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The avian subpallium: new insights into structural and functional subdivisions occupying the lateral subpallial wall and their embryological origins

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Abstract

The subpallial region of the avian telencephalon contains neural systems whose functions are critical to the survival of individual vertebrates and their species. The subpallial neural structures can be grouped into five major functional systems, namely the dorsal somatomotor basal ganglia; ventral viscerolimbic basal ganglia; subpallial extended amygdala including the central and medial extended amygdala and bed nuclei of the stria terminalis; basal telencephalic cholinergic and non-cholinergic corticopetal systems; and septum. The paper provides an overview of the major developmental, neuroanatomical and functional characteristics of the first four of these neural systems, all of which belong to the lateral telencephalic wall. The review particularly focuses on new findings that have emerged since the identity, extent and terminology for the regions was considered by the Avian Brain Nomenclature Forum. New terminology is introduced as appropriate based on the new findings. The paper also addresses regional similarities and differences between birds and mammals, and notes areas where gaps in knowledge occur for birds.

Keywords

Basal ganglia; striatum; pallidum; basal forebrain; extended amygdala; corticopetal system

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1. Introduction

A revised terminology of the avian forebrain was proposed in 2004 (Reiner et al., 2004a) as a result of an international Nomenclature Forum held at Duke University in July of 2002. The revision became necessary due to the longstanding existence of an inappropriate terminology for many forebrain structures based upon persistent but outdated and erroneous assumptions of homology to mammalian brain structures (Reiner et al., 2004a; Jarvis et al., 2005; Reiner, 2005). Historically, a single structure, the basal ganglia, was thought to comprise most of the forebrain of birds (Elliot-Smith, 1901; Edinger, 1908; Herrick, 1956). Forty years ago, a seminal hypothesis was put forth by Harvey Karten that the basal ganglia occupied a much more restricted basal region of the avian telencephalic hemispheres (Karten, 1969; Nauta and Karten, 1970). Numerous subsequent studies confirmed this hypothesis, and more broadly showed that the entire basal telencephalon (the subpallium) in birds contained homologues of many cell groups found in the subpallial telencephalon in mammals. One of the major goals of the Nomenclature Forum was to rename regions of the telencephalon in birds with terms that accurately reflect the new understanding of their homology to mammalian telencephalic regions. This resulted in the re-naming of nearly all structures in the two major regions (i.e. the pallium and subpallium) of the avian telencephalon. Since the time of the Forum, new anatomical, electrophysiological, embryological, behavioral and gene expression data have accrued on the organization and development of the somatic basal ganglia in birds, as well as the visceral basal ganglia, subpallial amygdala, basal forebrain cholinergic system, and septum. The new findings extend the understanding of these regions, especially with respect to their function and mammalian homologues. The present review seeks to provide an updated synthesis of the avian subpallium, focusing on the lateral subpallial wall.

2. Organization of the subpallium

2.1. Definition and components of the subpallium

The subpallium in birds consists of telencephalic structures ventral to the pallial-subpallial lamina (LPS), medial to the arcopallium/pallial amygdala, and rostro-dorsal to the diencephalon (Fig. 1). Subpallial structures can be organized into five major groups (Table 1), based on developmental, topographic, neurochemical, hodological and functional criteria. Four groups are located lateral to the ventral horns of the lateral ventricles, while the fifth group resides medial to the ventral horns of the lateral ventricles thereby occupying the medial wall of subpallium (Fig. 1). The five groups and their constituent major structures are:

1. Dorsal Somatomotor Basal Ganglia, consisting of the lateral striatum, dorsal part of medial striatum, the globus pallidus, and the intrapeduncular nucleus.
2. Ventral Viscerolimbic Basal Ganglia, consisting of the olfactory tubercle, ventral part of medial striatum, nucleus accumbens, and ventral pallidum.
3. Extended Amygdala, consisting of two components: (1) central extended amygdala which includes the so-called subpallial amygdala, an apparent central amygdala homologue, and the lateral bed nucleus of the stria terminalis, and, (2) the medial extended amygdala comprising the subpallial medial amygdala homologue (i.e. the subpallial nucleus taeniae) and the medial bed nucleus of the stria terminalis.
4. Basal Telencephalic Cholinergic and Non-cholinergic Corticopetal System, consisting of: the nucleus basalis magnocellularis, the nucleus of the diagonal band, and nucleus commissuralis septi.

5. Septum and Septal Neuroendocrine Systems, consisting of: the medial septum, the lateral septum, the nucleus of the hippocampal commissure (previously known as the bed nucleus of the pallial commissure), the lateral septal organ, the organum vasculosum of the lamina terminalis, and the subseptal organ.

Of these five systems, the first four residing within the lateral wall of subpallium will be reviewed here because of the close associations with intratelencephalic circuitry, motor function, and reward-motivated learning. The Septum and Septal Neuroendocrine System occurring medially between the ventral horns of the lateral ventricles and more closely associated with downstream diencephalon neuroendocrine functions and related social behaviors, will be reviewed in a later paper.

2.3. Developmental origin

The subpallium in both birds and mammals forms in the basal telencephalic anlage during development, and gives rise to the structures of the mature basal telencephalon, which are thus referred to as subpallial structures (Holmgren, 1925; Källén, 1951, 1953, 1962; Striedter, 1997; Puellas et al., 2000; Cobos et al., 2001b; Marín and Rubenstein, 2001; Pombero and Martínez, 2009). Current gene expression and fate mapping data indicate that the subpallium possesses three major radially-oriented histogenetic zones (Fig. 2) during development: 1) a dorsal, striatal zone termed the lateral ganglionic eminence (LGE) in mammals, which produces striatal subdivisions of the dorsal and ventral basal ganglia and the subpallial amygdala; 2) a ventral, pallidal subdivision called the medial ganglionic eminence (MGE) in mammals, which produces pallidal subdivisions of the dorsal and ventral basal ganglia and the subpallial amygdala; and 3) the preoptic subdivision (POC) in the telencephalic stalk, which contributes to the subpallial amygdala, and gives rise to most of the cholinergic cells of the basal forebrain corticopetal system (Puelles et al., 2000; Cobos et al., 2001a, b; Marín and Rubenstein, 2001; Redies et al., 2001; Flames et al., 2007; Puellas et al., 2007; García-López et al., 2008; Abellán and Medina, 2008; 2009). Recent data in the chicken and mouse indicate that each of these three zones is divided into further subzones, each giving rise to different parts of the striatum, pallidum and subpallial amygdala, as detailed below.

The entire subpallium in birds and mammals is defined by expression of the transcription factors *Dlx2/5* and the neurogenetic gene *Mash1* (or its orthologue in other vertebrates). These are involved in regulating the production of GABAergic neurons, which are the predominant and defining neuron type of the subpallium (Puelles et al., 2000; Garda et al., 2002; Wullimann and Mueller, 2004; Abellán and Medina, 2009). By contrast, the predominant and defining neuron type of the pallium is glutamatergic (Abellán et al., 2009). The striatal subdivision of the developing subpallium is distinct from the pallidal and preoptic zones in that it expresses *Gsh2*, *Pax6* and the LIM-only gene *Lmo4*, in addition to *Dlx2/5* and *Mash1*. This is particularly evident using coronal sections of embryonic chick(c) hybridized for *cLmo4* (Fig. 3C-3F) and *c substance P (cSP)* (Fig. 3A-3B) which mark major striatal components of the dorsal somatomotor and ventral viscerolimbic basal ganglia. By contrast, the pallidal and the preoptic zones additionally express the transcription factors *Nkx2.1*, *Lhx6* and *Lhx7/8*, with the preoptic subdivision also showing strong ventricular expression of Sonic *hedgehog* (Puelles et al., 2000; Garda et al., 2002; Flames et al., 2007; García-López et al., 2008; Abellán and Medina 2009). Thus, each of the three major subpallial histogenetic zones (striatal, pallidal and preoptic) expresses a unique and defining combination of genes that are thought to control development of those regions. Note that the so-called caudal ganglionic eminence of mammals, previously proposed to represent a separate subpallial subdivision (Nery et al., 2002), is now thought to represent the caudal parts of both the lateral and medial ganglionic eminences (Flames et al., 2007; García-López et al., 2008).

Studies in mice and other neurogenetic models have begun to clarify the role of these genes and their hierarchical interactions during development. *Gsh1/2* and *Nkx2.1* are among the earliest transcription factors expressed in the mouse subpallium, and they play key roles in patterning and specification of the striatal and pallidal subdivisions, respectively (Sussel et al., 1999; Yun et al., 2001, 2003). The role of *Gsh1/2* in striatal formation is evidenced by the absence or malformation of the striatum in *Gsh2*-null mice (Yun et al., 2001) or *Gsh1/2*-double null mice (Yun et al., 2003). Similarly, the role of *Nkx2.1* in pallidal development is evidenced by the severe pallidal malformation in *Nkx2.1*-null mice (Sussel et al., 1999). *Gsh1/2* and *Nkx2.1* are transcription factors that regulate the expression of downstream transcription factors, such as *Mash1*, *Dlx1/2*, *Lhx6*, and *Lhx7/8* (Sussel et al., 1999; Toresson et al., 2000; Yun et al., 2001, 2003). *Mash1* and *Dlx1/2* have been shown by studies in mice to be involved in the neurogenesis and differentiation of subpallial GABAergic neurons (Stühmer et al., 2002a,b; Cobos et al., 2005; Long et al., 2009a,b), while *Lhx7/8* plays a key role in the differentiation of cholinergic neurons (Zhao et al., 2003). Most of these transcription factors are expressed in chicken subpallium in patterns identical to those in mouse (e.g., *Dlx2/5*, *Nkx2.1*, *Lhx6*, *Lhx7/8*). While it seems likely their function is similar, this has not been directly demonstrated. Nonetheless, the correlated expression of *Dlx2/5* and GAD67 (a synthetic enzyme for GABA) in chicken and *Xenopus* suggests that Dlx transcription factors play a role in differentiation of GABAergic neurons in the forebrain of nonmammalian vertebrates as well (Brox et al., 2003; Abellán and Medina, 2009). In addition, the correlated expression of *Lhx7/8* and ChAT (the synthetic enzyme for acetylcholine) in chicken suggests that *Lhx7/8* plays a role in the differentiation of telencephalic cholinergic neurons in birds, much like it does in mammals (Abellán and Medina, 2009). Moreover, *Nkx2.1*-knockdown in *Xenopus* suggests that this transcription factor also plays an evolutionarily conserved role in pallidal specification and in the regulation of *Lhx7/8* expression (van der Akker et al., 2008).

The striatal and pallidal zones possess subdomains that are characterized by expression of distinct combinations of developmental regulatory genes, with each giving rise to specific subpopulations of subpallial neurons (Flames et al., 2007; Abellán and Medina, 2009). In chicken, the developing striatal progenitor zone includes three subdivisions. Early in development there are only two, a dorsal and ventral, with the ventral then later subdividing into separate ventrointermediate and ventrobasal zones to make three distinct striatal progenitor regions. These three striatal subdomains have been identified in mouse as well, and mice additionally possess a fourth zone, not evident in birds, interposed between the initial dorsal and ventral subdomains. In both chickens and mice, the two ventral subdivisions are the source of the bulk of the dorsal and ventral striatum. The dorsal subdivision is characterized by expression of the transcription factor *Pax6* in both mitotic and postmitotic cells, and the ventral subdivision expresses the transcription factor *Islet1* in the subventricular zone and mantle (Puelles et al., 2000; Yun et al., 2001; Stenman et al., 2003; Abellán and Medina, 2009). Based on the expression of *Pax6* and correlation with data on mammals, the dorsal striatal subdivision also appears to be the source of GABAergic and dopaminergic interneurons that migrate into the olfactory bulb (Abellán and Medina, 2009). The dorsal striatal subdivisions may thus also be the source of catecholaminergic-dopaminergic neurons in the olfactory tubercle of some birds (Roberts et al., 2002; Abellán and Medina, 2009), and in the striatum of mice and primates (Marín et al., 2005; Huot and Parent, 2007). The dorsal striatal subdomain also produces part of the lateral striatum in chicken (Abellán and Medina, 2009), and similarly in mouse some neurons of the dorsolateral striatum (Toresson and Campbell, 2001; Yun et al., 2003). At caudal hemispheric levels in both chicken and mouse, this dorsal striatal subdivision also appears to produce *Pax6*-expressing striatal neurons for the central amygdala in both chicken and mouse (Puelles et al., 2000; Tole et al., 2005; Abellán and Medina, 2009). Finally, a thin group of neurons directly below the palliosubpallial lamina also appears to be part of the

dorsal striatal subdivision. This region distinctly expresses *Lmo4* (Abellán and Medina, 2009) and the *Enc1* gene (ectodermal and neural crest cortex), a homolog of *Kelch* a *Drosophila melanogaster* gene essential for oogenesis (Puelles et al., 2007; García-Calero and Puelles, 2009), and it overlaps the subpallial area expressing *Pax6*. Since intercalated cell masses of the mammalian amygdala derive from the dorsal LGE based on gene expression and fatemap data (Tole et al., 2005; Kaoru et al., 2010; Waclaw et al., 2010), the *Lmo4*-expressing striatal capsular region in chicken has been proposed to be homologous to the amygdaloid intercalated cell masses of mammals (Abellán and Medina, 2009).

Based on genetic fate mapping of *Islet1* progenitors in mouse, most neurons of the striatal part of the basal ganglia (including the majority of projection neurons of dorsal and ventral striatum) derive from the two parts of the ventral striatal subdivision or ventral LGE (Stenman et al., 2003; Waclaw et al., 2010; reviewed in Medina and Abellán, 2009), and this appears to be true in chicken as well (Abellán and Medina, 2009). In contrast, most striatal interneurons in mouse and chicken derive from the pallidal or preoptic subpallial progenitor zones (Marin et al., 2000; Cobos et al., 2001a; Abellán and Medina, 2009; see below). The striatal part of the developing basal ganglia in birds, however, differs from that in mammals in the number of regions making up the striatal progenitor zone. As noted above, this region of the developing subpallium in birds comes to consist of separate dorsal, ventrointermediate and ventrobasal subdomains, while in mammals an additional zone is interposed between the dorsal and two ventral striatal zones. This additional zone may give rise to the striosomal dorsal striatal compartment in mammals, which may explain why this compartment seems absent in birds (Flames et al., 2007; Abellán and Medina, 2009). The ventrointermediate striatal-equivalent in mammals (LGE3 in mouse) then gives rise to the projection neurons of the matrix compartment of dorsal striatum, and in birds to the dorsal medial striatum and lateral striatum. The ventrobasal striatal zone (corresponding to LGE4 in mouse), in turn, gives rise to nucleus accumbens in birds and mammals (Abellán and Medina, 2009). The ventrobasal zone also appears to produce the INP in birds (Abellán and Medina, 2009).

The pallidal progenitor zone of mouse and chicken also has molecularly distinct subdivisions (Flames et al., 2007; García-López et al., 2008; Abellán and Medina, 2009). Again, the development of the pallidal subpallial regions is more complex in mouse than in chicken, with mouse having five distinct progenitor subdomains and birds only three evident ones (Flames et al., 2007; Abellán and Medina, 2009), although one of the avian pallidal progenitor subdomains appears to correspond to two MGE zones. Of those in mammals, the dorsalmost seems absent in birds, and the second and third MGE zones give rise to most neurons of the globus pallidus, and correspond to the dorsal pallidal zone of chick, which also gives rise to globus pallidus. As will be discussed below, these various pallidal zones also contribute to the bed nucleus of the stria terminalis and extended amygdala. In addition, recent data indicate that the adult mouse globus pallidus includes a neuron subpopulation that originates in the striatal progenitor zone (Nóbrega-Pereira et al., 2010). The neurons of this subpopulation of the globus pallidus do not contain parvalbumin, although they are GABAergic (Nóbrega-Pereira et al., 2010), and likely represents a striatal-type subpopulation of projection neurons that contain calbindin and enkephalin, and project back to the striatum (Hoover and Marshall, 2002; Medina and Abellán, 2009). A similar neuron subpopulation also appears to be present in the chicken globus pallidus (Molnar et al., 1994; Abellán and Medina, 2009). The mammalian ventral pallidum possesses a rostral, precommissural part that arises from MGE4, and a commissural ventral pallidum that arises from MGE2/3 (García-López et al., 2008; Abellán and Medina, 2009). The avian ventral pallidum, however, appears to arise only from the MGE4-equivalent (i.e. the ventral pallidal zone), and is thus homologous only to the precommissural ventral pallidum (García-López et al., 2008; Abellán and Medina, 2009). Both mouse and chicken possess a caudoventral pallidal subdivision (MGEcv), which is included as a caudal part of the fifth progenitor

subdomain of the medial ganglionic eminence (pMGE5; Flames et al., 2007), and is sometimes called the anterior peduncular area (AEP) (García-López et al., 2008; Abellán and Medina, 2009), that appears to give rise to part of the medial extended amygdala, as discussed in more detail in a later section.

Based on *Sonic hedgehog* (*Shh*) expression, the commissural preoptic area (POC) of both mouse and chicken also appears to contribute cells to the subpallial medial amygdala and other parts of the medial extended amygdala, and this has been shown experimentally in the mouse (Bupesh et al., 2011a). Pallidal (MGEcv) and POC cells intermingle in the subpallial medial amygdala of chicken, resembling in this respect the anterior part of the medial amygdala of mammals (García-López et al., 2008; Abellán and Medina, 2009). Recent data indicate that the *Lhx7/8* transcription factor is particularly highly expressed in the POC of mouse and chicken (including the ventricular zone where most progenitor cells are located) and that this subdivision may be the source of many cholinergic cells of the basal forebrain, including the corticopetal neurons of the basal magnocellular nucleus (NBM) and those overlapping the pallidum, as well as most of the cholinergic interneurons of the striatum (García-López et al., 2008; Abellán and Medina, 2008; 2009). Data in mouse indicate that *Lhx8* (also called *Lhx7/8*) is required for development of most cholinergic neurons of the telencephalon, since they are missing in *Lhx7/8* knockout mouse (Zhao et al., 2003; Manabe et al., 2007). The influence of *Lhx7/8* is partially mediated by the transcription factor *Islet1*, which is expressed in subventricular and postmitotic cells of POC. This interpretation is consistent since POC-derived cholinergic neurons of basal forebrain, pallidum and striatum are absent in conditional forebrain-specific *Islet1*-null mouse (Elshatory and Gan, 2008). Because most cholinergic neurons of the medial septum/diagonal band nuclei are preserved in conditional *Islet1*-null mice (Elshatory and Gan, 2008), these may derive from the rostroventral MGE, a subdomain that expresses *Lhx7/8* in its ventricular and subventricular zones, but not *Islet1*, in mouse and chicken (Flames et al., 2007; Abellán and Medina, 2009; reviewed in Medina and Abellán, 2009).

In summary, developmental and anatomical data suggest the following categorization of lateral subpallial structures (Table 1). Striatal regions derived from the striatal progenitor zone are the lateral and medial striatum, accumbens core and shell, intrapeduncular nucleus, part of the central extended amygdala, and part of the olfactory tubercle. The pallidal regions derived from the pallidal progenitor zone are the globus pallidus, ventral pallidum, part of the central and medial extended amygdala, and some neuron subpopulations of the diagonal band nuclei. The POC derivatives of the lateral subpallial wall are the basal magnocellular nucleus, the cholinergic neurons invading the pallidum and striatum, and part of the medial extended amygdala (Marín and Rubenstein, 2001; García-López et al., 2008; Abellán and Medina, 2008, 2009). Although cells of each subpallial nucleus/area primarily derive and primarily migrate radially from a specific striatal, pallidal or preoptic subdivision, there are important migrations that cross subdivision boundaries within the subpallium, or cell immigration from outside the subpallium, leading to a mixed cellular composition in most subpallial areas (Cobos et al., 2001a,b; Abellán and Medina, 2009). This is the case for some components of the extended amygdala, as will be discussed in more detail below. A striking case of tangential cell movement inside the avian subpallium is the massive migration of cells from the pallidal proliferative zone into the medial striatum demonstrated in chickens (Abellán and Medina, 2009). This will be discussed in more detail in the sections on the striatal part of the somatic basal ganglia and in the section on Area X, a striatal nucleus of songbirds that contains both striatal and pallidal neurons (Farries and Perkel, 2002; Reiner et al., 2004a; Person et al., 2008). Finally, in both chicken and mouse, the subpallium is the source of tangential migrations to the pallium, providing it with various neurochemically distinct subpopulations of GABAergic interneurons (Marín and Rubenstein, 2001, 2003; Cobos et al., 2001a, b; Abellán and Medina, 2009). The subpallium

also appears to produce some cholinergic interneurons for the pallium (Abellán and Medina, 2009).

Hence, the developing vertebrate subpallium, at least in tetrapods, appears to commonly possess the same three major progenitor zones or their correspondents: striatal, pallidal and POC (Fig. 2). Markers useful in identifying progenitor zones have likewise been shown to give rise to homologous subpallial cell groups of the lateral telencephalic wall in birds and mammals, as well as reptiles and amphibians (Fernández et al., 1998; Bachy et al., 2002; González et al., 2002a, b; Brox et al., 2003; Moreno et al., 2004; Moreno et al., 2008a,b,c; 2009). In the following sections, we review recent progress on the dorsal basal ganglia, the ventral basal ganglia, the subpallial amygdala/extended amygdala, and the basal forebrain corticopetal system of birds.

3. Four neural systems occupying the lateral subpallial wall

3.1. Dorsal somatomotor basal ganglia

Discovery in the 1960s of the abundance of dopamine and acetylcholinesterase in the avian subpallium began to reshape understanding of the location and extent of the avian basal ganglia (Spoonster and Winters, 1966; Juorio and Vogt, 1967; Karten, 1969; Nauta and Karten, 1970). The outdated and current understanding of components of the avian telencephalon in comparison to that of mammals is shown in Figure 4. Immunostaining with an antibody to tyrosine hydroxylase (TH) clearly demonstrated that the avian basal ganglia did not occupy the majority of the telencephalon as suggested by Nissl staining (Fig. 4, Fig. 5C) rather it occupied the ventromedial region similar to mammals (Fig. 4B, 4D). The avian dorsal somatomotor basal ganglia and its major structures in relation to the pallium are shown in Figures 4D and 5). Details of each of its components (medial striatum, lateral striatum, globus pallidus, and intrapeduncular nucleus) which have been more extensively studied than other parts of the avian subpallium are reviewed below. In this section, we also discuss area X of the songbird medial striatum.

3.1.1. Medial striatum—The medial striatum (MSt) together with the lateral striatum (LSt) has been known for many years to share numerous neurochemical, developmental and hodological traits with the mammalian dorsal striatum, and on this basis (including the presence of similar structures in reptiles) considered to be homologous to the mammalian caudate-putamen (Reiner et al., 2004a). The MSt and LSt differ in their connectivity, and are not considered strictly homologous to caudate and putamen, respectively, in a one-to-one manner. Thus, the MSt and LSt need to be discussed separately. In addition to embryological origin, shared traits that show MSt and LSt are striatal include a neuropil rich in acetylcholinesterase (AChE), choline acetyltransferase-containing terminals (ChAT; Medina and Reiner, 1994), dopamine (DA) – containing terminals (revealed by TH immunostaining), substance P (SP) – containing perikarya and processes, and enkephalin (ENK) – containing perikarya and processes (Fig. 5; reviewed in Reiner et al., 1998a). Concordant with its rich dopaminergic innervation, MSt and LSt have also been shown to be rich in D1_A, D1_B, and D2 dopamine receptors (Richfield et al., 1987; Dietl and Palacios, 1988; Casto and Ball, 1994; Schnabel and Braun, 1996; Stewart et al., 1996; Schnabel et al., 1997; Sun and Reiner, 2000; Kubikova et al., 2010), and the dopamine receptor signaling protein DARPP32 (Reiner et al., 1998b; Bálint et al., 2004). Associated with its rich cholinergic innervation, MSt and LSt are rich in muscarinic receptors (Dietl et al., 1988; Wächter and Ebinger, 1989; Kohler et al., 1995). In these regards, MSt resembles mammalian striatum, as well as in the expression of the developmentally regulated genes noted above.

One underlying reason for the neurochemical similarity between avian MSt and mammalian striatum is that they consist of the same major neuron types. This includes GABAergic projection neurons, which make up the bulk of MSt neurons. These projection neurons possess spiny dendrites, and about half also contain enkephalin while the other half show colocalization of substance P (SP) and dynorphin (Brauth et al., 1983; Reiner et al., 1983, 1984; Reiner and Anderson, 1990; Anderson and Reiner, 1990a; Anderson and Reiner, 1991; Veenman and Reiner, 1994; Sun et al., 2005). These neurons account for the SP+ and enkephalinergic projections of MSt to the dopaminergic neurons of the substantia nigra pars compacta and the GABAergic neurons of the substantia nigra pars reticulata (Anderson et al., 1991; Medina et al., 1995; Veenman and Reiner, 1994), of which the SP+ projection is more prominent. The MSt neurons projecting to the substantia nigra and the ventral tegmental area send their axons through the ventral pallidum, and some have terminations there (Kitt and Brauth, 1981; Medina and Reiner, 1997; Person et al., 2008). Interneurons make up most of the remainder of MSt neurons, although the percent projection neuron versus interneuron composition of MSt is not certain. The interneurons include: (1) large, aspiny cholinergic neurons that contain choline acetyltransferase (Medina and Reiner, 1994); (2) medium-sized aspiny GABAergic interneurons co-localized with somatostatin and neuropeptide Y (NPY) (Anderson and Reiner, 1990b); and (3) medium-sized aspiny neurons containing GABA, the calcium-binding protein parvalbumin, and the neurotensin-related hexapeptide LANT6 (Reiner and Carraway, 1987; Reiner and Anderson, 1993). These neurons appear to have similar electrophysiological properties to their mammalian counterparts (Farries and Perkel, 2000; Farries et al., 2005b). In mammals, a fourth type of interneuron contains GABA and the calcium binding protein calretinin (Bennett and Bolam, 1993; Figueredo-Cárdenas et al., 1996), and this cell type is rare or absent in bird MSt (Laverghetta et al., 2005).

One cell type that is present in MSt but absent in mammalian striatum is a neuron type that appears pallidal in its developmental derivation, neurochemistry, connectivity and physiology. As noted in the section above, during development a massive migration of cells occurs from the pallidal subdivision into the medial striatum in chickens. These cells can be recognized as pallidal since they express *Nkx2.1*, *Lhx6* and/or *Lhx7/8*, and they are distributed throughout MSt and continuous with the far more concentrated pallidal neurons of the globus pallidus, which have a similar gene expression signature (Abellán and Medina, 2009). Some of these neurons derived from the pallidal proliferative zone are likely to constitute striatal interneurons, such as those containing parvalbumin/LANT6 or somatostatin/neuropeptide Y (Cobos et al., 2001a; Carrillo and Doupe, 2004). The neurons expressing *Nkx2.1*, *Lhx6* and/or *Lhx7/8* are, however, more numerous than the parvalbumin/LANT6 or somatostatin/neuropeptide Y interneuron populations (Reiner and Carraway, 1987; Anderson and Reiner, 1990b; and Abellán and Medina, 2009), and at least some of them may be those shown to project to intralaminar thalamus in chickens and zebra finches, and possess pallidal electrophysiology (Farries and Perkel, 2002; Reiner et al., 2004b; Farries et al., 2005b; Person et al., 2008). Given the robustness of this trait in these two avian species, it seems likely that it is a general trait of MSt in birds. Consistent with this, the MSt in pigeons is rich in GABAergic woolly fibers that also contain either SP or enkephalin, especially along its medial wall (Reiner et al., 1983, 1984, 1998b). The woolly fiber pattern of SP+ and enkephalinergic terminal distribution is characteristic of pallidal neurons but not striatal interneurons. The putative intra-MSt pallidal neuron dendrite targets of this woolly fiber input are not rich in parvalbumin or LANT6 (Reiner and Carraway, 1987), and thus the pallidal neurons receiving this input in MSt have not been reported previously. The developmental data together with the neuropeptide immunolabeling data suggest that pallidal neurons may be numerous and widespread in MSt, but low in the conventional pallidal neuron markers parvalbumin or LANT6, at least in adults. While it is

known that some of these pallidal MSt neurons project to intralaminar thalamus, it is unknown if they have other projection targets as well.

The MSt also evidences a medial-lateral difference in neurochemical traits and connectivity. For example, medial MSt receives its dopaminergic input from the A10 dopaminergic neurons of the ventral tegmental area (VTA, Fig. 6A, 6B) (Kitt and Brauth, 1986b; Bailhache and Balthazart, 1993; Puellas and Medina, 1994; Reiner et al., 1994), while more lateral MSt receives its dopaminergic input from the A9 dopaminergic neurons of the substantia nigra pars compacta (SNc, Fig. 6A, 6C; Kitt and Brauth, 1986b; Bailhache and Balthazart, 1993; Puellas and Medina, 1994; Reiner et al., 1994; Smeets and Reiner, 1994; Székely et al., 1994; Medina and Reiner, 1995; Karle et al., 1996; Metzger et al., 1996; Durstewitz et al., 1998, 1999; Reiner et al., 1998a,b). Similar parcellation has been observed in the preferential origin of the projections to the ventral tegmental area or substantia nigra from the medial versus lateral MSt, respectively (Mezey and Csillag, 2002). The MSt also receives major excitatory afferents from pallial regions. As in mammals, the “corticostratial” projection utilizes glutamate, an excitatory amino acid neurotransmitter (Veenman and Reiner, 1996; Csillag et al., 1997; Reiner et al., 2001; Ding et al., 2003; Ding and Perkel, 2004; Farries et al., 2005a). More lateral MSt receives pallial input from somatic regions, such as those involved in somatosensory, visual, auditory and motor function (Karten and Dubbeldam, 1973; Nottebohm et al., 1976; Brauth et al., 1978; Wild, 1987; Wild et al., 1993; Veenman et al., 1995). By contrast, medial MSt appears more viscerolimbic, since its pallial input arises from such regions as hippocampus and olfactory bulb. Similarly, its excitatory thalamic input also arises from midline, more viscerolimbic intralaminar nuclei than does that to lateral MSt (Veenman et al., 1997). Thus, the two parts of MSt may differ in function, with medial MSt more viscerolimbic than lateral MSt. One possibility is that medial MSt is comparable to mammalian striosomes, since both are poor in calbindin (Roberts et al., 2002; Balint and Csillag, 2007). Abellán and Medina (2009), however, have suggested that birds may lack the part of the dorsal striatal proliferative zone that gives rise to striosomes. Thus, the medial MSt viscerolimbic traits may be comparable to those of medial mammalian caudate. Nonetheless, MSt seemingly differs from mammalian caudate in that its striatal neurons mainly project to the nigra and very few to globus pallidus. Additionally, a ventral and caudal part of what has been termed MSt may be part of the viscerolimbic striatum comparable to part of the shell of nucleus accumbens (Abellán and Medina, 2009). This region, however, may not be strictly equivalent to mammalian accumbens shell since unlike shell it is very rich in cholinergic neurons, dopaminergic terminals and SP+ and ENK+ woolly fibers. Accumbens core and shell are discussed in more detail in the viscerolimbic section.

3.1.2. Lateral striatum—As noted above, the LSt of birds possesses the neurochemistry and many of the neuron types characteristic of mammalian dorsal striatum, including neuropil enrichment in AChE, choline acetyltransferase-containing terminals, SP+ neurons, enkephalinergic neurons, D1, D1_A, D1_B, and D2 dopamine receptors, DARPP32 and muscarinic receptors. As true of MSt, the dopamine receptors and DARPP32 enrichment in LSt reflect the prominent dopaminergic input, in this case from the substantia nigra pars compacta (Fig. 6A, C) and A8 (Fig. 6D, E) tegmental cell groups. The LSt, except for its lateral edge, which may belong to the olfactory tubercle, receives its excitatory input mainly from somatic pallial and thalamic regions (Veenman et al., 1995, 1997). This feature of its input is consistent with its output circuitry to the globus pallidus, which gives rise to an output to motor pallium in the Wulst (thought to be an M1 homologue) via the avian motor thalamus (the ventrointermediate area, or VIA). The LSt neurons giving rise to this are likely to be SP+, and one of the so-called “direct pathway” outputs of the striatum for facilitating movement (Jiao et al., 2000). The enkephalinergic neurons of the LSt, by contrast, have been shown to give rise to the “indirect pathway” out of the avian striatum,

which projects to pallidal neurons innervating the subthalamic nucleus (Jiao et al., 2000; Person et al., 2008). This circuit appears to be involved in suppressing unwanted movements, as also the case in mammals (Jiao et al., 2000). With respect to its motor role as well as its presumed output to pallidal neurons projecting to intralaminar thalamus, the LSt may be comparable to the dorsolateral mammalian striatum. Moreover, the striatal neurons of primate dorsolateral striatum more heavily project to the globus pallidus than to nigra (Parent et al., 1995; Lévesque and Parent, 2005), as is also true of avian LSt. While at one time it seemed the avian LSt had no projections to the substantia nigra, recent evidence shows that some LSt neurons project to substantia nigra pars compacta and pars reticulata (Mezey and Csillag, 2002; Person et al., 2008).

Although the LSt contains most of the same striatal neuron types as the MSt, there are some notable differences. For example, while the LSt contains abundant SP+ spiny projection neurons, ENK+ spiny projection neurons and parvalbuminergic interneurons, immunolabeling suggests that LSt contains far fewer cholinergic and SS/NPY interneurons than MSt (Anderson and Reiner, 1990b; Medina and Reiner, 1995; see Fig. 6 and 13 in Abellán and Medina, 2009) or they may even be absent (Person et al., 2008). Nonetheless, the LSt is rich in cholinergic terminals and muscarinic receptors (Dietl et al., 1988; Wächter and Ebinger, 1989; Kohler et al., 1995; Medina and Reiner, 1995). Additionally, *in situ* hybridization for ChAT mRNA in day-old hatching chicks reveals some LSt cells positive for ChAT (Abellán and Medina, 2009), although the labeling is weaker than in MSt. It may be that immunostaining does not effectively label the somata of these cells or perhaps there is a developmental change in ChAT expression. Regardless, it is possible that the sparse and weakly labeled somata of LSt give rise to a dense cholinergic innervation. Alternatively, cholinergic neurons of MSt, globus pallidus or the intrapeduncular nucleus (see below) could provide the cholinergic innervation to LSt. Cholinergic innervation is important in regulating striatal projection neuron function and synaptic plasticity (Kreitzer and Malenka, 2008). The paucity of unambiguous resident cholinergic neurons in LSt (i.e. motor striatum) in birds indicates that the role of cholinergic neurons in striatal plasticity may differ from that in mammals. The functional implication of the apparent absence of somatostatinergic/NPY+ interneurons in LSt is uncertain.

3.1.3. Intrapeduncular nucleus—The intrapeduncular nucleus (INP), located below the inferior margin of the avian globus pallidus, is named for its location within the lateral forebrain bundle. Karten and Dubbeldam (1973) originally thought that its position resembled that of the mammalian internal pallidal segment, but subsequent immunolabeling studies showed that it lacked the pallidal-type neurons and the SP/DYN-containing striatal input characteristic of the internal pallidal segment (Reiner et al., 1983; Reiner and Carraway, 1987; Anderson and Reiner, 1990a; Veenman and Reiner, 1994; Reiner et al., 1999). More recent studies have shown that the INP contains densely packed GABAergic spiny neurons that express DARPP32 (Schnabel et al., 1997; Reiner et al., 1998b; Sun et al., 2005), and a very similar glutamate receptor profile to the striatum (Wada et al., 2004). Moreover, the INP has recently been found to develop from the ventralmost striatal progenitor zone, to show continuity with the medial striatum, and to contain neurons expressing *Lmo4* and cell-surface proteins (Cadherin-8) characteristic of striatal neurons (Abellán and Medina, 2009). The striatal neurons of INP include both SP-containing and enkephalinergic neurons. It also contains neurons derived from the pallidal and preoptic proliferative zones (identifiable as expressing *Lhx6* and/or *Lhx7/8*), as typical of the medial and lateral striatum proper (Abellán and Medina, 2009). The INP neurons expressing *Lhx6* and/or *Lhx7/8* may include the many cholinergic neurons and the few parvalbuminergic/LANT6 neurons it contains (Reiner and Carraway, 1987; Medina and Reiner, 1994). Like LSt, INP is poor in somatostatin/NPY interneurons (Anderson and Reiner, 1990b). Although the data thus suggest a largely striatal nature for the INP, it also possesses some traits that

differ from those of MSt and LSt. For example, INP is much richer than either MSt or LSt in LAMP, a limbic system marker (Yamamoto and Reiner, 2005), which is consistent with its derivation from the ventralmost part of the striatal sector of the developing subpallium, from which much of limbic striatum derives. The INP also contains many more immigrant cholinergic neurons than either MSt or LSt (Abellán and Medina, 2009). These cholinergic neurons appear to belong to the corticopetal system (Medina and Reiner, 1994). Finally, although seemingly a striatal territory, the INP is poor in dopaminergic terminals and dopamine receptors, making its enrichment in DARPP32 somewhat puzzling.

Given then that INP is a striatal derivative containing neurons with striatal traits, on what basis should it be assigned to dorsal striatum rather than ventral striatum, especially with its derivation from the ventral part of the striatal proliferative zone and its enrichment in LAMP? The relevant feature of INP that warrants this classification is that the INP is part of the circuitry controlling motor function via descending motor projections to the midbrain tectum. Karten and Dubbeldam (1973) had suggested that both globus pallidus and INP might project to the lateral spiriform nucleus of the pretectum (SpL). In later studies, SpL was found to project to deep layers of the optic tectum (Reiner et al., 1982a,b), and its neurons were shown to have pallidal morphology and neurochemistry (Reiner and Carraway, 1987; Reiner and Anderson, 1993; Veenman and Reiner, 1994). At that time, retrograde labeling with horseradish peroxidase only confirmed the GP projection to SpL but not the INP projection. More recent studies using biotinylated dextran amine (BDA) as the tracer have shown that neurons in INP give rise to a descending projection through the diencephalon (Jiao et al., 2000). Recent studies indicate that neurons in INP as well as some in LSt project to the SpL (Reiner and Medina, unpub. obs). The LSt flanking the INP receives a major projection from the internal division of the entopallium, a thalamorecipient zone, within the telencephalon, of the tectofugal visual system (Krütfeldt and Wild, 2005). The neurons in LSt at least contain SP, and are thus direct pathway neurons. SpL also receives input from globus pallidus neurons (Reiner et al., 1982a; Medina and Reiner, 1997), which themselves receive input from enkephalinergic LSt neurons (Reiner and Medina, unpub. obs.). These results indicate that the INP striatal neurons, together with SP+ neurons of LSt give rise to a “direct pathway” type output to SpL (Reiner et al., 1998a). A facilitatory role in tectally mediated head and eye movements seems likely for this circuit, based on its connectivity.

3.1.4. Globus pallidus—The globus pallidus (GP) in both mammals and birds is neurochemically distinct from striatum. For example, the globus pallidus has a low density of dopaminergic and cholinergic terminals and little acetylcholinesterase (Karten and Dubbeldam, 1973; Reiner et al., 1994). Correspondingly, it is poor in dopaminergic and muscarinic receptors (Richfield et al., 1987; Dietl and Palacios, 1988; Casto and Ball, 1994; Schnabel and Braun, 1996; Stewart et al., 1996; Schnabel et al., 1997; Sun and Reiner, 2000; Dietl et al., 1988; Wächtler and Ebinger, 1989; Kohler et al., 1995; Kubikova et al., 2010). The globus pallidus in birds and mammals is distinguished by the presence of large, aspiny GABAergic neurons, many of which also contain parvalbumin and LANT6 (Reiner and Carraway, 1987; Reiner and Anderson, 1993; Veenman and Reiner, 1994), and a dense mat of woolly fiber terminals containing GABA and SP, or GABA and enkephalin, which end on the aspiny GABAergic neurons (Reiner et al., 1998a). The pallidal neurons are rich in receptor types related to their predominant inputs. For example, the pallidal neurons of GP are rich in GABA receptors, as a consequence of their GABAergic input from LSt (Veenman et al., 1994). Similarly, as a consequence of the glutamatergic input from subthalamic nucleus, pallidal GP neurons are rich in NMDA-type and AMPA-type glutamate receptors (Jiao et al., 2000; Wada et al., 2004; Laverghetta et al., 2005).

The GABAergic neurons of the globus pallidus co-containing parvalbumin, which represent the majority of pallidal neurons in mammals and birds, derive from the pallidal progenitor zone (Xu et al., 2008; Abellán and Medina, 2009; Nóbrega-Pereira et al., 2010). In mammals, globus pallidus neurons remain *in situ* relatively near the lateral ventricle and inferior and medial to the striatum. In birds, the pallidal neurons migrate as a stream from their ventral position, sweeping along an arching ventromedial to dorsolateral course to invade the striatal sector between INP and LSt to form the globus pallidus (Puelles et al., 2007; Abellán and Medina, 2009). Some pallidal neurons remain in residence along this course, and one medial and ventral cluster forms the ventral pallidum. Nonetheless, the neurons of the globus pallidus and ventral pallidum derive from different sectors of the pallidal anlage, as noted above (Abellán and Medina, 2009). The entire migratory course of the pallidal neurons remains poor in striatal markers in adult birds, and largely contains a mix of pallidal GABAergic neurons and cholinergic neurons. The migration of pallidal neurons to the globus pallidus is, however, not precise and many pallidal neurons come to reside in MSt as well, as noted above. One consequence of pallidal invasion into a lateral striatal territory is that some striatal neurons remain in residence in the formerly striatal territory that has been “taken over” by pallidal neurons to create avian globus pallidus. Hence, SP+ and enkephalinergic spiny neurons are present in low abundance in avian GP (Reiner et al., 1983, 1984; Molnar et al., 1994; Abellán and Medina, 2009). In mammals, the globus pallidus also contains a subpopulation of enkephalinergic neurons, which have descending projections with collaterals to the striatum (Hoover and Marshall, 1999, 2002; Kita and Kita, 2001). The embryonic origin of these cells may be the striatal subdivision (Nóbrega-Pereira et al., 2010). In mice, this pallidal subpopulation is GABAergic, but does not express the pallidal gene *Nkx2.1*, and is spared in *Nkx2.1* knockout mouse (Nóbrega-Pereira et al., 2010), in which the pallidum is missing (Sussel et al., 1999). On the other hand, the cholinergic neurons that invade the pallidum are derived from the preoptic subpallial subdivision (POC) in both mouse and chicken (García-López et al., 2008; Abellán and Medina, 2009; Nóbrega and Pereira et al., 2010). Since these neurons belong to the corticopetal system, they will be treated in a later section.

The globus pallidus in mammals consists of two distinct segments that differ in the type of striatal neuron from which they receive input, and that differ in their projection targets. The external pallidal segment (GPe) receives enkephalinergic striatal input (from indirect pathway striatal neurons) and projects mainly to the subthalamic nucleus (STN), thalamic reticular nucleus and the substantia nigra pars reticulata, while the internal pallidal segment (GPi) receives SP+ striatal input (from direct pathway striatal neurons) and projects mainly to intralaminar and motor thalamus. In birds, the globus pallidus is a singular structure that contains both of these pallidal neuron types, as evidenced by the overlap of SP+ and enkephalinergic inputs to the avian GP and as evidenced by the projection of the avian GP to the targets of both the mammalian GPe and GPi (Medina and Reiner, 1997). These projections have been detailed in prior papers (e.g. Medina and Reiner, 1997; Farries et al., 2005a) and will be discussed in the following section on functional organization of the avian basal ganglia.

3.1.5. Functional considerations for dorsal basal ganglia—Models of the functional organization of the somatic basal ganglia in mammals have recognized two parallel output circuits that have opposing functions in motor control and that interact with one another. These two output circuits originate from differing sets of striatal neurons and are called the indirect (from enkephalinergic striatal neurons) and direct pathways (from SP + striatal neurons) (Albin et al., 1989; DeLong, 1990; Gerfen, 1992). The connections and functions of these two circuits have been detailed elsewhere and will not be reviewed here. Notably, the structure comprising the dorsal basal ganglia in birds is organized functionally into similar direct and indirect pathways. This too has been reviewed extensively elsewhere,

and the circuit details will not be repeated here (Reiner et al., 1998a). Of present interest are two major ways in which the direct-indirect pathway plan differs between birds and mammals. First, while mammals have two SP+ direct output pathways (to GPi and to the SNr), birds possess three, one from MSt SP+ neurons to SNr, one from LSt SP+ neurons to GPi-type neurons of globus pallidus, and one from presumptive SP+ neurons of LSt and INP to SpL. Secondly, it is not yet certain how the pallidal neurons of MSt fit into this circuit diagram. It is known that some of these neurons project to intralaminar thalamus, but it is unknown if they have additional projection targets, such as STN or SNr. Since both SP+ and enkephalinergic woolly fibers are present in MSt, it seems likely that MSt pallidal neurons include both GPe-type and GPi-type pallidal neurons. Despite these differences, the similarities between mammals and birds in the functional organization of the dorsal basal ganglia are extensive. Lesion studies and pharmacological manipulations in birds reinforce this view (Schwarcz et al., 1979; Goodman and Stitzel, 1977; Goodman et al., 1982, 1983; Rieke, 1982; Koster, 1957; Cheng and Long, 1974; Rieke, 1980; Sanberg and Mark, 1983; Rieke, 1981). Given these data and that avian species are similar to humans in being bipedal, warm-blooded, and capable of complex motor behaviors that can be readily measured, birds can potentially serve as useful models to explore the pathophysiology of basal ganglia-related disorders such as Parkinson's disease, Huntington's disease, obsessive-compulsive disorder and Tourette syndrome.

3.1.6. Area X: A specialized songbird striatal structure—The role of the anterior forebrain pathway (AFP) in song learning in songbirds has become of significant interest to basal ganglia researchers, due to the involvement of a specialized part of the songbird basal ganglia in this circuit. The serially connected components of the AFP include the following: nucleus HVC (proper name) of the pallium; area X of the MSt; the medial portion of the dorsolateral thalamic nucleus (DLM), a specialized intralaminar thalamic nucleus; and the lateral magnocellular nucleus of the anterior nidopallium (LMAN). These nuclei are serially connected with strictly ipsilateral projections (Fig. 7A). Moreover, area X, like the surrounding striatum, receives a strong dopaminergic input from the substantia nigra and VTA (Fig. 6A-C; Bottjer, 1993; Soha et al., 1996; Gale and Perkel, 2005). The AFP is required for song learning and adult song plasticity. Therefore its role appears comparable to that of cortico - basal ganglia - cortical circuits in the learning and execution of motor sequences in mammals (Bottjer et al., 1989; Sohrabji et al., 1990; Scharff and Nottebohm, 1991; Williams and Mehta, 1999; Brainard and Doupe, 2000; reviewed in Doupe et al., 2005). Reinforcing this notion is the observation that the language-related gene of humans *FoxP2* is expressed at very high levels in striatum and area X (Haesler et al., 2004; Teramitsu et al., 2004; Haesler et al., 2007; White et al., 2006 and Fisher and Scharff, 2009).

Area X contains a full complement of neurons typical of striatum such as spiny neurons, cholinergic interneurons, parvalbuminergic interneurons and somatostatinergic interneurons (Farries and Perkel, 2002; Reiner et al., 2004b). As true of striatum, the vast majority of Area X neurons are spiny neurons and essentially identical electrophysiologically to mammalian striatal spiny projection neurons (Fig. 7B; Farries and Perkel, 2002). In the zebra finch brain, high expression of D1A, D1B and D2 dopamine receptors has been found in striatum, including area X. Within area X, 77% of neurons expressed D1A, 70% expressed D2, and half appear to express both D1A and D2 receptors (Kubikova et al., 2010). As noted above, area X receives a “cortico-striatal” input from the HVC (Ding et al., 2003; Ding and Perkel, 2004; Farries and Perkel, 2005b). In contrast to any part of striatum that has been described in any mammalian species, however, area X projects directly to the thalamus (Okuhata and Saito, 1987; Bottjer et al., 1989; Parent and Hazrati, 1995). In mammals, it is a pallidal structure of the basal ganglia, the globus pallidus that projects to the thalamus. Area X has been discovered, however, to adhere to this pallidal output rule in a surprising way. The neurons of Area X that project to the medial dorsolateral nucleus of

the anterior thalamus (DLM) are pallidal in their traits - large, few in number, aspiny and pallidal in their neurochemistry, electrophysiology (Fig. 7B) and input from area X spiny neurons (Bottjer et al., 1989; Luo and Perkel 1999; Farries and Perkel, 2002; Reiner et al., 2004b; Goldberg and Fee, 2010; Goldberg et al., 2010). The mixing of striatal and pallidal neurons in area X is not unique to area X in songbirds, since the MSt region surrounding area X also contains pallidal neurons projecting to the DLM (Reiner et al., 2004b; Farries et al., 2005b). It is important to note, however, that not all properties of area X pallidal neurons are typical of those in mammalian pallidum. For example, area X neurons that project to DLM express enkephalin (Carrillo and Doupe, 2004). As noted above, chicken MSt also contains pallidal neurons, as part of the aftermath of the extensive migration of pallidal neurons dorsally toward GP during development. In this light then, the mixing of spiny striatal and pallidal aspiny neurons is not unique to area X of songbirds, but is instead a seemingly widespread feature of avian MSt. Songbird area X also projects to the ventral pallidum, via collaterals of axons projecting to the thalamic nucleus DLM, which then provides a route by which area X can modulate dopaminergic input back to itself during song learning and modification – ventral pallidum projects to regions of the ventral tegmental area and substantia nigra pars compacta that project back to area X (Gale et al., 2008; Gale and Perkel, 2010).

The key qualitative difference between area X and medial striatum is the apparent lack of an extrastriatal projection of the spiny neurons of area X. In MSt in zebra finches, chickens and pigeons, spiny neurons project to extrastriatal targets, as in mammalian striatum. To date, no substantial projection beyond area X itself has been identified for area X spiny neurons (Person et al., 2008). Instead, they contact and inhibit pallidal projection neurons within area X (Reiner et al., 2004b; Farries et al., 2005a, 2005b). The fraction of pallidal area X neurons that project to DLM versus VP remains uncertain (Reiner et al., 2004b; Farries et al., 2005a, 2005b; Leblois et al., 2009; Goldberg and Fee, 2010).

Finally, we have tentatively grouped area X with somatic striatum because of its location in rostralateral MSt, a somatic territory, and its role in a somatic motor function, song learning and in modulating song variability during learning (Ölveczky et al., 2005) or in adulthood (Kao et al., 2005; Leblois and Perkel, 2010). The interconnections of area X with ventral pallidum and VTA raise the possibility that it is perhaps allied with viscerolimbic striatum. More detail on its developmental derivation from the striatal proliferative zone and on its neurochemistry (e.g. LAMP) is needed to judge its classification as somatic, viscerolimbic, or mixed.

3.2. Ventral viscerolimbic basal ganglia

The ventral (viscerolimbic) basal ganglia in mammals possesses similar subdivisions, neurochemistry and input-output relations to that of the dorsal somatomotor basal ganglia. For example, it too consists of striatal subdivisions (nucleus accumbens and superficial olfactory tubercle) rich in spiny GABAergic projection neurons containing either substance P or enkephalin, and a pallidal subdivision (ventral pallidum and deep olfactory tubercle) to which the striatal subdivision projects. As true of the dorsal basal ganglia, the striatal part of the ventral basal ganglia receives pallial and dopaminergic input, and the pallidal part gives rise to major outputs of the ventral basal ganglia. Unlike dorsal basal ganglia, the inputs and outputs of the ventral basal ganglia are more related to visceral brain regions and functions. Consistent with this, the ventral basal ganglia appears more involved in reward and motivation underlying appetitive behavior (Kelley, 1999; Groenewegen and Uylings, 2000). Despite the many similarities to dorsal basal ganglia cellular organization and connectivity, and a basic understanding of the role of the ventral basal ganglia in reward-based behavior and functions, neuronal circuit models akin to those for the somatic basal ganglia have not yet been developed to provide a neuronal circuit-level explanation for the functions of the

ventral basal ganglia. As reward-motivated processes are a fundamental attribute of vertebrate behavior, it is not surprising that birds too possess a viscerolimbic basal ganglia (Reiner et al., 2004a). Although no distinct cytoarchitectonic boundary distinguishes the dorsal and ventral basal ganglia, the ventral basal ganglia in both mammals and birds, nonetheless, can be distinguished from the dorsal basal ganglia by a number of neurochemical distinctions, as detailed below. The components of the avian viscerolimbic basal ganglia including the olfactory tubercle, nucleus accumbens and ventral pallidum were recognized by the Avian Brain Nomenclature Forum, but several gaps in the understanding of these structures were noted and some have since been filled. Notably, the boundaries for structural components are more clearly established by developmental and neurochemical studies, including a distinction between the two main subdivisions of nucleus accumbens. Additionally, it is now evident that, like in mammals, the avian olfactory tubercle possesses striatal and pallidal subdivisions.

3.2.1. Olfactory tubercle—The olfactory tubercle (TuO) in mammals forms a prominent bulge (hence the term tubercle) at the base of the telencephalon, and is distinguished from other structures of the viscerolimbic basal ganglia by its prominent olfactory bulb input. The most ventral part of the olfactory tubercle that receives olfactory bulb input in mammals is striatal in derivation, neurochemistry and cytology, while a deeper lying portion is pallidal. This deeper lying pallidal part of the olfactory tubercle is cytoarchitectonically continuous with the ventral pallidum (see below). The striatal part of TuO contains medium-sized spiny neurons, as typical of striatal subpallium, and the medium-sized neurons project to the deeper lying pallidal TuO neurons and to the ventral pallidum (Heimer et al., 1976; Alheid and Heimer, 1988). The small-celled islets of Calleja interposed between the pallidal and striatal parts of the olfactory tubercle (Puelles et al., 2007) are derived from *Lmo4*-expressing neurons of the dorsalmost part of the LGE (Abellán and Medina, 2009). A ventral subpallial region receiving olfactory bulb input also is present in birds (Reiner and Karten, 1985), although it does not form a distinct ventral telencephalic bulge (Fig. 8A, 8B). The Nomenclature Forum recognized this as the olfactory tubercle in birds, noted its hodological and neurochemical similarities to mammalian olfactory tubercle, and described it as striatal in nature (Reiner et al., 2004a).

Recent developmental studies suggest, however, that the TuO in birds has both striatal and pallidal domains (Puelles et al., 2000, 2007; Abellán and Medina, 2009). Based on the expression of *Pax6* and *Lmo4*, but the absence of *Nkx2.1*, *Lhx6*, *Lhx7/8*, and *Shh*, the rostral and dorsolateral parts of the olfactory tubercle appear to be striatal derivatives, arising from the avian homologues of mammalian LGE1 and LGE3/LGE4, respectively. The transcription factor *cLmo4* further identifies cell aggregates in the striatal part of the avian TuO that resemble the islands of Calleja, which derive from the homologue of mammalian LGE1 (Puelles et al., 2007; Abellán and Medina, 2009). By contrast, the caudal and ventrolateral TuO in birds express pallidal markers reflecting an origin from the pallidal domain. The striatal nature of rostral and dorsolateral TuO is consistent with its neurochemistry, since it possesses numerous medium-sized neurons containing the striatal spiny projection neuron neuropeptide markers enkephalin and substance P (Reiner et al., 1983, 1984; Molnar et al., 1994; den Boer-Visser and Dubbeldam, 2002; Abellán and Medina, 2009). The striatal TuO has also been shown to contain presumptive interneurons possessing NADPH-diaphorase and nitric oxide synthase (NOS), as true in mammals as well (Vincent et al., 1983; Brünig, 1993; Brünig et al., 1994; Panzica et al., 1994). The striatal TuO additionally is rich in calcitonin gene-related peptide (CGRP)-containing fibers in budgerigar and quail (Lanuza et al., 2000; Roberts et al., 2002). Mammalian TuO also possesses CGRP+ fibers at rostral levels (Kawai et al., 1985). Additionally, the striatal TuO has been reported to be rich in thyroid hormone releasing hormone-containing fibers in ducks (Jozsa et al., 1988). The pallidal nature of caudal and ventrolateral TuO in birds is

consistent with the many GABAergic, substance-P containing, and enkephalinergic fibers and terminals it contains (Veenman and Reiner, 1994), and the presence of many neurons containing the pallidal neurotensin-related hexapeptide LANT6 (Reiner and Carraway, 1987). A striato-pallidal connectivity of avian TuO is suggested by the GABAergic, substance-P containing, and enkephalinergic fibers and terminals in pallidal TuO. In addition, striato-pallidal connectivity of avian TuO has been indicated in pigeon by a projection of striatal TuO to the ventral pallidum (Medina and Reiner, 1997). The TuO in birds has been shown to have widespread extratelencephalic projections to hypothalamus and midbrain dopaminergic neurons (Medina and Reiner, 1997), as also true in mammals. The relative contribution of striatal and pallidal TuO neurons to downstream projection areas is uncertain.

Consistent with its striatal nature, the rostral and dorsolateral TuO receives a dopaminergic input from the ventral tegmental area and substantia nigra of the midbrain (Fig. 6A-C; Kitt and Brauth, 1986b; Moons et al., 1994; Panzica et al., 1994, 1996), and contains numerous receptors and second messengers associated with this input, including D1A, D1B and D2 dopamine receptors, and DARPP-32 (Dietl and Palacios, 1988; Ball et al., 1995; Durstewitz et al., 1999; Sun and Reiner, 2000). In mammals, the piriform cortex and hippocampal formation are sources of pallial input to the TuO (Heimer and Wilson, 1975). Similarly, in pigeons the piriform cortex has been shown to project to the TuO (Bingman et al., 1994). The dorsomedial avian hippocampus has been shown to project indirectly to the avian TuO, projecting to the medial and lateral septum, with medial (striatal) septum having reciprocal connections with the TuO (Atoji and Wild, 2004). Other demonstrated sources of input to striatal TuO in birds include the lateral bed nucleus of the stria terminalis, the lateral hypothalamic area, the parabrachial region, the nucleus of the solitary tract, and the dorsal motor nucleus of the vagus (Berk and Hawkin, 1985; Wild et al., 1990; Arends et al., 1988; Atoji et al., 2006), structures associated with the autonomic nervous system. These various inputs to striatal TuO resemble those reported in mammals. Finally, avian TuO also contains numerous immigrant pallial/cortical derived glutamatergic neurons, as also true in mammals (Striedter et al., 1998; Puellas et al., 2000; Abellán and Medina, 2009; Abellán et al., 2009). Their functional significance is unknown.

3.2.2. Nucleus accumbens core and shell—The ventral striatum of mammals contains a prominent striatal structure called the nucleus accumbens. This structure is a major target of the mesolimbic dopaminergic system and an important part of the brain reward and motivation circuit. The nucleus accumbens of rats comprises a central core (AcC) surrounded on its medial, ventral and lateral sides by a shell (AcS; Herkenham et al., 1984; Záborszky et al., 1985). The core and shell were initially identified and distinguished by the relative enrichment of the core in acetylcholinesterase and the enrichment of the shell in argyrophilic fibers, respectively (Záborszky et al., 1985). Subsequently, immunolabeling showed differential labeling for substance P (Zahm, 1989) and calbindin 28kD (Voorn et al., 1989; Martin et al., 1991; Zahm and Heimer, 1993; Heimer et al., 1997) in rodents, with the core poor in substance P-containing fibers and rich in calbindinergic neuropil, and the shell moderate in substance P-containing fibers and calbindinergic neuropil. Other markers for the two sub-territories include calretininergic and neurotensinergic perikarya, which are relatively enriched in accumbens shell, and enkephalin and the GABA_A receptor, which are enriched in neurons of accumbens core (Zahm, 1999). The accumbens in mammals has also been shown to have a third sub-territory, a rostral pole (Zahm and Brog, 1992; Zahm and Heimer, 1993; Zahm, 2000).

The Nomenclature Forum suggested that the homologue of mammalian nucleus accumbens resides in the ventromedial striatum of birds (i.e. ventromedial MSt). Markers to confirm this and better define the relative locations of the avian accumbens core and shell, however,

were not available at that time. More recently, developmental (Abellán and Medina, 2009) and histochemical/hodological studies (Roberts et al., 2002; Bálint and Csillag, 2007; Husband and Shimizu, 2011; Bálint et al., 2011) have helped confirm the location of the avian nucleus accumbens, and clarify the components that appear homologous to the mammalian accumbens shell and core (Fig. 9). Specifically, the accumbens in chickens can be identified as a rostral ventromedial striatal territory that is derived from the ventrobasal striatal progenitor zone (LGE4 in mammals), and the its core subdivision can specifically be recognized as a region within accumbens at the base of the lateral ventricle that is very rich in neurons expressing genes for *SP*, *ENK*, and *NPY*, but moderate in *cLmo4* (Abellán and Medina, 2009). By contrast, the accumbens shell can be identified ventral and lateral to the core by its enrichment in *cLmo4*. This shell region has a caudal extension located medial to the intrapeduncular nucleus, within what has been regarded as ventral MSt. Thus, this caudal extension appears to be part of accumbens shell in birds (Fig. 3).

There is good agreement among recent neurochemical and hodological studies regarding the overall boundaries of the entire nucleus accumbens in birds (Roberts et al., 2002; Bálint and Csillag, 2007; Abellán and Medina, 2009; Husband and Shimizu, 2011; Bálint et al., 2011) and that a third accumbens sub-territory, a rostral pole, occurs in birds (Bálint and Csillag, 2007; Husband and Shimizu, 2011; Bálint et al., 2011) that may be comparable to that in mammals (Zahm and Heimer, 1993). Projections into the avian nucleus accumbens resemble those in mammals, and to some extent define its proposed subdivisions. For example, the nucleus tractus solitarius projects prominently to accumbens shell but not core in mammals. Bálint and Csillag (2007) showed by anterograde labeling in conjunction with immunolabeling that the nucleus tractus solitarius (NTS) also projects to accumbens in birds, and based on the differential projection within nucleus accumbens were able to distinguish an accumbens core-like region (poor in NTS input) and an accumbens shell-like region (rich in NTS input). Nucleus accumbens also receives dopaminergic input from the ventral tegmental area (Kitt and Brauth, 1981; Mezey and Csillag, 2002), and at least one study in budgerigars (Roberts et al., 2002) has suggested that the accumbens shell is especially high in tyrosine hydroxylase-containing (i.e. dopaminergic) fibers. Finally, a dense noradrenergic input from the A6 neurons of locus coeruleus to nucleus accumbens has been reported (Fig. 6F, 6G), ending more heavily in accumbens shell (Kitt and Brauth, 1986a; von Bartheld and Bothwell, 1992; Bailhache and Balthazart, 1993; Reiner et al., 1994; Moons et al., 1995; Mello et al., 1998). By contrast, somatic striatum receives only modest noradrenergic innervation (Bailhache and Balthazart, 1993; Reiner et al., 1994; Moons et al., 1995).

Bálint et al. (2011) recently showed projections from the chick AcS are similar to those reported in mammals, including extensive projections to the lateral preoptic area, substantia nigra pars compacta, ventral tegmental area, A8 dopaminergic cell group, and moderate projections to the periaqueductal gray, parabrachial complex and nucleus raphe (Groenewegen and Russchen, 1984; Zahm and Heimer, 1993; Usuda et al., 1998). Although projections from the avian AcC have been shown to be more extensive than reported for mammals, particularly in the caudal brainstem, significant projection areas comparable to those in mammals have been noted, including the substantia nigra pars compacta, the A8 dopaminergic cell group, periaqueductal gray and the ventral tegmental area (Groenewegen and Russchen, 1984; Zahm and Heimer, 1993; Usuda et al., 1998).

As pointed out in a recent publication, however, identification of subdivisions of avian nucleus accumbens as homologous to particular accumbens subdivisions in mammals is not unambiguous and suggests caution needs to be applied (Husband and Shimizu, 2011). They note that studies in budgerigars (Roberts et al., 2002), chickens (Bálint and Csillag, 2007) and pigeons (Husband and Shimizu, 2011) show that the two regions that some have

identified as avian accumbens core and shell do not match accumbens core and shell in rats (Tan et al., 1999; Bubser et al., 2000) or primates (Brauer et al., 2000) particularly in the localization of the calcium-binding protein calbindin. Husband and Shimizu (2011) have, thus, used the designations ventral (vAc) and dorsal (dAc) to subdivide the avian accumbens, with their vAc and dAc being topographically comparable to the accumbens shell (AcS) and accumbens core (AcC), respectively, of others (Fig. 9). On the other hand, the above noted molecular developmental, neurochemical, and hodological data and recent immunohistochemical and tract-tracing studies, support the notion that avian AcS and AcC resemble their similarly named mammalian counterparts in many regards. While further studies are needed to evaluate the proposed boundaries and homologies of the avian accumbens subdivisions with respective mammalian subdivisions, it may be that the counterparts will not resemble one another by all neurochemical and hodological criteria.

The nucleus accumbens in its entirety also receives input from central components of the autonomic nervous system such as the lateral hypothalamus (Berk and Hawkin, 1985), lateral part of the bed nucleus of the stria terminalis (Atoji et al. 2006), parabrachial nucleus (Wild et al., 1990), nucleus tractus solitarius (Arends et al., 1988; Bálint and Csillag, 2007) and dorsal motor nucleus of the vagus (Arends et al., 1988).

The avian accumbens also receives input from diverse telencephalic and midbrain regions regarded as limbic structures, including the hippocampus (Veenman et al., 1995; Székely and Krebs, 1996; Atoji et al., 2002; Atoji and Wild, 2004), piriform cortex (Veenman et al., 1995), posterior pallial amygdala (Atoji et al., 2006), and ventral tegmental area (Kitt and Brauth, 1981; Mezey and Csillag, 2002; Moons et al., 1994). Pallial input to avian accumbens is likely to be glutamatergic (Veenman and Reiner, 1996; Csillag et al., 1997; Reiner et al., 2001; Ding et al., 2003; Ding and Perkel, 2004; Farries et al., 2005a). Consistent with its input from limbic regions of brain, the nucleus accumbens core and shell in birds are enriched in the limbic system protein LAMP (Yamamoto and Reiner, 2005).

A 'limbic loop' involving medial regions of pallium (i.e. mesopallium and nidopallium), subpallium and thalamus has been described in birds (Husband and Shimizu, 2011). The circuit consists of a projection from a column of neurons in the medial pallium to the nucleus accumbens, from accumbens to ventral pallidum (VP), from VP to the anterior dorsomedial thalamic nucleus (DMA), and finally a return projection from DMA to the medial pallium (Fig. 13 in Husband and Shimizu, 2011). The restricted part of the medial pallium involved in this 'limbic loop' has been proposed to be equivalent to the mammalian prefrontal cortex (Husband and Shimizu, 2011). This medial pallial sector apparently corresponds to the medial pallial region previously shown to be involved in imprinting in chicks (Maier and Scheich, 1987; Gruss and Braun, 1996; Horn, 1998; Metzger et al., 1998; Bolhuis, 1999; Thode et al., 2005). Thus, the pallial part of this loop, as well as the loop itself, is associated with learning and memory. Nonetheless there are behavioral, anatomical and electrophysiological data showing that another brain region, the caudolateral nidopallium, may be the equivalent of the avian prefrontal cortex (Waldmann and Güntürkün, 1993; Güntürkün, 2005).

3.2.3. Ventral pallidum—The ventral pallidum (VP) of mammals is regarded as a medioventral extension of globus pallidus and the viscerolimbic component of the striatopallidal system. It occupies a relatively extensive area in the basal forebrain of rats and primates, extending ventrally and rostrally from the globus pallidus into the olfactory tubercle (Alheid and Heimer, 1988). The VP possesses a number of pallidal traits by which it can be identified, including enrichment in iron (Switzer et al., 1982), large aspiny glutamate decarboxylase (GAD)-containing neurons, a dense mat of terminals containing GAD, and dense mats of terminals containing enkephalin and SP (Beach and McGeer, 1984;

Haber and Nauta, 1983; Haber and Watson, 1985; Switzer et al., 1982). The terminals containing GAD, enkephalin and SP possess the distinctive pallidal woolly fiber morphology of striatopallidal terminals. The VP field in mammals contains two major neurochemically distinct output neuron types, GABAergic neurons with descending projections and cholinergic neurons with ascending projections within the telencephalon (Bengtson and Osborne, 1999). The GABAergic VP neurons have their origin in the pallidal progenitor zone of the developing subpallium, as do globus pallidus neurons (Xu et al., 2008), while cholinergic neurons have a preoptic origin (García-López et al., 2008; Nóbrega-Pereira et al., 2010). The globus pallidus and ventral pallidum in mammals, however, originate from different parts of the MGE, with the globus pallidus derived from MGE2/MGE3 and the ventral pallidum arising from MGE4 (precommissural part of VP) and MG3 (commissural part of VP). This is similar in birds, although the commissural part of VP (derived from MGE3) appears to be missing (Abellán and Medina, 2009).

The VP of birds (Fig. 8C, 8D) was originally termed the ventral paleostriatum, and the term was used for a large region that contained both striatal and pallidal neuron types (Kitt and Brauth, 1986a). The ventral paleostriatum was identified by the abbreviation PVT (paleostriatum ventrale) in a chick brain atlas (Kuenzel and Masson, 1988). Others used the term ventral pallidum instead, and the Nomenclature Forum officially renamed PVT as the ventral pallidum (VP). In doing so, the region defined as the ventral pallidum was narrowed to a territory exclusively having pallidal neurochemistry (Reiner et al., 2004a). Developmental studies in chicks have been instrumental in providing support for the identification of this region as the ventral pallidum, and the homologue of part of the mammalian structure of the same name. Specifically, the VP displays strong expression for *Nkx2.1* (Puelles et al., 2000), *Lhx6* and *Lhx7/8* (Abellán and Medina, 2009), which within subpallium are uniquely expressed by pallidal neurons. Like the avian globus pallidus, the avian VP is rich in fibers and terminals containing substance P, dynorphin, enkephalin and/or GABA that represent the terminals of striatal neurons (Reiner et al., 1983, 1984; Anderson and Reiner, 1990a; Veenman and Reiner, 1994; Veenman et al., 1995). Neurons in the avian VP also possess a similar glutamate receptor expression profile to that of neurons in the avian globus pallidus (Wada et al., 2001), as well as GABA receptors (Veenman et al., 1994). The GABAergic projection neurons of VP in birds co-contain parvalbumin and the neuropeptide LANT6 (Reiner and Carraway, 1987; Reiner and Anderson, 1993; Veenman and Reiner, 1994). As in mammals, the large GABAergic neurons of globus pallidus and ventral pallidum arise from separate parts of the pallidal domain, with the globus pallidus arising from the region homologous to mammalian MGE2/MGE3, and the ventral pallidum arising from the homologue of mammalian MGE4 (Abellán and Medina, 2009). The VP in birds only corresponds to the precommissural VP of mammals (Abellán and Medina, 2009) and contains a prominent group of cholinergic neurons, as it does in mammals (Medina and Reiner, 1994). The cholinergic neurons of avian VP (and those in globus pallidus and INP) derive from the POC subpallial subdivision (Abellán and Medina, 2009), as also true of the cholinergic neurons of mammalian VP (García-López et al., 2008). They constitute a separate system that will be discussed further in the section 3.4 (Basal telencephalic cholinergic and non-cholinergic corticopetal system).

As true of globus pallidus, the avian ventral pallidum receives striatal input (in this case viscerolimbic) and it gives rise to major descending output to targets very similar to those of mammalian VP (Medina and Reiner, 1997). Viscerolimbic striatal structures projecting to VP include the olfactory tubercle and nucleus accumbens (Medina and Reiner, 1997). The VP in birds also has been reported to receive pallial inputs from the temporo-parieto-occipital area and diencephalic inputs from the lateral hypothalamic area (Berk and Hawkin, 1985; Veenman et al., 1995; Medina and Reiner, 1997; Atoji and Wild, 2005). The avian VP, in turn, projects to a number of diencephalic sites including, the subthalamic nucleus,

paraventricular nucleus, dorsomedial thalamus, habenular nuclei, thalamic reticular nucleus, and lateral hypothalamic area (Kitt and Brauth, 1981; Berk and Hawkin, 1985; Veenman et al., 1995; Medina and Reiner, 1997). Several midbrain regions receive ventral pallidal input as well, including the ventral tegmental area, substantia nigra pars compacta, pedunculopontine tegmental nucleus, central gray, and raphe (Kitt and Brauth, 1981; Medina and Reiner, 1997).

3.2.4. Functional considerations for ventral basal ganglia—The dopaminergic input to viscerolimbic striatum in mammals, especially nucleus accumbens, is widely thought to mediate the rewarding effects of natural stimuli such as food, water and sex (Salamone et al., 1997). The many autonomic circuit inputs and outputs of the viscerolimbic basal ganglia are consistent with such a function. Nucleus accumbens, in particular, plays a major role in the initiation of reward-motivated behavior (Roberts et al., 1980). Because reward provides the motivation for learning, the nucleus accumbens has also been regarded as critical for reward- and incentive-based learning (Salamone et al., 1997). Moreover, drugs of abuse, such as cocaine, amphetamine, morphine and methamphetamine, produce their pleasurable sensations by release of dopamine and increased neuronal activation in nucleus accumbens, especially the accumbens shell (Pontieri, et al., 1994, 1995; Pierce and Kalivas, 1995). The dopaminergic input from the posteromedial ventral tegmental area to the medial olfactory tubercle and ventromedial accumbens shell appears particularly involved in reward, based on behavioral findings addressing the effects of intra-accumbens cocaine or amphetamine administration (Ikemoto, 2007). The role of the ventral basal ganglia, however, is more complex than a simple role in facilitating pursuit of reward (Salamone et al., 1997). Nucleus accumbens also plays a role in withholding responses so as to maximize reward, and lesions of accumbens core impair this ability and cause impulsive behavior (Cardinal et al., 2001). The nucleus accumbens, especially the shell, is also responsive to stress (Kalivas and Duffy, 1995; King et al., 1997). Although neural circuit models (e.g. the direct-indirect pathway model) have been developed to explain how the somatic basal ganglia mediates motor control at the neuronal level, how the striatopallidal circuitry of the viscerolimbic basal ganglia mediates its role in reward-motivated behavior, choice and learning is yet to be elucidated at the neuronal circuit level.

The viscerolimbic basal ganglia in birds appears to be involved in reward, and reward-motivated learning. For example, Delius et al. (1976) have shown that electrical stimulation of the accumbens region has rewarding properties in birds, and medial striatal neurons in chick show reward-related responses (Yanagihara et al., 2001). Similarly, chicks with electrolytic lesions of the ventromedial striatum, including the accumbens region, are impaired in their ability to associate color cues with reward (Izawa et al., 2003; Aoki et al., 2006). Such lesions also cause impulsivity in chicks. Additionally, the accumbens region is associated with passive avoidance learning in chicks (Stewart et al., 1996). One difficulty in relating the results of these studies to specific parts of viscerolimbic basal ganglia is that the stimulating, recording or lesion sites in the above studies spanned the somatic and viscerolimbic medial striatum. Thus, the relative contribution of limbic striatum and medial MSt to these functions is not certain. As true of medial caudate in mammals, medial MSt appears to be viscerolimbic in connectivity, function and neurochemistry (Yamamoto and Reiner, 2005). As discussed in the previous section on the nucleus accumbens, a 'limbic loop' circuit comprising prefrontal cortex-like medial pallial neurons, medial MSt/nucleus accumbens, ventral pallidum and a mediodorsal-like thalamic nucleus that may be involved in learning and memory has been demonstrated in pigeons (Husband and Shimizu, 2011).

3.3. Subpallial Amygdaloid Nuclei: The extended amygdala - central and medial amygdala, and bed nuclei of the stria terminalis

The amygdala in mammals has been recognized as consisting of two major subpallial cell groups, the central and medial amygdaloid nuclei (Swanson and Petrovich, 1998). Heimer and coworkers recognized, however, that these two amygdaloid nuclei were each confluent with neuronal corridors that extended from them, through the territory below the globus pallidus (i.e. sublenticular) to the bed nuclei of the stria terminalis or BST (Alheid and Heimer, 1988; Alheid et al., 1995). The distinctive feature of these neuronal corridors is that they possess similar neurochemical features and connections as the amygdaloid nuclei, with which they are confluent. The central and medial amygdaloid nuclei, directly or by way of the BST, are the major output nuclei of the amygdala (Paré et al., 2004; Swanson, 2000). The central extended amygdala, which we will use as a term to include the central amygdaloid nucleus (CeA) and its corridor to the lateral BST (BSTL), is involved in fear/anxiety and ingestive functions. The medial extended amygdala, which we will use as a term to include the medial amygdaloid nucleus (MeA) and its corridor to the medial BST (BSTM), is involved in reproduction and defense (Alheid and Heimer, 1988; Alheid et al., 1995). We will refer to the central extended amygdala together with the BSTL as the central extended amygdala-BSTL complex (or simply central extended amygdala complex), and the medial extended amygdala together with the BSTM as the medial extended amygdala-BSTM complex (or simply medial extended amygdala complex).

Developmental, neurochemical, hodological and behavioral evidence suggests that territories corresponding to the central and medial extended amygdala-BST complexes of mammals are present in the avian subpallium as well (Aste et al., 1998a; Jurkevich et al., 1997, 1999; Roberts et al., 2002; reviews in Reiner et al., 2004a; Yamamoto et al., 2005; Abellán and Medina, 2009; Xie et al., 2010). Moreover, both also appear to be present in amphibian and reptilian subpallia (Martínez-García et al., 2008; Morona and González, 2008), suggesting that amygdaloid regions were present in the common tetrapod ancestor (Martínez-García et al., 2007). Evidence for central and medial extended amygdala-BST complexes in birds is presented in the following two sections below, with constituents of the central extended amygdala and the BSTL, and constituents of the medial extended amygdala and BSTM presented under separate subheadings, respectively.

3.3.1. Central extended amygdala and BSTL—In mammals, neurons of the central extended amygdala are GABAergic and have descending projections to the lateral hypothalamus, central gray, the parabrachial nucleus and the nucleus of the solitary tract, which are autonomic centers that regulate behaviors related to ingestion, fear, and stress/anxiety (Alheid and Heimer, 1988; Alheid et al., 1995; Swanson, 2000; de Olmos et al., 2004). GABAergic neurons of the central extended amygdala projecting to these targets are typically enriched in any of several neuropeptides, including corticotropin-releasing hormone (CRH), neurotensin, enkephalin or somatostatin (Moga and Gray, 1985; Paré and Smith, 1994; Alheid et al., 1995; Swanson and Petrovich, 1998; Poulin and Timofeeva, 2008; Panguluri et al., 2009). Consistent with its role in autonomic functions, the central extended amygdala receives input from the posterior intralaminar thalamus, the parabrachial nucleus, the nucleus of the solitary tract, the insular cortex, and the pallial amygdala. It is distinctively rich in calcitonin gene related peptide (CGRP) terminals, representing the parabrachial and posterior intralaminar thalamic input (D'Hanis et al., 2007). The mammalian central amygdala itself is primarily a striatal derivative (Puelles et al., 2000; Tole et al., 2005; García-López et al., 2008; Waclaw et al., 2010; Bupesh et al., 2011b), and recent fate mapping data indicates that it contains *Pax6*-expressing cells derived from dorsal LGE and *Islet1*-expressing cells derived from ventral LGE (Waclaw et al., 2010; Bupesh et al., 2011b). However, recent evidence also indicates that the medial part of the central

amygdala), and possibly the sublenticular corridor of the central extended amygdala contain a mixture of neurons of striatal and pallidal origin (Bupesh et al., 2011b). Pallidal neurons invading the central amygdala and the corridor contain somatostatin (García-López et al., 2008; Bupesh et al., 2011b). The BSTL is primarily a pallidal derivative, but some striatal cells expressing *Pax6*, *Islet1* or *Lmo4* invade the BSTL (García-López et al., 2008; Bupesh et al., 2011b; reviewed in Medina and Abellán, 2009). The central extended amygdaloid complex in birds includes at least two components: the so-called subpallial amygdaloid area (SpA; Wild et al., 1990; Roberts et al., 2002; Yamamoto et al., 2005; Reiner et al., 2004a), and the BSTL (Aste et al., 1998b; Jurkevich et al., 1999; Roberts et al., 2002; Reiner et al., 2004a; Abellán and Medina, 2008, 2009). Both of these were recognized by the Nomenclature Forum, though not specifically in relationship to an entity termed the extended central amygdala. The Nomenclature Forum also did not recognize a central amygdaloid nucleus in birds. The current understanding of the subdivisions of avian central extended amygdala and the BSTL are discussed in the following sections.

3.3.1.1. The subpallial amygdaloid area (SpA) and the central amygdala: Abellán and Medina (2009) recognized that the central extended amygdala in chick includes a territory below the globus pallidus identified by the Nomenclature Forum as the SpA and a more lateral territory below the caudolateral striatum that the Forum did not recognize. Abellán and Medina termed these two regions the medial and lateral parts of the avian extended central amygdala (Fig. 10). They noted that the medial portion of the central extended amygdala, below the globus pallidus, may correspond to the sublenticular corridor of the central extended amygdala of mammals (Reiner et al., 2004a), and include striatal and pallidal cells (Abellán and Medina, 2009). They proposed that the lateral portion of the central extended amygdala may correspond to at least part of the mammalian central amygdala, by the criteria that it lies directly below the caudolateral striatum and is rich in striatal, *Pax6*-expressing (Fig. 10E, 10F) neurons (Abellán and Medina, 2009). They additionally recognized a caudolateral ventral part of LSt (which they termed CLSt) as part of the central extended amygdala as well, and suggested that this also was part of the avian homologue of mammalian central amygdala (Fig. 10E, 10F). Considerable neurochemical and hodological evidence shows a strong similarity between the mammalian sublenticular extended amygdala and the medial part of the avian central extended amygdala of Abellán and Medina (2009), or subpallial amygdala (SpA) as the Nomenclature Forum termed it. As true of mammalian sublenticular central amygdala, neurons of the avian central extended amygdala are GABAergic (Yamamoto et al., 2005; Abellán and Medina, 2009). Moreover, many of these neurons are striatal in neurochemistry, containing the characteristic striatal amygdaloid neuropeptides enkephalin, neurotensin and/or corticotropin releasing hormone (Molnar et al., 1994; Atoji et al., 1996; Roberts et al., 2002; Reiner et al., 2004a; Richard et al., 2004; Yamamoto et al., 2005). The inputs to the medial and lateral portions of the extended central amygdala of birds also resemble those of the mammalian central extended amygdala. In both, this region receives viscerolimbic input from the parabrachial nucleus (Wild et al., 1990), the nucleus of the solitary tract, and the pallial amygdala (Veenman et al., 1995; Atoji et al., 2006). Moreover, the avian central extended amygdala, as well as the CLSt, is enriched in CGRP terminals, (Lanuza et al., 2000; Roberts et al., 2002; Reiner et al., 2004a; Yamamoto et al., 2005). Note, however, that neither the lateral central extended amygdala nor the CLSt in birds is nearly as rich in CGRP+ fibers as their suggested mammalian homologue, the central amygdala. As in mammals, the GABAergic/neuropeptidergic neurons of the central extended amygdala in birds give rise to its outputs, notably to the BSTL and its sub-nuclei (Fig. 10) and the nucleus of the solitary tract/dorsal vagal nucleus (Berk, 1987; Richard et al., 2004; Yamamoto et al., 2005; Atoji et al., 2006; Abellán and Medina, 2009), and may account for some fibers in those regions containing enkephalin, neurotensin and/or corticotropin releasing hormone. In summary, considerable

data support the homology of the medial part of the avian central extended amygdala (i.e. the subpallial amygdala) to the mammalian sublenticular central extended amygdala, including the presence of a neurochemically and hodologically similar region in reptiles (Martínez-García et al., 2008). A homology of the lateral part of the avian central extended amygdala (CLSt) to the mammalian central amygdala also is supported by considerable data, although differences between these two structures suggest further study of this issue is needed.

3.3.1.2. Striatal capsule: The intercalated cell masses of the mammalian amygdala are subpallial neurons interposed between the central amygdala and the basal complex of the pallial amygdala and the ventral endopiriform nucleus. The amygdaloid intercalated cell masses appear to represent an integral part of the central extended amygdala in mammals, and develop from the dorsal part of the striatal subdivision of the developing subpallium, that is the LGE (García-López et al., 2008; Medina and Abellán, 2009; Kaoru et al., 2010; Waclaw et al., 2010). The amygdaloid intercalated cell masses have a GABAergic projection to the central amygdala and the cholinergic corticopetal cell groups of the basal telencephalon (including the basal magnocellular complex), and they are involved in extinction of fear memories (Paré et al., 2004). A distinctive set of subpallial neurons interposed between the nidopallium and the lateral striatum has recently been termed the avian striatal capsule (Puelles et al., 2007), and been proposed to be comparable to the intercalated cell masses of the mammalian amygdala (Abellán and Medina, 2009). Data supporting the proposal include similar developmental origin from the dorsal part of the avian LGE homologue, some molecular traits, and their position at the border between the subpallium and what Abellán and Medina (2009) identify as ventral pallium and thus regard as comparable to mammalian ventral pallium, including part of the basal amygdalar complex and the ventral endopiriform nucleus (Fig. 3C-3F). The connections of the avian striatal capsule are unknown and therefore no hodological support exists at this time. Moreover, the avian striatal capsule is not juxtapositioned to the proposed avian central amygdala (subpallial amygdalar area), unlike the intercalated cell masses of the mammalian amygdala.

3.3.1.3. Lateral bed nucleus of the stria terminalis (BSTL): As noted by the Nomenclature Forum, the BSTL in birds and mammals is located at the base of the lateral ventricle near the level of the septopallio-mesencephalic tract and anterior commissure (Fig. 8C, 8D). It is characterized by a relative abundance of neurotensinergic (Reiner and Carraway, 1987; Atoji et al., 1996; Reiner et al., 2004a), enkephalinergic (Molnar et al., 1994), and corticotropin-releasing hormone (CRH) neurons (Panzica et al., 1986; Richard et al., 2004), and many calcitonin gene related peptide (CGRP; Lanuza et al., 2000) and noradrenergic fibers (Reiner et al., 1994). In contrast a paucity of cholinergic cells/fibers (Medina and Reiner, 1994), sparse dopaminergic terminals (Bailhache and Balthazart, 1993; Reiner et al., 1994; Reiner et al., 2004a), and few substance P-containing neurons and fibers (Reiner et al., 1983; Reiner et al., 2004a) have been reported. Like the mammalian BSTL (van der Kooy et al., 1984; Gray and Magnuson, 1987; Moga et al., 1989), the avian BSTL is reciprocally connected with the hypothalamus, parabrachial nucleus, the nucleus of the solitary tract, and the dorsal motor nucleus of the vagus (Berk, 1987; Arends et al., 1988; Wild et al., 1990; Atoji et al., 2006; Balint et al., 2011). The BSTL in mammals and birds, however, appears to be a complex territory with striatal and pallidal cell subpopulations. In brief, the dorsal and medial parts of the BSTL in birds and mammals are rich in cells that develop from a comparable pallidal embryonic subdomain (García-López et al., 2008; Xu et al., 2008; Abellán and Medina, 2009), and in birds has been termed the dorsal BSTL by Abellán and Medina (2009). Lateral to this, in a region termed by them the dorsolateral BSTL, reside abundant neurons expressing *Pax6/Lmo4* that appear to derive from the striatal progenitor zone (Fig. 10E, 10F; García-López et al., 2008; Xu et al., 2008; Abellán and

Medina, 2008, 2009). The BSTL in mammals also contains a minor subpopulation of Pax6-expressing neurons derived from dorsal LGE, and an abundant subpopulation of Islet1-expressing neurons derived from ventral LGE (Bupesh et al., 2011b). The dorsolateral BSTL of birds is the subdivision rich in neurons possessing such striatal markers as corticotropin releasing hormone, enkephalin and neurotensin. In adult birds, however, even the dorsomedial BSTL contains some enkephalinergic and neurotensinergic neurons, as also true in mammals (Reiner et al., 2004a; Molnar et al., 1994). The dorsolateral BSTL in birds is confluent with the subpallial amygdala, or as Abellán and Medina termed it, the medial part of the central extended amygdala. Note that since the striatal central extended amygdala complex projects to the pallidal dorsal BSTL, this system shows a striato-pallidal organization in birds, as also noted in mammals (Alheid and Heimer, 1988; Swanson, 2000). Given that reptiles too possess a BSTL possessing these same various features, it seems likely that the BSTL is homologous across amniotes (Martínez-García et al., 2008).

3.3.2. Functional considerations for the central extended amygdala complex—

The central extended amygdala-BSTL in mammals is involved in food intake and fear/stress behaviors via its connections with the central parts of the autonomic nervous system (van der Kooy et al., 1984; Luiten et al., 1987; Paré et al., 2004). The connections of the avian central extended amygdala and BSTL complex with the lateral hypothalamic area, parabrachial nucleus, nucleus of the solitary tract, and dorsal motor nucleus of the vagus are consistent with the view that the homologous circuit in birds is involved with the same basic ingestive and visceral functions (Kuenzel and Blähser, 1993; Kuenzel, 1994; 2000). In mammals, the central extended amygdala-BSTL complex projections involving neurons containing corticotropin-releasing hormone (CRH) are particularly important for expression of stress and anxiety, and for regulation of appetite (Heimer and Alheid, 1991; Clark and Kaiyala, 2003; Krogh et al., 2008; Gallagher et al., 2008). This peptide is also enriched in the projections of the central extended amygdala complex in birds and reptiles, particularly in the BSTL projections (Richard et al., 2004; Martínez-García et al., 2008), and the CRH+ amygdaloid neurons may thus play a similar role in non-mammals as mammals (Meade and Denbow, 2003; Crespi and Denver, 2005; Tachibana et al., 2006).

3.3.3. Medial extended amygdala and BSTM—In mammals, the medial extended amygdala consists of the medial amygdala itself and a sublenticular neuronal corridor leading from it to the BSTM. This medial amygdaloid corridor lies inferior to the sublenticular central extended amygdala corridor. The medial amygdala receives main olfactory and vomeronasal input, is rich in neurons with receptors for gonadal steroids, and projects to medial preoptic and hypothalamic regions involved in reproduction and defense (Alheid et al., 1994, 1995; Swanson, 2000). Many of the projections of the medial amygdala and BSTM are GABAergic (Swanson and Petrovich, 1998; Swanson, 2000), but some are glutamatergic (Choi et al., 2005). The complexity of these subpallial cell groups is further evidenced by the multiple subdivisions described for the medial amygdala and BSTM (de Olmos et al., 1985; de Olmos and Heimer, 1999; Alheid et al., 1995; Dong et al., 2001; de Olmos et al., 2004). Recent molecular and fate mapping data in mouse aid understanding of the developmental basis of this complexity. The medial amygdaloid nuclear complex originates primarily from the caudoventral pallidal progenitor subdivision (MGEcv, also sometimes called the anterior entopeduncular area, or AEP) and the commissural preoptic area (POC) of the subpallium, as confirmed by the numerous *Nkx2.1*-lineage neurons in the mature medial amygdala (Xu et al., 2008) and by recent experimental fate mapping (Bupesh et al., 2011a). MGEcv-derived neurons in the medial amygdala can be distinguished from POC-derived neurons because the former express the transcription factor *Lhx6*, while the latter express *Shh* (García-López et al., 2008). The distribution of neurons expressing *Lhx6* and *Shh* indicates that MGEcv-derived and POC-derived cells in mammals are segregated in

the posterior medial amygdala, but intermingled in the anterior medial amygdala (García-López et al., 2008; Bupesh et al., 2011a). The preoptic origin of part of the medial amygdala has been confirmed by a fatemap of *Dbx1*-lineage cells, showing that most of the nitroergic neurons (co-containing GABA) of the medial amygdala originate in the preoptic subdivision (Hirata et al., 2009). In addition, the medial amygdala appears to include neurons that originate either in ventral pallium (expressing the transcription factor *Lhx9*; García-López et al., 2008; Bupesh et al., 2011a) or the supraopto-paraventricular domain (SPV) of the hypothalamus (expressing the transcription factors *Otp* and *Lhx5*; Bardet et al., 2008; Abellán et al., 2010; García-Moreno et al., 2010; Bupesh et al., 2011a). The ventral pallial and SPV-derived neurons of medial amygdala are presumably glutamatergic (García-López et al., 2008; Abellán et al., 2010), and possibly the source of the glutamatergic projections of the medial amygdala. The mammalian BSTM also includes cells derived from MGEcv, POC and extralencephalic sources (García-López et al., 2008), including the supraopto-paraventricular domain (Abellán et al., 2010; Bupesh et al., 2011a).

The Nomenclature Forum recognized the subpallial part of nucleus taeniae in birds as a medial amygdala homologue (Reiner et al., 2004a; Yamamoto et al., 2005). They also noted the evidence for a BSTM in birds (Aste et al., 1998a; Jurkevich et al., 1997, 1999; Roberts et al., 2002; Reiner et al., 2004a). In addition to arginine vasotocin, the BSTM likewise was shown to contain galanin (Klein et al., 2006). More recently, Abellán and Medina (2009) termed the subpallial part of nucleus taeniae the subpallial medial amygdala (MeAs; Fig. 11). They suggested that it formed a functional unit with the BSTM (Fig. 11B) shown as BSTM1 (dorsolateral) and 2 (ventromedial) in chicks (Jurkevich et al., 1999; Abellán and Medina, 2008, 2009), and possibly the ventral part of BSTL (BSTLv, Fig. 11A; Abellán and Medina, 2008, 2009). A glutamatergic population of neurons has been identified in the avian medial amygdala (Puelles et al., 2007; Bardet et al., 2008; Abellán and Medina, 2008, 2009; Abellán et al., 2009), which include neurons derived from the ventral pallium, and *Otp*-expressing neurons of supraopto paraventricular origin. Additionally, a sub-nucleus termed the amygdaloid taenial nucleus (ATn shown in Fig. 17 of Puelles et al., 2007) has been identified in chickens located dorsal and medial to the MeAs (Fig. 11 and last cross-sectional plate of Fig. 1) suggesting that the avian medial amygdala (MeAs) may comprise more than the traditional nucleus taeniae.

A medial amygdala and BSTM have also been described in reptiles and amphibians (Martínez-García et al., 2008; Morona and González, 2008), suggesting that a medial amygdala - BSTM corridor was present in the forebrain of the common tetrapod ancestor.

3.3.3.1 Subpallial medial amygdala: In chickens, the subpallial medial amygdala (called the subpallial amygdaloid nucleus of the taeniae by the Nomenclature Forum) includes intermingled neurons derived from pallidal/MGEcv and preoptic progenitor zone subdivisions (expressing *Lhx6* and *Shh*, respectively), resembling in this respect the anterior subnucleus of the medial amygdala of mammals (Abellán and Medina, 2009). Moreover, the subpallial medial amygdala of birds (Fig. 11) contains GABAergic neurons (Sun et al., 2005; Yamamoto et al., 2005; Abellán and Medina, 2009) and nitroergic neurons (Panzica et al., 1994; Balthazart et al., 2003), resembling the finding of GABAergic and nitroergic neurons in the mammalian medial amygdala (Tanaka et al., 1997; Swanson, 2000). In addition, the avian subpallial medial amygdala receives olfactory input from the main olfactory bulb (Reiner and Karten, 1985) and piriform cortex (Bingman et al., 1994; Veenman et al., 1995), and projects to the BST complex and medial preoptic region (Balthazart and Absil, 1997; Cheng et al., 1999). As true of the mammalian medial amygdala, the avian subpallial medial amygdala is reciprocally connected with the hippocampal formation (Atoji et al., 2002; Atoji and Wild, 2004). Importantly, the avian subpallial medial amygdala is enriched in sex-steroid concentrating neurons possessing

estrogen and androgen receptors and the enzyme aromatase (Martinez-Vargas et al. 1976; Balthazart et al., 1998; Foidart et al., 1999). Their abundance is more striking in males (Watson and Adkins-Regan, 1989), and reflects the role of the steroid receptors and the neurons that contain them in male sexual behavior (Panzica et al., 1996; Thompson et al., 1998; Absil et al., 2002). In summary, data in birds, reptiles and amphibians (Martínez-García et al., 2008; and Morona and González, 2008) strongly support the homology of avian subpallial medial amygdala and the medial amygdala of mammals, particularly its anterior subnucleus. A distinct sublenticular corridor from the avian medial amygdala to the BSTM has not, however, been clearly delineated.

3.3.3.2. Medial bed nucleus of the stria terminalis (BSTM): The BSTM of chicken also includes neurons of pallidal/MGEcv and preoptic origins, thus resembling the BSTM of mammals (Abellán and Medina, 2008, 2009). In quail, a single BSTM nucleus has been documented by neurochemical criteria (Aste et al., 1998a), while in chickens BSTM has been shown to consist of two subnuclei (Fig. 11B), as evidenced by immunocytochemistry and in situ hybridization histochemistry (Jurkevich et al., 1999). The two BSTM nuclei of chickens were termed the BSTMdl and BSTMvm by Jurkevich et al. (1999), and adopted as the BSTM1 and BSTM2, respectively, by the Nomenclature Forum (Reiner et al., 2004a). Similar to the mammalian BSTM, steroid-responsive neurons of the avian BSTM include cells containing aromatase (Balthazart et al., 1990; Roselli, 1991; Shinoda et al., 1994; Aste et al., 1998b; Xie et al., 2011), and cells containing vasotocin (Kiss et al., 1987; Viglietti-Panzica et al., 1992; De Vries et al., 1994; Aste et al., 1998b; Jurkevich et al., 1999; Xie et al., 2011). As also true of mammalian BSTM, the avian BSTM (and potentially the embryologically-related ventral part of BSTL) receives olfactory input from the piriform cortex (Bingman et al., 1994; Veenman et al., 1995), and possibly the subpallial medial amygdala (Balthazart and Absil, 1997), and projects to the medial preoptic nucleus and medial hypothalamus, which are involved in male mating behavior (Absil et al., 2001, 2002; Xie et al., 2010). In Japanese quail, AVT neurons of the BSTM are the projection neurons targetting the POM and hypothalamus (Absil et al., 2002) and some of their axons also reach the subpallial medial amygdala (Balthazart and Absil, 1997).

3.3.4. Functional considerations for subpallial medial amygdala and BSTM—In mammals, the medial extended amygdala - BSTM complex plays a key role in mating, sexual, defensive, and aggressive behaviors, for which olfactory information to the medial amygdala is extremely important (Swanson, 2000; Choi et al., 2005). In birds, the hodological and behavioral data indicate that the medial amygdala and BSTM play a similar role (Panzica et al., 1998; Thomson et al., 1998; Absil et al., 2002; Xie et al., 2010). Although birds are relatively microsmatic, electrophysiological responses in the avian olfactory bulb to odorants are comparable to those in mammals (McKeegan, 2002), and olfactory cues are used by birds in social and sexual interactions (Caro and Balthazart, 2010). The medial amygdala and BSTM, which receive olfactory information (Bingman et al., 1994; Veenman et al., 1995), are involved in olfactory-related behaviors (Balthazart and Schoffeniels, 1979). Numerous studies directly demonstrate the role of the avian subpallial medial amygdala and BSTM in reproductive behavior. For example BSTM1 and BSTM2 are significantly larger in males, are steroid-responsive, and play a role in male copulatory behavior (Del Abril et al., 1987; Kiss et al., 1987; Voorhuis et al., 1988; Viglietti-Panzica et al., 1992; Guillamón and Segovia, 1997; Aste et al., 1998b; Panzica et al., 1998; Jurkevich et al., 1999). The avian BSTM2 is involved specifically in male appetitive sexual behavior (Xie et al., 2010, 2011). Arginine vasotocin (AVT) is the non-mammalian homologue of vasopressin (Acher et al., 1993), and castration in quail eliminates AVT-expressing neurons and decreases the number of aromatase-expressing neurons in the BSTM and medial preoptic hypothalamus (Aste et al., 1998b; Panzica et al., 1999).

3.4. Basal telencephalic cholinergic and non-cholinergic corticopetal system

In mammals, the basal telencephalic corticopetal system consists of large cholinergic neurons dispersed over the pallidal-substantia innominata region, the medial septum-diagonal band nucleus, and the magnocellular preoptic nucleus (Gritti et al., 1993; 2003). These cells partly overlap the globus pallidus and ventral pallidum of the basal ganglia and the extended amygdala in the so-called substantia innominata, but they represent functionally distinct neurons that typically project to cortical regions. The cholinergic corticopetal projections are in contrast to the major descending GABAergic projections typical of the basal ganglia and BST-extended amygdala systems (Alheid et al., 1995; Gritti et al., 1997). Corticopetal cholinergic neurons play an important role in modulation of cortical activity, and in attentional and arousal processes (Záborszky et al., 1999) that affect learning and memory (Metherate et al., 1988, 1992; Cape and Jones, 2000; Cape et al., 2000). Similarly, the avian corticopetal system consists of scattered large cholinergic neurons that are dispersed over the pallidum-substantia innominata, and septal-diagonal band regions (Medina and Reiner, 1994; Medina et al., 1995). In birds, telencephalic structures containing cholinergic neurons (Reiner et al., 2004a) include the basal magnocellular nucleus (NBM, Fig. 11A, Fig. 12), nucleus of the diagonal band, horizontal limb (NDBh, Fig. 11A, Fig. 12A), nucleus of the diagonal band, vertical limb (NDBv, Fig. 12B) and commissural nucleus of the septum (CoS, Fig. 11A).

3.4.1 Nucleus basalis magnocellularis—Cholinergic cells of nucleus basalis magnocellularis (NBM) in birds take residence primarily in and about the lateral and medial forebrain bundle but also dispersed in the globus pallidus, ventral pallidum and intrapeduncular nucleus (Medina and Reiner, 1994; Reiner et al., 2004a). This field of cholinergic neurons thus overlaps GABAergic neurons in each region. The cholinergic neurons of the avian NBM (Fig. 11A, Fig. 12) are comparable to those in the mammalian nucleus basalis of Meynert, which overlaps the globus pallidus, ventral pallidum and substantia innominata. Perikarya of the basal forebrain cholinergic system of mammals project topographically to pallial and cortical areas, including hippocampus, neocortex, and pallial amygdala (Záborszky et al., 1999). Various pallial regions in birds also receive cholinergic innervation, including rostromedial nidopallium, temporo-parieto-occipital area (TPO), hippocampal complex and dorsal arcopallium (Medina and Reiner, 1994). Tract-tracing and double-labeling data indicate that cholinergic neurons of the basal forebrain in birds project to the pallium in a roughly topographic manner (Krebs et al., 1991; Bagnoli et al., 1992; Medina et al., 1995). Since the intrapeduncular nucleus is rich in cholinergic neurons and projects to the TPO, its cholinergic neurons appear to be part of the NBM system in birds (Brauth et al., 1978). The cholinergic innervation of the pallium in birds and mammals is associated with their enrichment in muscarinic cholinergic receptors (Brann et al., 1988; Dietl et al., 1988; Wächtler and Ebinger, 1989; Kohler et al., 1995). In mammals, the basal forebrain cholinergic corticopetal cell fields receive input from the pallial amygdala, and the central and intercalated nuclei of the subpallial amygdala (Price and Amaral, 1981; Russchen, 1982; Russchen et al., 1985a, 1985b; Grove, 1988; Paré and Smith, 1994), and the brainstem reticular formation, including the pedunculopontine nucleus (Pal and Mallick, 2004; Datta and Prutzman, 2005). In birds, it appears that the region of the NBM cholinergic neurons receives input from limbic striatum (including nucleus accumbens) and from the arcopallium-amygdaloid complex (Veenman et al., 1995; Medina and Reiner, 1997). Tract-tracing data also suggest that the NBM receives input from a rostral rhombencephalic tegmental region (Kitt and Brauth, 1986b) that contains the pedunculopontine nucleus. Thus, inputs, outputs, and neurochemistry of the NBM in birds closely resemble those in mammals.

3.4.2. Nucleus of the diagonal band—Cholinergic neurons in the diagonal band and ventromedial septum are also part of the mammalian basal forebrain cholinergic system (Woolf, 1991). Cholinergic neurons of the nucleus of the diagonal band (NDB) occur as far caudally as the nucleus of the septal commissure. Neurons from the vertical limb of the diagonal band and medial septum provide major cholinergic innervation of the hippocampus while those of the horizontal limb of the diagonal band project to the olfactory bulbs. Similarly, the avian NDB (Fig. 11A, Fig. 12B) projects heavily into the hippocampal and parahippocampal areas (Benowitz and Karten, 1976; Casini et al., 1986; Atoji et al., 2002; Montagnese et al., 2004). Tract-tracing and double-labeling data indicate that cholinergic neurons of the NDB are at least partly the source of this projection to the hippocampal complex, as well as to medial pallial territories of the Wulst and dorsal ventricular ridge (Medina et al., 1995).

3.4.3. Nucleus commissuralis septi (Commissural septal nucleus)—The avian commissural septal nucleus (CoS) can be observed just dorsal to the anterior commissure and lateral to the nucleus of the hippocampal commissure (Fig. 11). The nucleus projects heavily to the hippocampal and parahippocampal areas (Benowitz and Karten, 1976; Casini et al., 1986; Atoji et al., 2002; Montagnese et al., 2004). In general, its inputs resemble those to the NBM and NDB.

3.4.4. Functional considerations for corticopetal system—The basal forebrain system has been implicated in cortical learning and memory in mammals (Záborszky et al., 1999), and there is a strong correlation between the loss of cholinergic neurons and the loss of memory (Auld et al., 2002). Little is known, however, about the role of these cholinergic neurons in learning and memory in birds. The similarities between mammals and birds in the inputs, outputs, and neurochemistry of this system of cholinergic neurons suggest that they likely play a key role in learning and memory in birds as well. Pharmacological blockade of muscarinic cholinergic receptors, in fact, has been shown to impair learning and memory in diverse avian species (Patterson et al., 1990; Mineau et al., 1994; Savage et al., 1994; Kohler et al., 1996; Zhao et al., 1997). Moreover, beta-amyloid toxicity, which is known to damage the basal forebrain cholinergic system in mammals, is known to impair memory in chicks (Gibbs et al., 2010).

4. Conclusions

The present goal was to provide current developmental, hodological, chemoarchitectonic and behavioral/functional data that further refine understanding of the avian subpallium and its relationship to that in mammals. We have organized the cell groups of the lateral wall of the avian subpallium into four distinct neural systems, and pointed out similarities and differences between mammals and birds in the constituent parts of these systems. Noteworthy similarities that had not been previously recognized are apparent, as well as some differences that advance understanding of the evolution and function of the avian subpallium. A subsequent paper will address septal structures residing in the medial subpallial wall that comprise a fifth neural system in the avian subpallium.

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Abbreviations

6-OHDA	6-hydroxydopamine
A	Arcopallium
A6	Locus coeruleus, noradrenergic cell group
A8	Dopaminergic cell group
Ac, AcS, AcC	Nucleus accumbens (shell and core)
AChE	Acetylcholine esterase
AEP	Anterior peduncular area
AFP	Anterior forebrain pathway
AHi	Amygdalo-hippocampal area
AMPA	Glutamate agonist specific for AMPA-gated glutamate receptor subtype
APH	Parahippocampal area
ARCO	Arcopallium
Av	Arcopallium ventrale
AVT	Arginine vasotocin
BDA	biotinylated dextran amine
BG, dBG, vBG	Basal ganglia; dorsal, ventral BG
BO	Bulbus olfactorius, olfactory bulb
BST, BSTL, BSTLdl,vm	Bed nucleus of the stria terminalis, lateral BST (BSTL), BSTL pars dorsolateralis (BSTLdl), BSTL pars ventromedialis (BSTLvm)
BSTM1, BSTM2	Medial BST sub-nucleus 1(dorsolateralis, dl), sub-nucleus 2(ventromedialis, vm)
CA	Commissura anterior, anterior commissure
CCS	Caudocentral septal area
CeA	Central amygdalar nucleus
CGRP	Calcitonin gene-related peptide
ChAT	Choline acetyltransferase
CHCS (FiHp)	Tractus cortico-habenularis and tractus cortico-septalis (fimbria of hippocampus)
CLSt	Caudolateral part of striatum
CoS	Nucleus commissuralis septi, commissural septal nucleus
CPa (HpC)	Pallial commissure (hippocampal commissure)
CPu	Caudate putamen

CRH	Corticotropin releasing hormone
CSFcn	Cerebrospinal fluid contacting neuron/s
cSP, SP	Chicken substance P
CVO	Circumventricular organ/s
DA	Dopamine
DARPP	Dopamine and cAMP-regulated phosphoprotein
DIEN	Diencephalon
DL CPu	Dorsolateral part of caudate putamen
DLM	Medial dorsolateral nucleus of the anterior thalamus
DMA	Anterior dorsomedial thalamic nucleus
DVR	Dorsal ventricular ridge
DYN	Dynorphin
E14, E16, E18	Embryonic day 14, 16 and 18 in developing chick
EA	Extended amygdala
EAce, cel, cem	Central EA, lateral part of EAce (EAcel), medial part of EAce (EAcem)
EAmes	Medial EA, subpallial part
EAp	Pallial part of the medial EA
ENK	Enkephalin
GABA	Gamma-aminobutyric acid
GAD	Glutamic acid decarboxylase
GnRH-1	Gonadotropin releasing hormone-1
GP, GPe, GPi	Globus pallidus, GP externus (GPe), GP internus (GPi)
H	Hyperpallium (dorsal pallium)
HVC	HVC, used as a letter based name (associative center of the caudal nidopallium)
IHA	Interstitial nucleus of the apical hyperpallium
INP	Intrapeduncular nucleus
IP	Interpeduncular nucleus
ITC	Intercalated amygdalar cells
LAMP	Limbic-associated membrane protein
LFB	Lateral forebrain bundle
LGE	Lateral ganglionic eminence
LMAN	Lateral magnocellular nucleus of the anterior nidopallium
LoC	Locus coeruleus (A6), noradrenergic cell group
LPS	Pallial-subpallial lamina

LS	Lateral septum
LSO, LSOm, LSOl	Lateral septal organ, pars medialis (LSOm), pars lateralis (LSOl)
LSt	Lateral striatum
M	Mesopallium (lateral pallium)
MeA	Medial amygdala
MeAs	Subpallial medial amygdala
MFB	Medial forebrain bundle
MGE, MGEcv	Medial ganglionic eminence, caudalventral area
MPTP	1-methy-4-phenyl-1,2,3,6-tetrahydropyridine
MSIB	Medial septum, internal band
MSt	Medial striatum (MSt)
MStm	Medial striatum, magnocellular part
N	Nidopallium
NBM	Nucleus basalis magnocellularis (of Meynert), basal magnocellular n.
NCPa (NHpC)	Bed nucleus of pallial commissure, replaced by NHpC
NDB, NDBh,v	Nucleus of the diagonal band, horizontal limb, ventricular limb
N-III	Third cranial nerve (oculomotor nerve)
NHpC	Nucleus of hippocampal commissure
NMDA	Glutamate agonist specific for NMDA-gated glutamate receptor subtype
NOS	Nitric oxide synthase
NPY	Neuropeptide Y
NTS	Nucleus tractus solitarius
OB	Olfactory bulb
OVLT	Organum vasculosum of the lamina terminalis
PO	Preoptic area
PoA, PoAc	Posterior nucleus of the pallial amygdala, compact division
POC	Commissural preoptic area
PPN	Pedunculopontine nucleus
Pt	Pretectum
RSv	Ventral reticular superior nucleus
S, Se	Septum
SL	Nucleus septalis lateralis, Lateral septal nucleus
SM	Nucleus septalis medialis, Medial septal nucleus

SNe	Substantia nigra pars compacta
SNr	Substantia nigra pars reticulata
SpA	Subpallial amygdaloid area
SpL	Lateral spiriform nucleus
SPV	Supraopto-paraventricular domain
SS	Somatostatin
SSO	Subseptal organ
ST	Stria terminalis
StC	Striatal capsule
Std	Dorsal striatal subdivision
STN	Subthalamic nucleus (formerly, anterior nucleus of the ansa lenticularis)
Stvb, Stvi	Ventral striatal subdivision, basal domain, intermediate domain
Supv	Subparaventricular nucleus (part of suprachiasmatic domain of embryo)
TEO	Optic tectum
Th	Thalamus
TH	Tyrosine hydroxylase
TnA	Nucleus taeniae of the amygdala, currently proposed as the subpallial medial amygdala (MeAS)
TPO	Area temporo-parieto-occipitalis
TRH	Thyroid releasing hormone
TSM	Tractus septopallio-mesencephalicus
TuO	Olfactory tubercle
Tup, Tus	Pallidal olfactory tubercle, striatal olfactory tubercle
vaf	Ventral amygdalofugal tract (formerly occipitomesencephalic tract)
VIA	Ventrointermediate thalamic area
VL	Lateral ventricle
VP, VPa	Ventral pallidum
VTA	Ventral tegmental area

Fig. 1.

Schematic diagram of five neural systems comprising the avian subpallium

Red Dorsal somatomotor basal ganglia: structures include the lateral striatum (LSt), medial striatum (MSt), globus pallidus (GP), intrapeduncular nucleus (INP) and pallial-subpallial lamina (LPS; the dorsal border of LSt and MSt).

Tan Ventral viscerolimbic basal ganglia: structures include the olfactory tubercle (TuO), nucleus accumbens (shell and core, AcS, AcC) and ventral pallidum (VP).

Blue Extended amygdala and bed nuclei of the stria terminalis: structures include the *central extended amygdala* - subpallial amygdaloid area (SpA), striatal capsule (StC) and lateral bed nucleus of the stria terminalis (BSTL); and, the *medial extended amygdala* - subpallial medial amygdala (MeAs) and medial bed nucleus of the stria terminalis (BSTM1, BSTM2).

Green Basal telencephalic cholinergic and non-cholinergic corticopetal system: structures include the basal magnocellular nucleus (NBM), diagonal band nucleus (NDB) and commissural septum (CoS).

Yellow Septum and Septal Neuroendocrine Systems: structures include the medial Septum (SM), lateral septum (SL), nucleus of the hippocampal commissure (NHpC) and circumventricular organs - lateral septal organ (LSO), organum vasculosum of the lamina terminalis (OVLT) and subseptal organ (SSO).

Other abbreviations: ARCO – arcopallium, DIEN – diencephalon.

Derivatives	Mouse	Chicken	Derivatives
GABA/DA interneurons of OB (Pax6), DL CPU, striatal TuO (Pax6), ITC, capsular amygdala and lateral CeA (Pax6), Subset of Pax6 cells of BSTL	LGE1	Dorsal St	GABA/DA interneurons of OB (Pax6), LSt, CLSt, striatal TuO (Pax6), Striatal capsule, lateral EAc (Pax6), Subset of Pax6 cells of BSTL and medial EAc
Dorsolateral CPu	LGE2		
CPu matrix, striatal TuO (Islet1), medial and lateral CeA (Islet1), Subset of Islet1 cells of BSTL	LGE3	Ventrint St	Part of MSt and LSt, striatal TuO (Islet1) part of INP?
accumbens, striatal TuO (Islet1)	LGE4	Ventrobass St	accumbens, striatal TuO (Islet1), INP
GABA interneurons of Pallium	MGE1		
GPe, GPi, Pallidal TuO (Nkx2.1, Lhx6), commissural VP (Nkx2.1, Lhx6), BSTLd (Nkx2.1, Lhx6), GABA interneurons of Pallium	MGE2		
	MGE3	Dorsal Pa	GP, Pallidal TuO (Nkx2.1, Lhx6), BSTLd and medial EAc (Nkx2.1, Lhx6), GABA interneurons of Pallium
precommissural VP, Pallidal TuO (Nkx2.1, Lhx6, Lhx7/8)	MGE4	Ventral Pa	VP, Pallidal TuO (Nkx2.1, Lhx6, Lhx7/8)
GPe, MeA - BSTM (Nkx2.1, Lhx6), GABA interneurons of Pallium	MGE5	AEP	MeA - BSTM (Nkx2.1, Lhx6), GABA interneurons of Pallium
Subset of cells in MeA - BSTM (Shh), basal magnocellular complex (Lhx7/8, ChAT)	POC	POC	Subset of cells in MeA - BSTM (Shh), basal magnocellular complex (Lhx7/8, ChAT)

Fig. 2.

Schematic diagram of the three major, developmental subpallial proliferative zones and their derivatives, comparing mouse and chicken. The three major subpallial divisions are: lateral ganglionic eminence (LGE) in mouse, and the corresponding striatal division (St) in chicken; medial ganglionic eminence (MGE) in mouse, and the corresponding pallidal division (Pa) in chicken; and the preoptic division (PO) in mouse and commissural preoptic division (POC) in chicken. Based on differential gene expression patterns (for example, differential expression of the transcription factors Pax6, Islet1 or Nkx2.1), each major division is subdivided into several subdomains, although some differences are found in the number of subdivisions between mouse and chicken. For example, four LGE subdivisions are found in mouse, but only three striatal subdivisions appear to be present in chicken: 1) dorsal striatal (dorsal st.), 2) ventrointermediate striatal (ventrint. st.) and 3) ventrobasal striatal (ventrobass. st.) subdivisions which may be related to some of the differences found in the mature striatum of these two species. Similarly, although five MGE subdivisions are present in mouse, only three have been described in chicken: 1) dorsal pallidal (dorsal pa.), 2) ventral pallidal (ventral pa.) and 3) caudal pallidal (formerly termed the anterior peduncular area (AEP)) subdivisions. Regarding the preoptic area, two comparable subdivisions are found in mouse and chicken, although here we only refer to one of them (the commissural preoptic subdivision or POC) due to its contribution of cells to the lateral telencephalic wall. See text for more details and list of abbreviations for other abbreviations shown in figure.

Fig. 3.

A-F present low-magnification digital images of frontal sections of the telencephalon of chicken at prehatching stages (E18) or at hatching (P0), hybridized for *cSP* (A, B), *cLmo4* (C-F). The images show the major subdivisions of the developing somatic and limbic basal ganglia, with striatal subdivisions enriched in *cSP* and *cLmo4*. Scale bar = 1 mm in A (applies to A, B), and Scale bar = 1 mm in C (applies to C-F). AcC = accumbens core; AcS = accumbens shell; StC = striatal capsule; Tup = pallidal olfactory tubercle; Tus = striatal olfactory tubercle. From Abellán and Medina (2009). See list of abbreviations for other abbreviations shown in this figure.

Fig. 4.

A-D A series of schematic line drawings of midtelencephalic transverse brain sections of pigeon and rat. **A.** The outdated interpretation of the organization of the telencephalon in birds and the outdated nomenclature that view engendered for the telencephalon of birds. **B.** The longstanding interpretation of mammalian telencephalic organization and the established nomenclature consistent with that view. **C.** The current interpretation of the organization of avian telencephalon and the outdated avian telencephalic nomenclature, which highlights the inappropriateness of this nomenclature. **D.** The current interpretation of the organization of avian telencephalon and new avian telencephalic nomenclature adopted by the Avian Brain Nomenclature Forum that is consistent with current findings on telencephalic organization in birds. In each schematic interpretation of telencephalic organization, the speckled region represents pallium, the striped region represents striatum, and the checked region represents globus pallidus. The new avian terminology (D) avoids the erroneous misimpressions about correspondences between avian and mammalian

telencephala perpetuated by the old nomenclature. Hp = hippocampus. From Reiner et al., (2004).

Fig. 5. Images of transverse sections of pigeon brain immunolabeled for **A.** Substance P (SP) and **B.** Choline acetyltransferase (ChAT). Transverse section of chicken brain immunolabeled for **C.** Tyrosine hydroxylase (TH). Note the enrichment of the ventral pallidum (VP) in SP fibers and ChAT neurons and the paucity of SP fibers and relative paucity of ChAT neurons in the lateral part of the bed nucleus of the stria terminalis (BSTL). In B, the field of cholinergic neurons spanning the VP and lateral forebrain bundle (LFB) represents the basal magnocellular cholinergic cell group (NBM). Image C shows the enrichment of striatal parts of the basal ganglia in fibers containing TH, and identifies the parts of the dorsal somatic basal ganglia. Abbreviations: GP = globus pallidus; LSt – lateral striatum; MSt = medial

striatum; SL = lateral septal nucleus; TSM = tractus septopallio-mesencephalicus. Scale bar = 1 mm in A and C (scale bar in A applies to A, B). See list of abbreviations for other abbreviations shown in this figure.

Fig. 6.

Sources of afferent inputs to the basal ganglia in chick brain. **A.** Brain atlas plate A3.4 (Kuenzel and Masson, 1988). Boxed areas show locations of images 6B and 6C. **B.** Ventral tegmental area (VTA) or A10 dopaminergic cell group. Scale bar = 200 μ m. **C.** Substantia nigra pars compacta (SNc) or A9 dopaminergic cell group. Scale bar = 200 μ m. **D.** Chick brain atlas plate A2.4; boxed area shows location of photomicrograph 6E. **E.** A8 dopaminergic cell group. Scale bar = 200 μ m. **F.** Chick brain atlas plate A1.4. Boxed area shows location of photomicrograph 6G. **G.** Locus coeruleus or A6 noradrenergic cell group. Scale bar = 100 μ m. Neurons in figure immunolabeled with antibody to tyrosine hydroxylase.

Fig. 7.

The songbird anterior forebrain circuit. **A.** A simplified, neuroanatomical schematic representation of the avian song system. The direct motor pathway arises from nucleus HVC (proper name), which projects to the robust nucleus of the arcopallium (RA), which in turn projects to the tracheosyringeal half of the hypoglossal nucleus (nXIIts) and other respiratory premotor neurons in the brainstem. Another projection from HVC leads to area X of the MSt. Area X projects to the medial portion of the dorsolateral nucleus of the thalamus (DLM), which projects to the lateral magnocellular nucleus of the anterior nidopallium (LMAN). LMAN sends a projection to RA, with axon collaterals projecting to area X. As part of the MSt, area X receives a strong dopaminergic input from the ventral

tegmental area (VTA). Axon collaterals of the area X projection to DLM terminate in the ventral pallidum (VP), an area that sends projections to the region of the dopaminergic midbrain (VTA) that ultimately projects to area X. **B.** Combined electrophysiological and cell morphological classification of neurons of area X. There are four classes of neurons that correspond to mammalian striatal neurons: spiny neurons; cholinergic; fast spiking (FS); and low-threshold spiking (LTS). In addition, there is a neuron with pallidal properties, an aspiny fast firing cell (AF). Images and traces from Farries and Perkel (2002).

Fig. 8. Sections of chick brain showing selected structures of the viscerolimbic basal ganglia (BG). **A.** Sagittal section near midline and **B.** Transverse section showing the ventral portion of medial striatum (MSt) and tuberculum olfactorium (TuO). **8B, C, D.** Transverse sections of BG depicting major components of the ventral viscerolimbic BG including the tuberculum olfactorium (TuO), medial striatum (MSt), and ventral pallidum (VP). Immunolabeled with antibody to substance P. Scale bars for 8A – 8D = 1.0mm. Refer to list of abbreviations for names of other structures identified.

Fig. 9.

Transverse sections of chick brain showing nucleus accumbens (Ac) core (AcC) and shell (AcS) subdivisions processed with antibodies made to the following neuropeptides/proteins: **A.** Substance P (SP), **B.** Neuropeptide Y (NPY), **C.** Dopamine and cAMP-regulated phosphoprotein (DARPP-32), and **D.** Calbindin (CB). Scale bars = 500 μ m. The lateral border of AcC is particularly well delineated in section A, however, the border with the dorsomedial MSt is not marked clearly. The NPY immunoreactivity (B) is useful for demarcation of the shell. The putative core is dorsolateral to the BSTl while the putative shell occurs ventrolateral to the AcC and BSTl. Refer to list of abbreviations for names of other structures identified.

Fig. 10.

Major structures comprising the avian central extended amygdala (EACE) complex, as seen in frontal (A,B) or oblique-horizontal (C-F) sections showing mRNA expression of *Lmo3* (A,B), *SP* (C,D) or *Pax6* (E,F). Scale bars in A and C = 1mm (applies to A-F). Expression of the gene *Lmo3* helps to delineate the dorsal part of lateral bed nucleus of the stria terminalis (BSTLd) and part of a lateral corridor that includes the intrapeduncular nucleus (INP) and the EACE cell corridor, located below the globus pallidus (GP). The striatal division is rich in cells expressing substance P (SP) or Pax6, and both markers are enriched in the striatal (lateral) part of the EACE complex. In addition, many cells expressing Pax6 or SP also invade (apparently by tangential migration) the pallidal (more medial) parts of the EACE complex, including the EAcem and part of the dorsal BSTL. Refer to list of abbreviations for names of other structures identified. From Abellán and Medina (2009).

Fig. 11.

Major structures comprising the avian medial extended amygdala (EAmc) complex, as seen in frontal sections showing mRNA expression of the transcription factor Lhx6. These structures include the subpallial medial amygdala (MeAs) and the BSTM (which show two subdivisions in chicken, called BSTM1 and BSTM2). Scale bar = 1mm. Note the expression of Lhx6 in other pallidal structures of the telencephalon, including the globus pallidus (GP), the BSTLd and the medial EAc. Refer to list of abbreviations for names of other structures identified. Modified from Abellán and Medina (2009).

Fig. 12.

Major structures of the cholinergic corticopetal system seen with markers of ChAT (mRNA or protein), which label cholinergic cells. **A.** Nucleus basalis magnocellularis (NBM). **B.** Nucleus of the diagonal band (NDB). **C.** Higher magnification of the NBM of Fig. 12A showing more detail of *ChAT* expression in NBM, GP and low expression in LSt. Scale bars in A and B = 1mm. Modified from Abellán and Medina (2009).

TABLE 1**Structures Comprising the Subpallium****Structures within the Lateral Wall of Subpallium**

- 1 Somatic Basal ganglia**
 - a. Somatic striatum (striatal region)**
 - i. Dorsal and ventral parts of medial striatum**
 - ii. Lateral striatum**
 - iii. Nucleus intrapeduncularis**
 - iv. Area X (mixed striatal and pallidal region)**
 - b. Globus pallidus (GP; pallidal region)**
- 2 Limbic Basal Ganglia**
 - a. Limbic Striatum (striatal region)**
 - i. Ventral part of medial striatum**
 - ii. Nucleus accumbens Shell and Core**
 - iii. Olfactory Tubercle – rostral and dorsolateral**
 - b. Limbic Pallidum (pallidal region)**
 - i. Ventral pallidum**
 - ii. Olfactory Tubercle – posterior and caudomedial**
- 3 Extended Amygdala Complex**
 - a. Extended central amygdala complex (mixed striatal and pallidal region)**
 - i. Subpallial amygdaloid area**
 - ii. Lateral bed nucleus of stria terminalis**
 - b. Extended medial amygdala complex (pallidal region)**
 - i. Nucleus taeniae amygdala (subpallial medial amygdala)**
 - ii. Medial bed nucleus of stria terminalis**
- 4 Cholinergic Corticopetal System (commissural preoptic areal derivatives)**
 - a. Nucleus basalis magnocellularis**
 - b. Nucleus of the diagonal band (mixed commissural preoptic area and pallidal region)**
 - c. Nucleus of the septal commissure**

Structures within the Medial Wall of Subpallium

- 1 Septum and Septal Neuroendocrine System**
 - a. Medial septum**
 - b. Lateral septum**
 - c. Nucleus of hippocampal commissure (formerly termed the bed nucleus of pallial commissure)**
 - d. Circumventricular organs: (lateral septal organ, organum vasculosum of the lamina terminalis and subseptal organ)**