projects back to AreaX and also interconnects AFP and SMP via its projections to RA.

The SMP generates and coordinates the activity of syringeal and respiratory muscles and is important for song production and certain aspects of song learning (Nottebohm et al., 1976; Wild, 1997; Brainard and

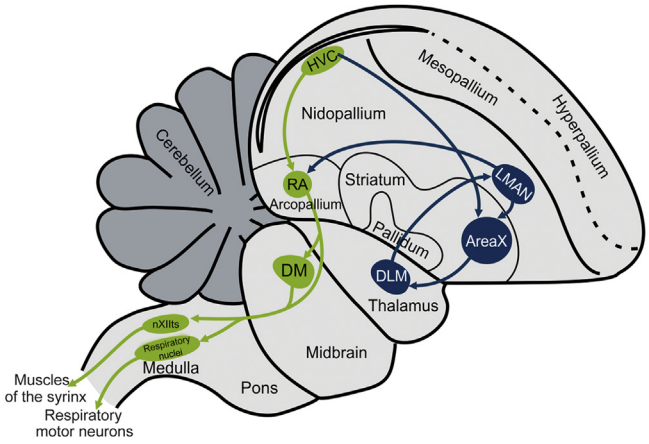

FIGURE 8.23 The figure shows the anterior forebrain pathway (*blue*) and the posterior song motor pathway (*green*) of the song control system in songbirds. Neurons in the HVC project either to the robust nucleus of the arcopallium (RA) or to AreaX in the medial striatum. The pallidal-like neurons of AreaX project to the dorsal lateral nucleus of the medial thalamus (DLM) which projects to the lateral magnocellular nucleus of anterior nidopallium (LMAN). LMAN projects back to AreaX and also connects the two pathways via its projection to RA. RA projects directly and indirectly, via the dorsal medial nucleus of the midbrain (DM), to the tracheosyringeal part of the nucleus hypoglossus (nXIIts) and to some respiratory nuclei in the brain stem. These nuclei innervate syringeal muscles and respiratory motor neurons in the spinal cord, respectively. *Reproduced from Moorman, S., Mello, C.V., Bolhuis, J.J., 2011. From songs to synapses: molecular mechanisms of birdsong memory. Molecular mechanisms of auditory learning in songbirds involve immediate early genes, including zenk and arc, the ERK/MAPK pathway and synapsins. Bioessays 33, 377–385.*

Doupe, 2002; Bolhuis et al., 2010). Consequently, lesions of HVC or RA practically abolish complex vocalizations without impacting the bird's disposition to sing (Nottebohm et al., 1976; Aronov et al., 2008). Interestingly, although the axons of HVC neurons start to grow and reach the dorsal border of RA already during the sensory phase of song development, they do not enter this nucleus until the onset of the motor phase (Mooney and Rao, 1994; Nowicki et al., 1998). Thus, the developmental time point of the SMP underlines its importance for song production. Electrophysiological investigations revealed that the population of RA-projecting HVC neurons seems to represent the temporal sequence of song syllables (Vu et al., 1994; Yu and Margoliash, 1996; Hahnloser et al., 2002). This sequence is then conveyed to the myotopic map in RA (Vicario, 1991; Hanloser et al., 2002), where neurons exhibit temporally precise and structured patterns of burst activity associated with specific notes (Vu et al., 1994; Yu and Margoliash, 1996). Thus, the plasticity of HVC-RA synapses is possibly a key component in the production of learned complex vocalizations (Mooney, 1992; Hahnloser et al., 2002). In addition, the study of Day et al. (2008) suggests that the HVC might control song plasticity during sensorimotor learning.

The AFP is necessary for song learning and adult song plasticity, and it might be involved in memorization of the tutor song (Bolhuis et al., 2010; Bolhuis and Moorman, 2015). Functional connections within this pathway are already established during the sensory phase, considerably earlier than those of SMP (Mooney and Rao, 1994; Nowicki et al., 1998). Lesions within this pathway in juvenile birds have clearly deteriorating effects on the learned song (Scharff and Nottebohm, 1991). However, the consequences for song development differ between AreaX and LMAN lesions (Scharff and Nottebohm, 1991). Lesions of AreaX produce an abnormal song with more variability in terms of notes, intervals, and syllable sequence. On the other hand, lesions of LMAN significantly reduce the number of notes used by the birds. Thus, this and other studies indicate that the LMAN seems to induce variability in the song of juvenile birds necessary for them to acquire the crystallized birdsong by trial-and-error learning (Ölveczky et al., 2005). In contrast, adult lesions of AreaX or LMAN do not alter the birdsong indicating the main role of AFP in song learning rather than adult song production (Scharff and Nottebohm, 1991; Aronov et al., 2008). LMAN and its projection to RA seem especially relevant for producing subsong (Aronov et al., 2008). Neurons in LMAN exhibit premotor activity related to onset (or offset) of syllables of subsong, and inactivation of LMAN entirely eliminates subsong production (Aronov et al., 2008). Although the exact role of the AFP in song learning is still not exactly understood (Bolhuis and Moorman, 2015), the presence of auditory neurons responsive to bird's own song (BOS) within this pathway (Doupe and Konishi, 1991) and the connections to the SMP indicate that AFP provides auditory feedback about the bird's own vocal outcome to match the BOS to the tutor song memory (Doupe, 1993). Such a role of AFP in modification of the own vocalizations by means of auditory feedback is supported by the fact that LMAN lesions prevent song deficits which normally develop after deafening in birds with an intact LMAN (Brainard and Doupe, 2000).

As stated previously, songbirds learn their song from a conspecific tutor and later adjust their own song according to the memorized tutor song (Brainard and Doupe, 2002). Which brain areas are involved in the storage of the tutor song has been the subject of extensive research (for reviews, see Bolhuis and Gahr, 2006; Bolhuis and Moorman, 2015). Although several studies suggested that the AFP might contain the neuronal substrate for the memory of the tutor song, other evidence suggests that the secondary auditory areas NCM and CM are the sites for birdsong storage (Bolhuis and Gahr, 2006; Gobes and Bolhuis, 2007; Bolhuis and Moorman, 2015). In particular, NCM may store the tutor song in male zebra finches, while CM may be relevant for the

memory of the father's song in females (Bolhuis and Moorman, 2015). However, the picture is perhaps not that simple. The tutor song is most probably stored in a distributed brain network that also involves the SMP (Roberts et al., 2012; Roberts and Mooney, 2013). In an elegant study, Roberts et al. (2012) demonstrated that the HVC plays a crucial role in encoding the tutor song on a very precise timescale during the sensory phase. They manipulated the activity in HVC of a juvenile zebra finch while listening to the tutor song. When HVC activity was disrupted during the utterance of a specific syllable in the tutor song motif, the bird developed poor copies of the manipulated syllable while producing accurate copies of syllables flanking the target syllable. Thus, the auditory system, as well as several structures of the song system, seems to be involved in the internal representation of the tutor song. Furthermore, differences between species may also exist (Prather et al., 2010; Roberts and Mooney, 2013).

As mentioned above, human speech and birdsong share many features (Doupe and Kuhl, 1999; Elemans et al., 2015). Moreover, the neurobiology of human speech production and birdsong is strikingly similar in numerous respects (Jarvis, 2004; Simonyan et al., 2012). Humans seem to have evolved a specific region in the primary motor cortex that projects monosynaptically to the nucleus ambiguus, which innervates the muscles of the larynx, the vocal organ of humans (Jarvis, 2004; Simonyan and Horwitz, 2011; Simonyan et al., 2012). This region is called the laryngeal motor cortex (LMC) and has not been identified in the primary motor cortex of nonhuman primates (Simonyan and Horwitz, 2011). In nonhuman primates, only the premotor cortex contains a laryngeal region, and it lacks direct projections to laryngeal motor neurons (Simonyan and Horwitz, 2011). It has been suggested that the direct projection from LMC to nucleus ambiguus in humans is crucial for producing human speech (Simonyan et al., 2012). It is also reminiscent of the RA-nXIIts projection in songbirds. These observations indicate that a direct projection from the primary motor areas to the neurons controlling vocal organ muscles is a prerequisite for complex vocalizations (Petkov and Jarvis, 2012). Consistent with this idea, a recent study found that ultrasonic sound production in mice shares several features with the birdsong and involves a direct projection from the primary motor cortex to nucleus ambiguus (Arriaga et al., 2012). The fact that this projection is weak in mice led the authors to suggest that the strength of such projection is proportional to the complexity of vocalizations produced by an animal.

Together with premotor cortical areas, the human LMC is part of a corticobasal ganglia-thalamocortical loop that is comparable to AFP in songbirds (Jarvis, 2004; Simonyan and Horwitz, 2011; Simonyan et al., 2012). Premotor cortical areas in mammals project to the striatum and from there to motor nuclei of the thalamus via the internal part of the globus pallidus (Reiner et al., 1998; Jarvis, 2004; Simonyan et al., 2012). The thalamus then closes the loop via its projection back to the cortex. This loop is similar to the LMAN-AreaX-DLM-LMAN loop described earlier (Jarvis, 2004; Kuenzel et al., 2011; Simonyan et al., 2012).

These similarities between distantly related species indicate that the neuronal correlates of vocal learning and production may have evolved as specializations of preexisting system present in ancestral amniote (or even vertebrate) brains. The motor theory of vocal learning origin proposes that brain systems for vocal learning and production evolved from ancestral motor system (Feenders et al., 2008; for alternative theories, see Petkov and Jarvis, 2012). This could have happened, for instance, by duplication of whole pathways (Chakraborty and Jarvis, 2015) or by strengthening of existing projections in vocal learners which are sparse or absent in nonvocal learners (Arriaga et al., 2012; Petkov and Jarvis, 2012). Feenders et al. (2008) used molecular imaging to map brain activity of vocal learning and nonlearning birds during body movements. They found movement-associated activity in comparable regions in both vocal learners and nonlearners. Most interestingly, movement-activated areas in vocal learners were adjacent to song system nuclei. The song system nuclei were activated by singing but not by body movements. The findings of this study therefore provide intriguing evidence for the notion that song system in birds emerged from the existing motor system and subsequently specialized for vocal control.

Further support for the motor theory comes from anatomical, electrophysiological, and pharmacological–behavioral studies on motor sequence execution in vocal nonlearning species including pigeons and chickens. Pigeons performing a sequence learning task require brain regions that are similar to the song system nuclei of songbirds (Helduser and Güntürkün, 2012; Helduser et al., 2013). Especially crucial for correct sequence execution are the nidopallium intermedium medialis pars laterale (NIMl), which is comparable to LMAN in songbirds in terms of topology and connectivity (Kröner and Güntürkün, 1999), and the NCL. Furthermore, HVC is adjacent to NCL in songbirds, and the NCL in pigeons contains separate populations of neurons projecting to medial striatum and arcopallium, just as HVC does in songbirds. These findings are consistent with the motor theory.

As mentioned above, the AreaX in the medial striatum of songbirds contains both spiny striatal neurons and aspiny pallidal-like neurons (Kuenzel et al., 2011). However, unlike mammalian medium spiny neurons, the spiny striatal neurons of AreaX do not appear to

project outside of the striatum (Reiner et al., 2004b). Rather, these neurons project to a small population of large aspiny neurons which are the output neurons of the AreaX projecting to DLM (Farries et al., 2005a). These neurons show pallidal-like morphology and physiology and express the pallidal marker LANT6 (Farries and Perkel, 2002; Reiner et al., 2004b). The spiny striatal neurons of AreaX seem to express SP, the cotransmitter also presents in mammalian striatal neurons belonging to the direct pathway of basal ganglia (Reiner et al., 2004b). Thus, AreaX consists of both striatal and pallidal components and is possibly part of the direct pathway of the basal ganglia in songbirds (Faries and Perkel, 2002; Carrillo and Doupe, 2004). However, Carillo and Doupe (2004) suggest that functionally, AreaX may contain both the direct and the indirect pathway. This idea was further supported by anatomical and electrophysiological data showing monosynaptic pallial excitatory projections to pallidal-like output neurons as well as a connection between pallidal-like neurons lacking thalamic efferents and pallidal-like output neurons (Farries et al., 2005a). Both of these findings describe pathways that are not anatomically identical to the indirect pathway of mammals but nevertheless elicit an effect opposite to that of the direct pathway.

Farries et al. (2005b) investigated neurons in the striatum of domestic chickens, a vocal nonlearner distantly related to songbirds. Although striatal neurons in chickens exhibit a high diversity in their electrophysiological properties, Farries et al. (2005b) identified aspiny neurons that exhibited properties akin to pallidal neurons. This indicates that mixing of striatal and pallidal features within the striatum might be common to all birds and that AreaX in songbirds might be a specialized subset of these neurons, thus supporting the motor theory of vocal learning origin.

The above mentioned similarities in the pathways and their function raise the question whether similar specialized molecular regulatory mechanisms are responsible for the development and control of vocal behavior in different species. The transcription factor FoxP2 has received particular attention because of its association with the developmental verbal dyspraxia (a speech disorder) in humans and song deficits in songbirds (Bolhuis et al., 2010; Wohlgemuth et al., 2014). In recent years, considerable progress has been made toward mechanistic explanations of FoxP2 function in songbirds (Wohlgemuth et al., 2014). The evidence points to a role of the FoxP2 in the development and proper function of the circuitry required for sensorimotor learning. In a recent study, Pfenning et al. (2014) applied a computational algorithm to analyze a large gene expression database for vocal learning and vocal nonlearning birds and primates. They identified striking similarities between songbird's RA and the human lateral motor cortex as well as between AreaX and a part of the human striatum activated during speech. The relationships of HVC and LMAN to human brain areas were weaker and had the highest correlation values with the Wernicke and Broca area, respectively. Importantly, none of these relationships were found in vocal nonlearners. Although it is not clear whether such similarities reflect the molecular machinery for the development of vocal learning circuits or whether they are the consequence of these circuits, these data nevertheless indicate that convergent behavioral and anatomical traits of vocal learners are associated with convergent molecular mechanisms.

8.5 Conclusion

There are more than 17 000 different sauropsid species, and they inhabit all major ecosystems of our planet (Shine, 2013). The phylogenetic heterogeneity of this group of animals is mirrored in the diversity of brain organizations of which a small fragment was outlined in this chapter. Comparative neuroscientists traditionally follow one of two scientific traditions to reveal the commonalities and the differences of these sauropsid brains. One tradition primarily analyzes brain anatomy and its ancestral relationships. The other tradition is interested in animal behavior and tries to map functions onto neural entities. Ideally, these two approaches should result in overlapping results. As we have seen, this is by far not always the case. Why?

Comparative neuroanatomists compare not only adult brains but often also expression patterns of genes that are involved in brain development. And they do this in the context of a topological framework of structures. This allows both to detect homologies between brain areas and to reconstruct the changes of brain components during evolution. This approach is quite successful in reconstructing the evolution of the brain, but it has only limited predictive power with regard to behavior. Current studies in the area of evolutionary developmental biology (evo-devo) would not easily expect that nearly identical arrangements of spinal motor pools generate the undulation of snakes, the walking pattern of rodents, or the flight of birds (Section 8.3.1.1). Similarly, a prefrontal-like area in the most posterior corner of the avian ventral pallium (Section 8.3.3.3.2.4) or the existence of an avian song system within the DVR that shows astonishing similarities to the human cortical language circuit comes as a surprise (Section 8.4.5).

The functional approach to comparative neuroscience has its own merits and problems. It is able to identify similar functional circuits in the brains of different animals, but it often fails to provide a strong hypothesis on the evolutionary background of such systems. Functional analyses may support evo-devo conclusions on ancestral

conditions in some cases, but they are not useful in establishing conclusions on homologies on their own. Thus, comparative neuroanatomy can reconstruct the phylogeny of brains but often falls short in predicting behavior. Behavioral neuroscience provides insights about function–structure mappings but is mostly unable to conclude on homologies and so to reconstruct ancestral conditions.

A key factor that can explain the differential strengths and weaknesses of these two approaches is neural connectivity. Scientists in the evo-devo field usually try to avoid resting their conclusions on connectivity analyses since axonal pathways are often structured by genes that control late functional maturation and are under less tight evolutionary constraint. In addition, neural connectivity always goes through cycles of massive early maturational overproduction and late maturational pruning. During overproduction, many aberrant connections to nontarget areas are produced that are later eliminated when they do not contribute to proper functioning. But this is possibly exactly the way how new connections can be established rather quickly during evolution when animals are under selection for new perceptual, cognitive, or motor abilities. The seemingly aberrant connections can then contribute to new abilities, thereby increasing the fitness of the individual. This is due to the fact that the function of a neuron is largely determined by its input and far less by its location in the brain. So, if a visual neuron in the tectum of a rattlesnake starts receiving trigeminal thermal input, it will process infrared information in addition to classic vision (Section 8.3.2.1). If a light-dependent molecule in the photoreceptors of birds gains the ability to alter its function relative to the Earth's magnetic field lines, the respective visual pathway starts to see the position of the pole overlayed on object vision (Section 8.4.1.1). If auditory information is funneled to a trigeminal forebrain area, birds start combining the tactile and the auditory feedback of their pecking movements (Section 8.4.1.2). These kinds of changes can happen independently multiple times in evolution since they possibly require only few neural alterations to gain functionality for the individual.

Other neural functions depend on a large number of interwoven circuits to be functional. The mammalian PFC and its control over executive functions is a good example. In such cases, comparative neuroanatomists assumed that a certain macroanatomy is required to enable prefrontal functions. The discovery of a prefrontal-like area in the nonlaminated posterior DVR of birds shows that similar complex functions can be generated in brains with quite a different macroanatomy (Section 8.3.3.3.2.4). The same can be said for the avian telencephalic connectome in comparison to the respective connectomes of mammals (Section 8.3.3.3). Such examples reveal the degree of independence that functional circuits can have from their macroanatomical framework. At this point it is important to make clear which aspect of macroanatomy we are talking about. The avian prefrontal-like area NCL is not positioned within a laminated dorsal pallium, but still it produces executive functions. But for its functionality, the NCL requires a certain connectivity pattern and, most importantly, input from the dopaminergic system that acts via D1 receptors. This dopaminergic D1 cascade could constitute a "deep homology" between mammalian and avian prefrontal structures that is independent from the overall macroanatomy (Shubin et al., 2009).

In other cases, we have seen that different neural computations can result from a highly comparable macroanatomy. For example, the visual cortex of turtles is homologous to the mammalian visual cortex and holds with its three-layered organization at least some of the critical macroanatomical features of the mammalian cortex. But, as outlined in Section 8.3.3.2.1, the visual cortex of turtles shows a visual representation that does not even remotely resemble the mammalian condition. Thus, even with a similar macroanatomy, local computations can differ substantially. In other cases, however, lamination evolved independently in nonhomologous locations: Sensory areas in the avian DVR show a laminated connectivity pattern with columnar arrangements like found in the sensory cortices of mammals (Section 8.3.3.3.2.3). Similar observations were recently reported from the fish dorsolateral pallium (Trinh et al., 2016).

Taken together, this chapter shows that both studies on homology and studies on function deliver important insights. We cannot replace one of them for the other since these two strands of inquiries often result in very different findings, with both of them telling a part of the truth. Without proper evo-devo-based analyses of homologies, we lose the framework to correctly interpret what has changed in which line of animals during convergent evolution. But a sole analysis of homologies falls far too short to explain the myriads of fascinating observations on sauropsid brains of which some were recapitulated here. We have to appreciate that the ability to properly respond to sensory inputs was the driving force for the evolution of brains. Comparative neuroscience that ignores this most fundamental aspect of brain evolution is prone to neglect the most vital part of its studies.

Nothing in neuroscience makes sense, except in the light of behavior.

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