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Visual circuits of the avian telencephalon: evolutionary implications

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Abstract

Birds and primates are vertebrates that possess the most advanced, efficient visual systems. Although lineages leading to these two classes were separated about 300 million years ago, there are striking similarities in their underlying neural mechanisms for visual processing. This paper discusses such similarities with special emphasis on the visual circuits in the avian telencephalon. These similarities include: (1) the existence of two parallel visual pathways and their distinct telencephalic targets, (2) anatomical and functional segregation within the visual pathways, (3) laminar organization of the telencephalic targets of the pathways (e.g. striate cortex in primates), and (4) possible interactions between multiple visual areas. Additional extensive analyses are necessary to determine whether these similarities are due to inheritance from a common ancestral stock or the consequences of convergent evolution based on adaptive response to similar selective pressures. Nevertheless, such a comparison is important to identify the general and specific principles of visual processing in amniotes (reptiles, birds, and mammals). Furthermore, these principles in turn will provide a critical foundation for understanding the evolution of the brain in amniotes. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Vision is probably more important to birds than to any other class of vertebrates. It is used for their navigation/migration, feeding/prey-catching, escape from predators, and elaborated social behavior. There is a bulk of psychophysical and behavioral evidence that birds (pigeons, in particular) have excellent visual acuity, color vision, discrimination ability, and visual memory [12,18,57]. Some of these abilities are comparable, or in some aspects, even superior, to those of humans.

This raises the intriguing question of how the small avian brain is able to function so superbly in various visual tasks. Without any scientific examination of the avian brain, one might come up with two possible answers. First, birds and humans have essentially the same underlying neural mechanisms to process visual information, and the avian brain is simply a miniature replica of the human brain. Thus, the difference in visual ability between birds and humans is quantitative, rather than qualitative. The alternative answer is that birds have a unique neural mechanism, which is fundamentally different from that of humans. That is, birds accomplish visual performance in a very different manner from humans.

The real answer is probably found somewhere between these two extreme ideas. Comparative anatomical studies have indicated that the basic design of each brain is essentially the same for all amniotes (reptiles, birds, and mammals), although there are quantitative and organizational differences as a result of individual evolutionary history in accordance with the adaptive demands of the environment [37]. There are significant structural and functional similarities in the brainstem [5]. However, similarities between birds and mammals are not so manifest in the forebrain, particularly the telencephalon [6]. Birds, as well as reptiles, lack a laminar neocortical structure, which is evident in the mammalian telencephalon. In mammals, the neocortex receives sensory input from the thalamus, and processes

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the information for further analysis. In contrast, non-mammals have a nuclear mass protruding into the ventricle, called the dorsal ventricular ridge (DVR), which receives a major projection from the thalamus [7,48,52]. Because of these significant organizational differences in the telencephalon, comparisons between the nonmammalian and mammalian forebrains have been difficult and complicated.

Recent anatomical, physiological, and behavioral studies of the avian forebrain have provided detailed information about the similarities and differences between the avian and mammalian brains, especially the visual system [58]. These data suggest that, despite the evolutionary and environmental differences, there are uncanny similarities in the basic neural organization for visual processing. These similarities include: (1) the existence of two parallel visual pathways and their distinct telencephalic targets (collothalamic and lemnothalamic pathways) [7], (2) anatomical and functional segregation within individual pathways, (3) the laminar organization of the lemnothalmic targets (e.g. striate cortex in mammals), and (4) possible interaction between the two pathways. This paper will discuss these four similarities from a viewpoint based on recent findings about the avian visual telencephalon. By providing comparative information regarding the avian and mammalian visual systems, the general and specific principles of visual processing can be identified, which in turn provide a critical foundation necessary to understand the evolution of the brain in amniotes.

2. Evolution of the brain

Before describing the avian visual system, a brief discussion of the evolution of amniotes is in order to clarify the phyletic relationships between birds and mammals. It is our contention that a comparative analysis between the avian and mammalian brains should be embedded in an understanding of the evolutionary histories of the two classes. If necessary, more comprehensive reviews of the brain evolution of vertebrates are readily available elsewhere [7,30].

For a long period of time, theories of brain evolution have been largely dominated by the idea of the phylogenetic scale. In this anthropocentric model, each species was placed on a unilinear, progressive, evolutionary scale based on its relative 'complexity' and 'evolutionary age'. It was assumed that phylogenetically 'older' life forms (e.g. fish) are not as advanced, or as well developed, as the 'modern' life forms (e.g. mammals). It was also assumed that the brain evolved from small, simple, and undifferentiated to large, complex, and differentiated. Thus, one can discern the relative 'evolutionary age' of a species by how different its brain is from the 'most advanced brain'—the human brain [7].

The concept of the phylogenetic scale was elaborated by many additive theories, whereby it was postulated that new structures are needed to allow for the adaptations of organisms to new environments [7]. One of the most well known additive theories is the triune brain theory by MacLean [29]. According to this theory, the human brain is composed of three individually inherited major structures: the reptilian complex (the basal ganglia), the paleomammalian brain (the limbic system), and the neomammilian brain (the dorsal thalamus and isocortex). MacLean [29] maintains that, throughout the evolution of amniotes, the new structures, such as the limbic system, dorsal thalamus, and isocortex, were added to the basic reptilian complex for new, higher cognitive functions. Thus, although every amniote species—including birds and reptiles—has the reptilian core, only mammals have the additional limbic system; and furthermore, only the most advanced mammals—such as humans—have the neomammilian brain.

Analyses based on fossil records, however, completely refute the fundamental idea of the phylogenetic scale. The amniote lineages leading to reptiles and mammals were separated about 300 million years ago, and each lineage evolved individually in a parallel fashion (Fig. 1) [8]. Indeed, the lineage eventually leading to mammals evolved before reptiles, and birds were derived from the reptilian lineage about 200 million years ago [8]. Therefore, extant reptiles and birds do not represent a primitive state of mammals.

Neuroanatomical studies since the late 1960's also concluded that many previous theories of brain evolution, derived from the idea of the phylogenetic scale, were erroneous. There are few neuroanatomical data that support the idea that telencephalic size is inversely related to phylogenetic age [37]. Ostensibly "simple, lower" animals often have complex, sophisticated neural structures. In particular, nonmammalian amniotes have not only the reptilian complex, but also equivalent structures of the paleomammalian and neomammalian brain structures that, according to the additive theories, should not be present in nonmammals. Recent anatomical studies based on connections, histochemistry, and functions clearly demonstrate that only a small portion of the sauropsid telencephalon (i.e. the paleostriatum of birds) corresponds to the mammalian basal ganglia (Fig. 2). The evolutionary origin of the rest, including DVR, is still controversial [7], and the DVR in particular, has been compared to the mammalian pallium, claustrum, and/or amygdala [4,6,11,22–24,27,29,37,38, 41,42,51]. Notwithstanding the common reptilian ancestry, therefore, the avian and mammalian brains and their visual systems have evolved independently over about 300 million years as they have adapted to their own specific environment.
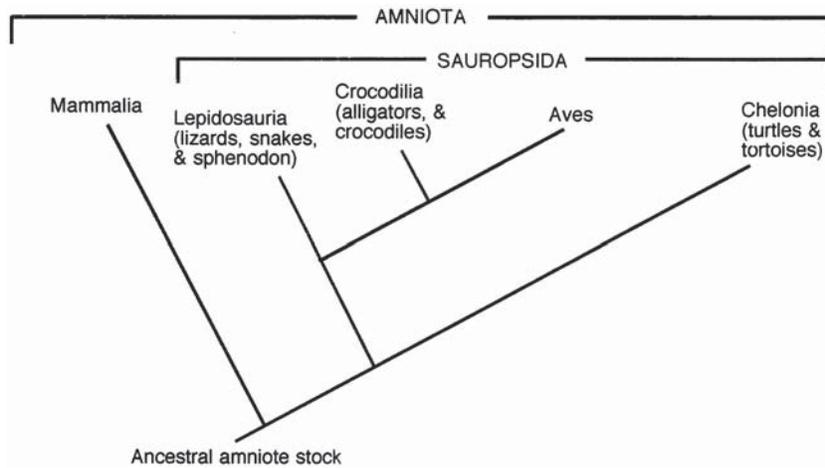
Fig. 1. A schematic figure illustrates the phyletic relations of amniotes (reptiles, birds, and mammals). Adapted from Carroll [8].

3. Two parallel visual pathways

In all amniotes, there are two main visual pathways from the retina to the telencephalon: the collothalamic (or tectofugal) and the lemnothalamic (or thalamofugal) pathways [7]. In primates, the collothalamic pathway travels from the retina to the superior colliculus to the pulvinar of the thalamus to part of the extrastriate cortices, whereas the lemnothalamic pathway runs from the retina to the lateral geniculate nucleus of the thalamus (LGd) to the visual cortex (Fig. 3). The lemnothalamic pathway (the geniculo–striate pathway) of primates plays the dominant role in various visual discrimination tasks, including detecting fine detail and color [28]. In contrast, the primate collothalamic pathway is involved in visuomotor behaviors, such as orienting and paying attention to a visual stimulus [10,54].

In birds, the connection patterns of the two pathways are similar to those of mammals, although the functional roles are quite different. The avian collothalamic pathway runs from the retina to the optic tectum, and then to the thalamic nucleus rotundus (n.Rt) of the thalamus, and finally to the ectostriatum in DVR [7]. This pathway is reminiscent of the primate collothalamic pathway in that both pathways process visual information from the optic tectum/superior colliculus, which is one of the most phylogenetically conservative structures in the brain [7,49]. The avian n.Rt is compared to the primate pulvinar as the primary thalamic recipient of the tectal efferents, and the avian ectostriatum is compared to part of the extrastriate cortices as the telencephalic target of the collothalamic pathway. The avian lemnothalamic pathway runs from the retina to the dorsal thalamic nuclei (named the principal optic nuclei of the thalamus, OPT) to the telencephalic area called the visual wulst [7]. The OPT and the visual wulst are, respectively, compared to the mammalian LGd and striate cortex in that they are the thalamic targets of the direct retinal input and the telencephalic targets of the thalamic nuclei.
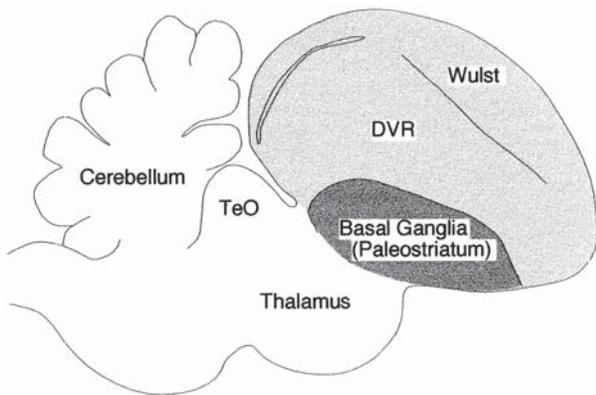

Fig. 2. A schematic avian (pigeon) sagittal brain shows major neural structures. The shaded area is the telencephalon, which includes the wulst, DVR, and basal ganglia. DVR, dorsal ventricular ridge; TeO, optic tectum.
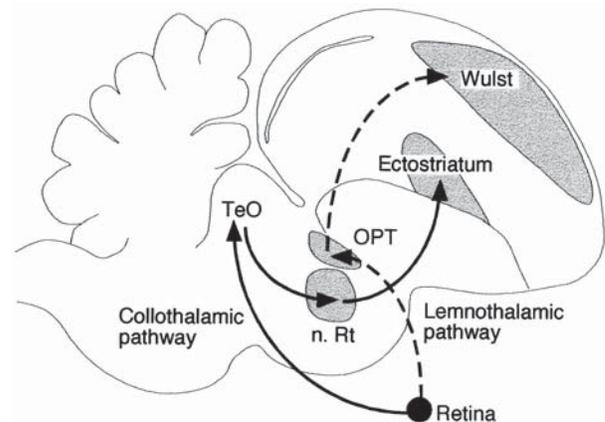

Fig. 3. The two visual pathways from the retina to the telencephalon in the avian sagittal brain. The dotted lines represent the lemnothalamic pathway, and the solid lines represent the collothalamic pathway. n. Rt, nucleus rotundus; OPT, principal optic nuclei.

Extensive anatomical, histo- and bio-chemical, and physiological studies have been conducted to compare these two pathways, their subcortical structures in particular, in not only primates and birds, but many species of amniotes [7,49]. These studies have shown that the two pathways have many similarities between nonmammals and mammals in terms of topological and topographical organization, connections, chemistry, and response characteristics [7,49]. These striking similarities suggest that ascending parallel visual pathways to the telencephalon are almost certainly traced back to the amniote ancestral brain [7,27,50]. Furthermore, impressive similarities in the basic design throughout amniotes suggest that two parallel pathways—the lemnothalamic and collothalamic pathways—must be efficient, useful, and probably necessary for terrestrial animals (amniotes) to survive in a visually rich environment.

However, there are also clear differences between the mammalian and nonmammalian pathways. One of the major differences is the degree of development of the two pathways. The mammalian—especially the primate—lemnothalamic pathway is well developed and differentiated much more than the collothalmic pathway. For instance, the primate LGd is highly segregated based on cytoarchitecture and function (magnocellular and parvocellular layers) and connections (ipsi- and contra-lateral retinal input). On the other hand, in many sauropsids (birds and reptiles), the lemnothalamic pathway is rather underdeveloped and undifferentiated compared to the collothalamic pathway, which includes the optic tectum, the major visual center for nonmammals [7,49].

4. Anatomical and functional segregation within visual pathways

Recently, the focus of research has extended from the subcortical structures to the telencephalic targets of the avian visual pathways [19,20,47]. In particular, this paper will discuss the subsequent circuits of the ectostriatum and visual wulst in order to compare them with those of the visual cortex and the extrastriate cortices. Does an examination of the avian telencephalic neural circuits provide more similarities in the visual processing between birds and mammals? Or does it provide information that supports the uniqueness of the avian system which is divergent from the mammalian system?

The ectostriatum is a large longitudinal structure embedded in the DVR. The ectostriatum can be divided into two divisions: the core region (Ec) which receives the thalamic input from n.Rt, and the belt region (Ep) which receives the input from the core region and projects to other telencephalic areas [25]. The Ec can also be divided along the anterior–posterior axis into
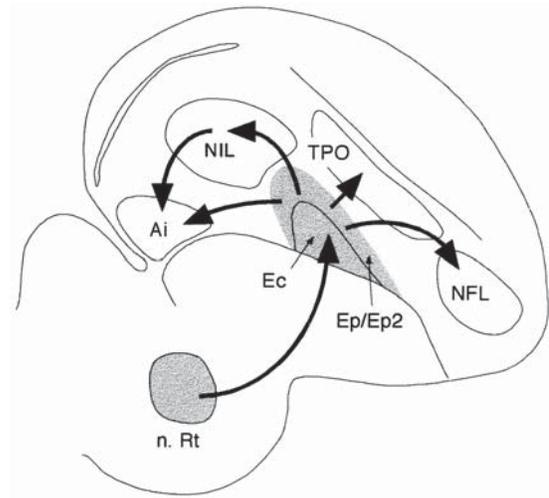

Fig. 4. The major visual output from the ectostriatum. Ai, intermediate archistriatum; Ec, core region of the ectostriatum; Ep, belt region of the ectostriatum; Ep2, neostriatal region surrounding the ectostriatum; NFL, lateral portion of the neostriatum frontale; NIL, lateral portion of the neostriatum intermediale; TPO, tempero-parieto-occipital area.

several subdivisions based on their afferent connections with n.Rt [3,36]. Each of the subdivisions, which are arranged roughly along the anterior–posterior axis, receives a projection from each of the corresponding subdivisions of n.Rt [3,36]. There are also studies showing the heterogeneous nature of the Ec with regard to response characteristics [13] and the staining pattern of cytochrome oxidase [17].

Using tract-tracing methods, recent studies show that there are multiple telencephalic projections from the ectostriatum [18,19]. These data suggest that at least three major regions in the neostriatum receive projections from the ectostriatum, in addition to minor terminations in other telencephalic structures, such as the archistriatum (Ai) (Fig. 4). The three target areas are organized along the anterior–posterior axis: a restricted region in the lateral portion of the neostriatum frontale (NFL), dorsolateral portion of the tempero-parieto-occipital area (TPO), and lateral portion of the neostriatum intermediale (NIL, [46]). Furthermore, the ectostriatal sources of these three targets are also organized roughly along the anterior–posterior axis (Fig. 4). Thus, the anterior Ec sends a projection to the anterior Ep and an immediate surrounding neostriatal area of Ep (Ep2, [46]), both of which in turn give rise to projections rostrally to NFL and dorsolaterally to the rostral portion of TPO. Similarly, the posterior Ep and Ep2 receive projections from the posterior Ec, and send a dorsolateral projection to the caudal TPO and a dorsocaudal projection to NIL. In our laboratory, we are currently analyzing the exact correspondence between the ectostriatal subdivisions based on efferent connections [18,19] and those subdivisions by afferent

connections [3,36], physiology [13], and chemistry [17]. Whatever the findings of this analysis, our previous results suggest three important features of the ectostriatal efferents: (1) the information from the ectostriatum is widely distributed in the neostriatum, (2) the ectostriatum–neostriatum connection is organized in a parallel fashion along the anterior–posterior axis, and (3) there are no direct major projections from the ectostriatum to structures dorsal to the neostriatum, such as the wulst and hyperstriatum ventrale (HV).

The significance of the third feature is that there is a possible hierarchical organization within the telencephalic structures, including the neostriatum, wulst, and HV. This issue will be discussed later. In contrast, the first two features are important in that they indicate that there is a parallel organization within the collothalamic pathway. This notion concerning the subcortical portion of the pathway is not new. Previous studies have already shown that the collothalmic visual pathway is comprised of parallel connections from the tectum to the ectostriatum. For instance, in addition to the tecto–rotundo–ecstostriatal pathway, there are at least two other collothalamic pathways: (1) one is from the tectum to the neostriatum intermedium via the dorsolateral posterior nucleus of the thalamus [14], and (2) the other is from the tectum to the ectostriatum via the triangular nucleus of the thalamus [3]. Even within the tecto–rotundo–ecstostriatal pathway, the existence of parallel connections has been reported [3,36]. Findings of the visual circuits in the telencephalon thus suggest that this parallel system extends to higher telencephalic levels, beyond the ectostriatum. Together with the previous studies, these data indicate that there are parallel and independent connections within the collothalamic pathway from the tectum to the thalamus to the ectostriatum then to the neostriatum.

Like the ectostriatum, n.Rt can be divided into several subdivisions based on tectal afferents [3,34], as well as cytoarchitecture and chemical contents [31]. In particular, each subdivision of n.Rt receives a projection from different sublayers of layer 13 of the tectum [3]. Although the numbers and topographical organization of the subdivisions have not been closely examined, they are all generally organized along the anterior–posterior axis. Furthermore, these sagittally organized subdivisions appear to correspond to those with distinct response characteristics [44,56]. Thus, neurons of the dorsoanterior n.Rt (DA) [34] tend to respond selectively to the color of a stimulus, whereas many cells in the posterior n.Rt are excited by motion stimuli [56]. The same study also reports that a small group of cells sensitive to illuminance are located between the anterior-color area and the posterior-motion area[56]. In the tecto–rotundo–ectostriatal pathway, therefore, there are at least two parallel connections: (1) one travels from superficial sublayers of layer 13 of the tectum to DA in n.Rt to the anterior ectostriatum to NFL, and (2) the other runs from deeper sublayers of layer 13 to posterior n.Rt to posterior ectostriatum to NIL. Based on studies of n.Rt neurons [56], the former appears to be specialized for color whereas the latter is for motion.

The ectostriatum sends a projection to TPO, as well as to the neostriatum. As yet, we have little information regarding the organization and relationships of ectostriatal neurons sending projections to the neostriatal targets and those sending to TPO. Do they belong to the same cell groups or are there distinct subdivisions? This issue needs to be further studied in light of the fact that cells of the dorsolateral TPO are putative motor neurons which project to the paleostriatum (basal ganglia) [55].

The similarity between this avian system and the primate system is striking. In primates, the lemnothalamic pathway consists of two functionally distinct subdivisions: the magnocellular (M) and parvocellular (P) pathways [28,32]. The M pathway travels from large M retinal ganglion cells to magnocellular layers in LGd to layer $4C\alpha$ of the striate cortex, whereas the P pathway travels from smaller P ganglion cells to parvocellular layers of LGd to layer $4C\beta$ of the striate cortex [28]. Physiological properties of neurons in the M pathway include high sensitivity to moving objects whereas cells in the P pathway are able to detect fine details and analyze information concerning color [28]. Functional segregation is also found in the parietal and temporal pathways in the cortex [2,53]. Thus, the parietal pathway includes areas in the posterior parietal lobe, and is associated with evaluating object motion. The temporal pathway includes areas in the temporal lobe, and is important for identifying colors and patterns of visual objects. Based on anatomical, physiological, and behavioral evidence, the parietal and temporal cortical pathways are thought to depend largely on the contributions of M and P pathways, respectively. It has been proposed that the parallel visual pathways extend from the retina to the higher cortical areas in primates [2,53]. However, further studies also show that there are extensive interactions between the two cortical pathways, suggesting that a relationship between the subcortical and cortical pathways may not be so straightforward [32].

Both the avian collothalamic pathway and the primate lemnothalamic pathway have at least two distinct subdivisions, each of which contributes to a large extent to either motion or color processing (Fig. 5). Both pathways play a prominent role in various visual discrimination tasks, and lesions of the pathways yield devastating effects on their performance in birds and primates [18]. Given the fact that the avian collothalamic and the primate lemnothalamic pathways do not share any common heritage in the ancestral amniote

stock, these similarities are apparently the result of convergent evolution. The similarities clearly indicate, not only that such parallel processing is a highly efficient mechanism to process visual information, but also that the two properties, color and motion, need to be independently processed in the parallel neural mechanism. However, the cumulative evidence warrants further comparative analysis between the avian and primate visual systems. For instance, physiological characteristics of the avian retinal ganglion cells are only poorly understood [35].

5. Laminar organization of the striate cortex and the visual wulst

In contrast to the collothalamic pathway, the lemnothalamic pathway is not well developed in birds, particularly those species with eyes laterally located, such as pigeons and chickens. For these birds, the lemnothalamic pathway is involved in processing the lateral visual
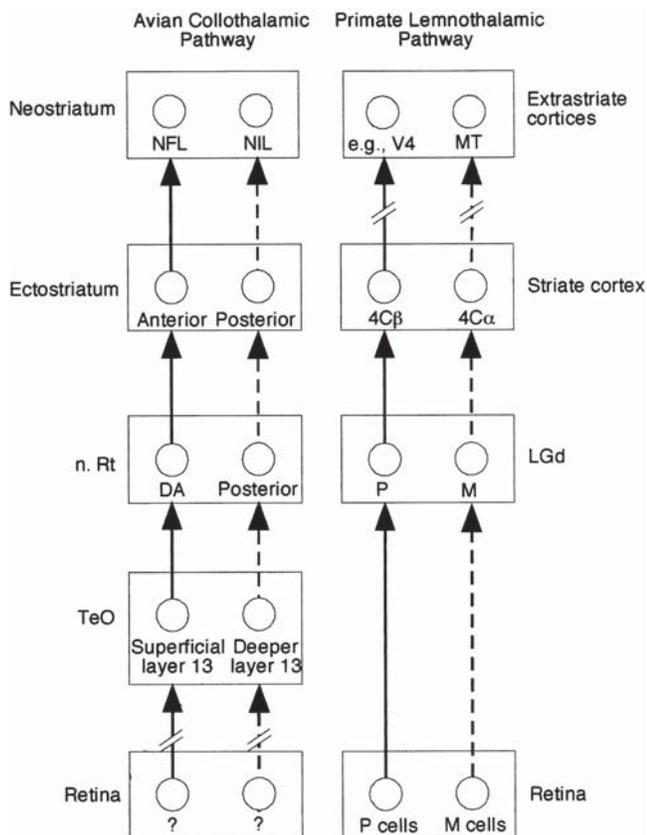

Fig. 5. Comparison between the avian collothalamic pathway and the primate lemnothalamic pathway. The simplified figure shows that each pathway includes two functionally and anatomically distinct parallel connections (dotted and solid lines). DA, dorsoanterior division of n. Rt; LGd, dorsal division of the lateral geniculate nucleus; M, magnocellular layer; M cells, M ganglion cells; MT, middle temporal area; P, parvocellular layer; P cells, P ganglion cells.

field [15,16], although the lemnothalmic pathway of birds of prey (e.g. owls and hawks) is more developed for processing the frontal binocular field [39,40]. Nevertheless, an examination of the avian lemnothalamic pathway is important for understanding the evolution of the pathway in amniotes. Both the mammalian and avian lemnothalamic pathways first send a retinal projection to the dorsal visual thalamus. Like LGd, the avian visual thalamus (OPT) consists of multiple components, which are cytoarchitectonically and chemically distinct [16,26], suggesting the existence of additional parallel processes within the lemnothalamic pathway.

The telencephalic target of the avian lemnothalamic pathway, the visual wulst, is a parasagittal bulge on the dorsomedial part of the pallium. Even a cursory glance at the striate cortex and visual wulst suggests remarkable similarities. The similarities include laminar organization [26], afferent and efferent connections [1,26], physiological characteristics [33,39,40], and chemical contents [48]. However, there are also many differences between the two structures. Here, we will focus on the intratelencephalic connections of the striate cortex and visual wulst in particular [47]. Based on the connections, six cytoarchitectonically distinct layers of the striate cortex can be divided into three major layers: supragranular, granular, and infragranular layers. Layer 4 is the granular layer, layers 1, 2, and 3 are the supragranular, and layers 5 and 6 are the infragranular layers. The granular layer (layer 4) receives the visual input from LGd. The supragranular layers (layers 2 and 3) are the major sources of intratelencephalic projections to other cortices, whereas neurons of the infragranular layers (layers 5 and 6) send feedback projections to subcortical visual structures, including the superior colliculus and GLd [21]. Thus, the striate cortex can be broken down into two layers, which are distinct based on the targets of their projections: intratelencephalon or extratelencephalon.

Like the striate cortex, the visual wulst has supragranular, granular, and infragranular layers. The granular layer is called the intercalated nucleus of the hyperstriatum accessorium (IHA), the supragranular layer is the hyperstriatum accessorium (HA), and the infragranular layers include the hyperstriatum calatus superior (HIS) and hyperstriatum dorsale (HD). A projection from the avian visual thalamus (OPT) terminates, as in the striate cortex, mainly in the granular layer, IHA, as well as the lateral portion of HD [27]. Then, neurons in IHA give rise to a massive projection to the supragranular layer, HA [47]. Like in mammals, the supragranular layer distributes the information to multiple telencephalic areas, including NFL, the lateral portion of the caudal neostriatum (NCL), and paleostriatum augmentatum (PA, the avian equivalent of the caudate-putamen) [47]. However, HA is also the main source of projections to extratelencephalic visual struc-

tures, such as OPT and optic tectum, via the septomes-encephalic tract (TSM) [43]. In contrast, although neurons of the infragranular layers have minor projections to the same telencephalic structures which receive HA efferents, they predominantly project dorsocaudally to the hippocampal complex and its surrounding areas [47]. Thus, the lemnothalamic visual information is primarily sent to the supragranular layer HA, which in turn sends dominant projections to both telencephalic structures and the brainstem. Although we do not know whether both intratelencephalic and extratelencephalic projections originate from the same cells, HA may have at least two kinds of neurons which correspond to some of those in the supragranular and infragranular layers of the mammalian striate cortex [47]. These differences between the visual wulst and striate cortex indicate that, despite the fact that both structures are organized in a trilaminar fashion, the functional significance of such a lamination may be different between the two structures.

Another important issue regarding the telencephalic target of the lemnothalamic pathway is that the wulst is a large heterogeneous structure, which also contains areas for another modality (i.e. somatosensory) and limbic function [7]. It is important to note that the visual area is only a part of the whole wulst which occupies about 12% of the total telencephalic volume even for the laterally-eyed pigeon with its diminutive lemnothalamic pathway (Shimizu, unpublished data). The wulst receives multiple direct and indirect projections from diverse telencephalic areas [1]. In particular, part of the wulst is also closely associated with the limbic system based on connections with the hippocampal complex [9,47] and non-visual thalamic nuclei [26]. Since there are extensive intrinsic connections within the wulst [47], such diverse information to the wulst must have, at least to some degree, interactions with one another. Although the functional significance of the heterogeneous nature is unknown, this contrasts to the ectostriatum which is specialized only for visual processing for the collothalamic pathway. Therefore, the visual wulst is not only the telencephalic target of the lemnothalamic pathway, but it may also be involved in part of the qualitatively different functions, whether visual or nonvisual. A comparison between the visual wulst and striate cortex should be carried out with regard to this possibility. For instance, it is possible that only part of the visual wulst corresponds to part of the striate cortex in terms of connections and functions. Indeed, an immunohistochemical examination of the visual wulst shows that there are chemically distinct multiple subdivisions within individual layers [48], suggesting that further analysis is necessary with special attention to such subdivisions instead of assuming layer-to-layer correspondence between the wulst and striate cortex.
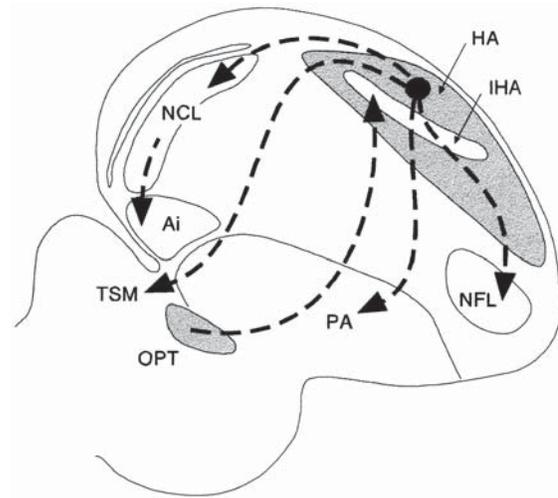

Fig. 6. The major visual output from the wulst. HA, hyperstriatum accessorium; IHA, intercalated nucleus of the hyperstriatum accessorium; NCL, lateral portion of the neostriatum caudale; PA, paleostriatum augmentatum; TSM, septomesencephalic tract.

6. Interactions of the visual pathways

Finally, we briefly discuss the interactions between the two visual pathways. After the two visual pathways reach the telencephalon, does the information from the two pathways interact within the telencephalon? There has been no conclusive anatomical evidence of integration within the telencephalon. However, lesion studies strongly indicate that there is a significant interaction between the two pathways [18,45]. As shown in Figs. 4 and 6, although there are two areas that receive direct or indirect visual information from the two pathways—NFL and Ai, these two areas are cytoarchitectonically and chemically heterogeneous nuclei. An investigation is in progress to examine whether the information from the two pathways converges in the same cell groups or diverges into different subnuclei within NFL and Ai.

By comparing Figs. 4 and 6, a hierarchical relationship between the two visual pathways can be noted. As mentioned previously, the ectostriatum does not project directly onto those structures dorsal to the neostriatum, such as HV and the wulst. On the other hand, the visual wulst sends projections to multiple areas in the DVR, including the neostriatum and archistriatum. This connectivity suggests that there is a general direction of streams for visual information, which runs from the wulst to DVR. Provided that the wulst is the avian equivalent of the striate cortex and the ectostriatum corresponds to part of the extrastriate cortices, the pattern of the streams in the avian telencephalon is similar to that of the streams beginning in the striate cortex and ending in the extrastriate cortices of primates. Again, there is no available information to

determine whether this similarity is ascribed to inheritance or convergent evolution. Nevertheless, the common principle in birds and primates is that some of the visual information from the two visual pathways is processed in the subsequent neural circuits of the collothalamic pathway (i.e. DVR and extrastriate cortices).

7. Concluding remarks

The goal of comparative studies of the avian visual system is two-fold. The immediate significance of comparative analysis is to aid us in comprehending the basic design of the best and most efficient neural system to process visual objects in diverse environments. Birds and primates live in and are adapted to very different environments. Even though they have been under different environmental pressures, birds can detect, recognize, analyze, and memorize complex visual objects as quickly and efficiently as humans. As shown here, there are striking similarities in the underlying neural mechanisms for such visual processing, regardless of the evolutionary histories of the two classes. Comparative studies will provide important information about the general role of the central nervous system as generated by the independent evolution. The visual system of birds and primates may be the prime example of the most advanced and sophisticated neural mechanisms of all vertebrate sensory systems.

The long-term impact of comparative studies of the avian visual system lies unquestionably in the development of a hypothesis concerning the evolution of the amniote brain. No evolutionary theory can be complete without considering the avian visual circuits, in order to delineate the whole picture of brain evolution. But one caution should be noted. The possible evolutionary scenario of the visual system should be inferred from a viewpoint in which studies using a variety of species and classes, not only birds and primates, are coalesced. We often use a very small number of avian species (e.g. pigeons and chickens) and primate species (e.g. macaque monkeys and humans) for visual studies. Simply by comparing two species, however, we cannot formulate a hypothesis about how a particular neural trait, such as a visual pathway, evolved. Evolutionary reconstruction is most likely to succeed with a cladistic analysis, which uses out-group comparisons [7]. Thus, whether a particular structure is plesiomorphic (ancestral) or apomorphic (derived) is inferred based on comparisons of the trait in sister species and sister groups. Further information about cladistic analysis and its application for the brain evolution will be found in the recent book by Butler and Hodos [7].

References

[1] Bagnoli P, Burkhalter A. Organization of the afferent projections to the wulst in the pigeon. J Comp Neurol 1983;214:103–13.

[2] Baizer JS, Ungerleider LG, Desmone R. Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. J Neurosci 1991;11:168–90.

[3] Benowitz LI, Karten HJ. Organization of the tectofugal visual pathway in the pigeon: a retrograde transport study. J Comp Neurol 1976;167:503–20.

[4] Bruce LL, Neary TJ. The limbic system of tetrapods: a comparative analysis of cortical and amygdalar populations. Brain Behav Evol 1995;46:224–34.

[5] Butler AB. The evolution of the dorsal thalamus of jawed vertebrates, including mammals: cladistic analysis and a new hypothesis. Brain Res Rev 1994;19:29–65.

[6] Butler AB. The evolution of the dorsal pallium in the telencephalon of amniotes: cladistic analysis and a new hypothesis. Brain Res Rev 1994;19:66–101.

[7] Butler AB, Hodos W. Comparative Vertebrate Neuroanatomy: Evolution and Adaptation. New York: Wiley-Liss, 1996, 514 pp.

[8] Carroll RL. Vertebrate Paleontology and Evolution. New York: Freeman, 1988, 698 pp.

[9] Casini G, Bingman VP, Bagnoli P. Connections of the pigeon dorsomedial forebrain studied with WGA-HRP and 3H-proline. J Comp Neurol 1986;245:454–70.

[10] Chalupa LM. Visual function of the pulvinar. In: Leventhal AG, editor. Vision and Visual Dysfunction, vol. 4: The Neural Basis of Visual Function. London: Macmillan, 1991:140–159.

[11] Díaz C, Yanes C, Medina L, Monzon M, Trujillo CM, Puelles L. Golgi study of the anterior dorsal ventricular ridge in a lizard. I. Neuronal typology in the adult. J Morphol 1990;203:293–300.

[12] Donovan WJ. Structure and function of the pigeon visual system. Physiol Psychol 1978;6:403–37.

[13] Engelage J, Bischof HJ. The organization of the tectofugal pathway in birds: a comparative review. In: Zeigler HP, Bischof HJ, editors. Vision, Brain, and Behavior in Birds. Cambridge (MA): MIT Press, 1993:137–158.

[14] Gamlin PDR, Cohen DH. A second ascending visual pathway from the optic tectum to the telencephalon in the pigeon (*Columba livia*). J Comp Neurol 1986;250:296–310.

[15] Güntürkün O, Hahmann U. Functional subdivisions of the ascending visual pathways in the pigeon. This volume.

[16] Güntürkün O, Miceli D, Watanabe, M. Anatomy of the avian thalamofugal pathway. In: Zeigler HP, Bischof HJ, editors. Vision, Brain, and Behavior in Birds. Cambridge (MA): MIT Press, 1993:15–135.

[17] Hellman B, Waldmann C, Güntürkün O. Cytochrome oxidase activity reveals parcelllations of the pigeon's ectostriatum. NeuroReport 1995;6:881–5.

[18] Hodos W. The visual capabilities of birds. In: Zeigler HP, Bischof HJ, editors. Vision, Brain, and Behavior in Birds. Cambridge (MA): MIT Press, 1993:63–76.

[19] Husband SA, Laverghetta AV, Bosco GL, Edwards SC, Shimizu T. Some observations on the connections of the ectostriatum in the avian telencephalon. Soc Neurosci Abstr 1995;21:653.

[20] Husband SA, Shimizu T. Anatomical evidence for parallel processing within the avian collothalamic visual pathway. Soc Neurosci Abstr 1997;23:172.

[21] Kaas JH, Huerta MF. The subcortical visual system of primates. In: Steklis HD, Erwin J, editors. Comparative Primate Biology, vol. 4: Neurosciences. New York: Plenum, 1988:409–430.

[22] Karten HJ. The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon. Ann New York Acad Sci 1969;167:164–79.

[23] Karten HJ. Homology and evolutionary origin of the 'neocortex'. Brain Behav Evol 1991;38:264–72.

[24] Karten HJ. Evolutionary developmental biology meets the brain: the origins of mammalian cortex. Proc Natl Acad Sci USA 1997;94:2800–4.

[25] Karten HJ, Hodos W. Telencephalic projection of the nucleus rotundus in the pigeon (*Columba livia*). J Comp Neurol 1970;140:35–52.

[26] Karten HJ, Hodos W, Nauta WJH, Revzin AM. Neural connections of the 'visual wulst' of the avian telencephalon. Experimental studies in the pigeon (*Columba livia*) and owl (*Speotyto cunicularia*). J Comp Neurol 1973;150:253–77.

[27] Karten HJ, Shimizu T. The origins of neocortex: connections and lamination as distinct events in evolution. J Cogn Neurosci 1989;1:291–301.

[28] Livingstone MS, Hubel DH. Segregation of form, color, movement, and depth: anatomy, physiology, and perception. Science 1988;237:740–9.

[29] MacLean PD. The Triune Brain in Evolution. New York: Plenum, 1990, 672 pp.

[30] Macphail, E.M., Brain and Intelligence in Vertebrates. New York: Oxford University Press, 1982, 423 pp.

[31] Martinez-de-la-Torre M, Martinez S, Puelles L. Acetylcholinesterase-histochemical differential staining of subdivisions within the nucleus rotundus of the chick. Anat Embryol 1990;181:129–35.

[32] Merigan WH, Maunsell JHR. How parallel are the primate visual pathways? Ann Rev Neurosci 1993;16:369–402.

[33] Miceli D, Gioanni H, Repérant J, Peyrichoux J. The avian visual wulst: I. An anatomical study of afferent and efferent pathways. II. An electrophysiological study of functional properties of single neurons. In: Granda AM, Maxwell JH, editors. Neural Mechanisms of Behavior in the Pigeon. New York: Plenum, 1979:223–254.

[34] Mpodozis J, Cox K, Shimizu T, Bischof H-J, Woodson W, Karten HJ. GABAergic inputs to the nucleus rotundus (pulvinar inferior) of the pigeon (*Columba livia*). J Comp Neurol 1996;374:204–22.

[35] Mpodozis J, Letelier JC, Concha ML, Maturana H. Conduction velocity groups in the retino-tectal and retino-thalamic visual pathways of the pigeon (*Columba livia*). Int J Neurosci 1995;81:123–36.

[36] Nixdorf B, Bischof HJ. Afferent connections of the ectostriatum and visual wulst in the zebra finch (*Taeniopygia guttata castanotis Gould*)—an HRP study. Brain Res 1982;248:9–17.

[37] Northcutt RG. Evolution of the telencephalon in nonmammals. Ann Rev Neurosci 1981;4:301–50.

[38] Northcutt RG, Kaas JH. The emergence and evolution of mammalian neocortex. TINS 1995;18:373–9.

[39] Pettigrew JD. Binocular visual processing in the owl's telencephalon. Proc R Soc Lond 1979;204:435–55.

[40] Pettigrew JD, Konishi M. Neurons selective for orientation and binocular disparity in the visual wulst of the barn owl (*Tyto alba*). Science 1976;193:675–8.

[41] Reiner A. A comparison of neurotransmitter-specific and neuropeptide-specific neuronal cell types present in turtle cortex: implications for the evolution of mammalian isocortex. Brain Behav Evol 1991;38:53–91.

[42] Reiner A. Neurotransmitter organization and connections of turtle cortex: implications for the evolution of mammalian isocortex. Comp Biochem Physiol 1994;104A:735–48.

[43] Reiner A, Karten HJ. The laminar source of efferent projections from the avian wulst. Brain Res 1983;275:349–54.

[44] Revzin AM. Functional localization in the nucleus rotundus. In: Granda AM, Maxwell JH, editors. Neural Mechanisms of Behavior in the Pigeon. New York: Plenum, 1979:165–175.

[45] Riley NM, Hodos W, Pasternak T. Effects of serial lesions of telencephalic components of the visual system in pigeons. Vis Neurosci 1988;1:387–94.

[46] Ritchie TLC. Intratelencephalic visual connections and their relationship to the archistriatum in the pigeon (*Columba livia*), Unpublished PhD dissertation. University of Virginia, 1979, 217 pp.

[47] Shimizu T, Cox K, Karten HJ. Intratelencephalic projections of the visual wulst in pigeons (*Columba livia*). J Comp Neurol 1995;359:551–72.

[48] Shimizu T, Karten HJ. Immunohistochemical analysis of the visual wulst of the pigeon (*Columba livia*). J Comp Neurol 1990;300:346–69.

[49] Shimizu T, Karten HJ. Central visual pathways in reptiles and birds: evolution of the visual system. In: Gregory R, Cronly-Dillon JR, editors. Vision and Visual Dysfunction, vol. 2. London: Macmillan, 1991:421–441.

[50] Shimizu T, Karten HJ. The avian visual system and the evolution of the neocortex. In: Zeigler HP, Bischof HJ, editors. Vision, Brain, and Behavior in Birds. Cambridge (MA): MIT Press, 1993:103–114.

[51] Stiedter GF. The telencephalon of tetrapods in evolution. Brain Behav Evol 1997;49:179–213.

[52] Ulinski PS. Dorsal Ventricular Ridge: a Treatise on Forebrain Organization in Reptiles and Birds. New York: Wiley, 1983, 284 pp.

[53] Ungerleider LG, Mishkin M. Two cortical visual systems. In: Engle DJ, Goodale MA, Mansfield RJW, editors. Analysis of Visual Behavior. Cambridge (MA): MIT Press, 1982:549–586.

[54] Vanegas H, editor. Comparative Neurology of the Optic Tectum. New York: Plenum, 1984, 850 pp.

[55] Veenman CL, Wild JM, Reiner A. Organization of the avian 'corticostriatal' projection system: a retrograde and anterograde pathway tracing study in pigeons. J Comp Neurol 1995;354:87–126.

[56] Wang YC, Jiang S, Frost BJ. Visual processing in pigeon nucleus rotundus: luminance, color, motion, and looming subdivisions. Vis Neurosci 1993;10:21–30.

[57] Wasserman EA. The conceptual abilities of pigeons. Am Sci 1995;83:246–55.

[58] Zeigler HP, Bischof HJ, editors. Vision, Brain, and Behavior in Birds. Cambridge (MA): MIT Press, 1993, 415 pp.