The Vertebrate Mesolimbic Reward System and Social Behavior Network: A Comparative Synthesis

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ABSTRACT

All animals evaluate the salience of external stimuli and integrate them with internal physiological information into adaptive behavior. Natural and sexual selection impinge on these processes, yet our understanding of behavioral decision-making mechanisms and their evolution is still very limited. Insights from mammals indicate that two neural circuits are of crucial importance in this context: the social behavior network and the mesolimbic reward system. Here we review evidence from neurochemical, tract-tracing, developmental, and functional lesion/stimulation studies that delineates homology relationships for most of the nodes of these two circuits across the five major vertebrate lineages: mammals, birds, reptiles, amphibians, and teleost fish. We provide for the first time a comprehensive comparative analysis of the two neural circuits and conclude that they were already present in early vertebrates. We also propose that these circuits form a larger social decision-making (SDM) network that regulates adaptive behavior. Our synthesis thus provides an important foundation for understanding the evolution of the neural mechanisms underlying reward processing and behavioral regulation. J. Comp. Neurol. 519:3599–3639, 2011.

INDEXING TERMS: social behavior; comparative neuroanatomy; amphibian; reptile; bird; teleost; reward system; social behavior network; limbic system; neural circuits

Throughout their lives, all animals constantly face situations that provide either challenges (e.g., aggression, predation) or opportunities (e.g., reproduction, foraging, habitat selection) (for a detailed review, see O'Connell and Hofmann, 2011). In all cases, environmental cues are processed by sensory systems into a meaningful biological signal while internal physiological cues (e.g., condition, maturity) and prior experience are integrated at the same time. This process usually results in behavioral actions that are adaptive, i.e., beneficial to the animal. To accomplish this, an animal's nervous system must evaluate the salience of a stimulus and elicit a context-appropriate behavioral response. Despite tremendous progress in understanding the ecology and evolution of social behavior (Lorenz, 1952; Tinbergen, 1963; Lehrman, 1965; von Frisch, 1967; Krebs and Davies, 1993; Stephens, 2008), it is less understood where in the brain these decisions (e.g., about mate choice or territory defense) are made and how these brain circuits have arisen over the course of vertebrate evolution.

Recent research has begun to decipher the neural basis of social decision-making. In mammals in particular, the neural circuits that evaluate stimulus salience and/or regulate social behavior have been uncovered to some degree: the mesolimbic reward system and social behavior network (Fig. 1). It is becoming increasingly clear that the reward system (including but not limited to the midbrain dopaminergic system) is the neural circuit where the salience of an external stimulus is evaluated (Deco and Rolls, 2005; Wickens et al., 2007), as appetitive behavior seems to be regulated by this network. In mammals, this circuit contains mostly telencephalic brain regions and dopaminergic projections from the midbrain ventral tegmental area. The neural substrate of social

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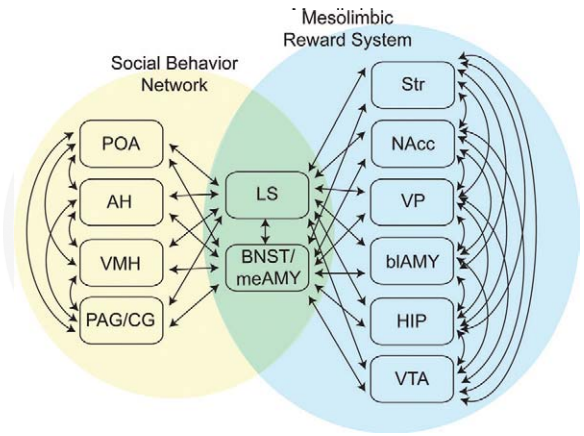

Figure 1. Interactive nodes of the networks regulating social decision-making. Brain regions in the social behavior network (left) and mesolimbic reward system (right), as well as brain regions involved in both systems (center), are shown. Arrows indicate anatomical connections between these brain regions within each system in mammals. AH, anterior hypothalamus; blAMY, basolateral amygdala; BNST/meAMY, bed nucleus of the stria terminalis/medial amygdala; HIP, hippocampus; LS, lateral septum; NAcc, nucleus accumbens; PAG/CG, periaqueductal gray/central gray; POA, preoptic area; Str, striatum; VMH, ventromedial hypothalamus; VP, ventral pallidum; VTA, ventral tegmental area. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

behavior has been described by Newman (1999) as a "social behavior network" (SBN) in mammals, and has been expanded to reptiles, birds, and teleosts (Crews, 2003; Goodson, 2005). The core nodes of Newman's network are involved in multiple forms of social behavior (sexual behavior, aggression, and parental care), are reciprocally connected, and—by definition—contain sex steroid hormone receptors. Unfortunately, very little is known about the neural basis of other opportunistic nonsocial behaviors, such as foraging or habitat selection. However, there is evidence that some of these amygdalar and hypothalamic regions also regulate feeding behavior (Buntin et al., 1999; Choi and Kim, 2010).

Social decision-making requires the evaluation of stimulus salience before an adaptive behavioral response can be carried out. We therefore argue here that the mesolimbic reward system and SBN are best understood as an integrated and evolutionarily ancient social decision-making (SDM) network that regulates and implements responses to salient stimuli (both social and nonsocial). The reasoning for this integration of neural circuits into a larger framework is as follows: historically, the study of the neural and endocrine mechanisms underlying social behavior (aggression, parental care, sexual behavior), and more generally, sociality (Goodson and Kabelik, 2009), focused on specific candidate fore- and midbrain areas (e.g., preoptic area, ventromedial hypothalamus, septal regions). Newman (1999) was the first to propose a comprehensive set of criteria (see below for detailed discussion) that allowed her to integrate these individual regions into the SBN, an advance that has greatly facilitated our understanding of the neural and hormonal underpinnings of social life across major vertebrate lineages (Newman, 1999; Crews, 2003; Goodson, 2005). However, to be adaptive, social behavior must be reinforcing (or rewarding) in some way. This is where we can take advantage of the rich literature on the mesolimbic reward system, which shares overlapping nodes with the SBN (lateral septum and bed nucleus of the stria terminalis) and has been studied extensively in mammals in the context of addiction (Adinoff, 2004) and regulating appetitive behavior (Alcaro et al., 2007). This neural system can reinforce responses to salient stimuli such as sex with a conspecific (Paredes, 2009), winning a fight (Fuxjager et al., 2010), or caring for offspring (Numan, 2007) and—as we argue here—was likely already in place in early vertebrates. Taken together, the SDM network as the union of the reward system and SBN is intimately concerned with regulating and implementing adaptive behavioral outputs in response to salient environmental challenges and opportunities. We would therefore predict that the SDM network is highly conserved and has played a fundamental role in vertebrate social evolution.

In order to test this hypothesis, we must first establish the homology relationships of the SDM network nodes across vertebrates. In principle, this provides the opportunity to integrate insights into the neural basis of social decision-making gathered from many species across vertebrates into a comprehensive understanding of how decision-making processes have evolved. This type of cross-species comparison supports the idea that elements of these circuits are phylogenetically ancient, with evidence for their existence in a wide variety of vertebrates, including both amniote and anamniote lineages. In the following review, we will endeavor to describe what we suggest to be homologous systems in four vertebrate groups: mammals, birds/reptiles, amphibians, and fish. Specifically, we focus on the fish subclass of teleosts, due to the

Abbreviations

AH	Anterior hypothalamus
blAMY	Basolateral amygdala
BNST	Bed nucleus of the stria terminalis
HIP	Hippocampus
LS	Lateral septum
meAMY	Medial amygdala
NAcc	Nucleus accumbens
PAG/CG	Periaqueductal gray/central gray
POA	Preoptic area
STR	Striatum
VMH	Ventromedial hypothalamus
VP	Ventral pallidum
VTA	Ventral tegmental area

paucity of neural studies in nonteleost fish. These vertebrate groups should not be considered to represent a linear sequence of evolution, but instead as representatives of four different clades that diverged at different points during vertebrate evolution. Commonalities between these divergent groups suggest, but do not prove, that the circuits we describe were present in some form at the common origin of these lineages, as our descriptions only *suggest* similarity in circuitry and neurotransmitters based on several lines of evidence. Importantly, space does not permit a rigorous review of the limitations or caveats on the suggested homologies that we draw, and for this the reader should refer to the original articles referenced herein.

Efforts to determine homology relationships for nodes of the mesolimbic reward system and SBN in other vertebrate classes have often proved controversial and have been hampered by inconsistent nomenclatures and incomplete information. However, a consensus is emerging from hodological, neurochemical, and developmental studies that provide support for putative homologies for most of the relevant areas in the avian, reptilian, amphibian, and teleost brains (Fig. 2) (Marín et al., 1998a; Redies and Puelles, 2001; Reiner et al., 2004; Wullimann and Mueller, 2004; Moreno and González, 2007a; Bruce and Braford, 2009). Here we present a synthesis of decades of research that has led to a greater understanding of the putative homologies across the major vertebrate lineages. This work builds on an extraordinary body of literature in comparative neuroanatomy, but is presented here for the first time within the functional context of a network of brain regions that regulate social decision-making. Our synthesis has four goals: First, we aim to provide a comprehensive neuroanatomical resource to researchers interested in studying the neural basis of social decision-making in vertebrates. Second, we hope to provide a framework that will facilitate the systematic comparison of species-specific insights across vertebrate classes, so that we may better understand how the mechanisms governing complex social decisions evolved. Third, we see the current synthesis as part of a program that will move the field toward comprehensive electronic repositories of neuroanatomical, neurochemical, developmental, and functional data on all SDM network nodes and beyond. Finally, we discuss how this framework will increase our understanding of variation in social decision-making across lineages.

Before discussing the evolution of brain homologies across vertebrates, it is important to note the caveats that accompany such a daunting task and contentious topic (Striedter, 1998; Wullimann and Mueller, 2004; Jarvis, 2005). Discussions of the homology concept itself have often been contentious (Striedter and Northcutt, 1991; Striedter, 2002). Homologous traits (i.e., organismal characteristics that exhibit "structural correspondence" and are derived from a common ancestor; Owen, 1843) are usually discussed using morphological criteria, which in the case of brain structures include topographical position, hodology (Fig. 3), and gene expression or neurochemical profiles. It is important to add here that in the case of complex characters homologies can also be incomplete or "partial" (sensu van der Klaauw, 1966; Sattler, 1984) in that the structure of interest may comprise both subparts derived from the common ancestor as well as other subparts that do not have this property (for a contemporary discussion, see also Wake, 1999). It should also be noted that inferring homology for a brain region does not imply conserved function, although the idea of functional homology has served molecular and developmental biologists well (Striedter, 2002). In cases where functional (i.e., lesion or stimulation) studies have determined that a given (possibly homologous) brain region regulates similar behavioral processes across lineages we consider it functionally similar. To further complicate this issue, brain regions may be homologous in morphology but may subserve different functions, whereas functionally similar brain regions may not be morphologically homologous. Thus, we use here a combination of insights from developmental studies, tract tracing, and neurochemistry to discuss brain homologies, and functional lesion-stimulation studies to assess whether these potential brain homologies are functionally similar (Table 1; see also Supplementary Excel file for individual studies). Along these lines, another useful approach utilizes careful comparisons of neuronal characteristics at the level of well-defined cell types (Tessmar-Raible et al., 2007; Tomer et al., 2010; Wang et al., 2010), although such analyses are available for very few taxa and will not be discussed here. Finally, any analysis of brain homologies across vertebrate classes is dependent on decades of research by many investigators and thus liable to biases as a consequence of how results were reported and which particular techniques were used. While the synthesis we attempt here is thus bound to be incomplete, we strongly believe that the time has come for an integrative and comparative neural framework of social behavior and its evolution.

SOCIAL BEHAVIOR NETWORK

The neural substrates regulating social behavior in mammals have been described as the "social behavior network" (SBN), based on decades of work investigating the role of sex steroid-sensitive regions of the brain (Newman, 1999). By definition, the core nodes of the SBN are involved in the regulation of multiple forms of social behavior, are reciprocally connected, and contain sex

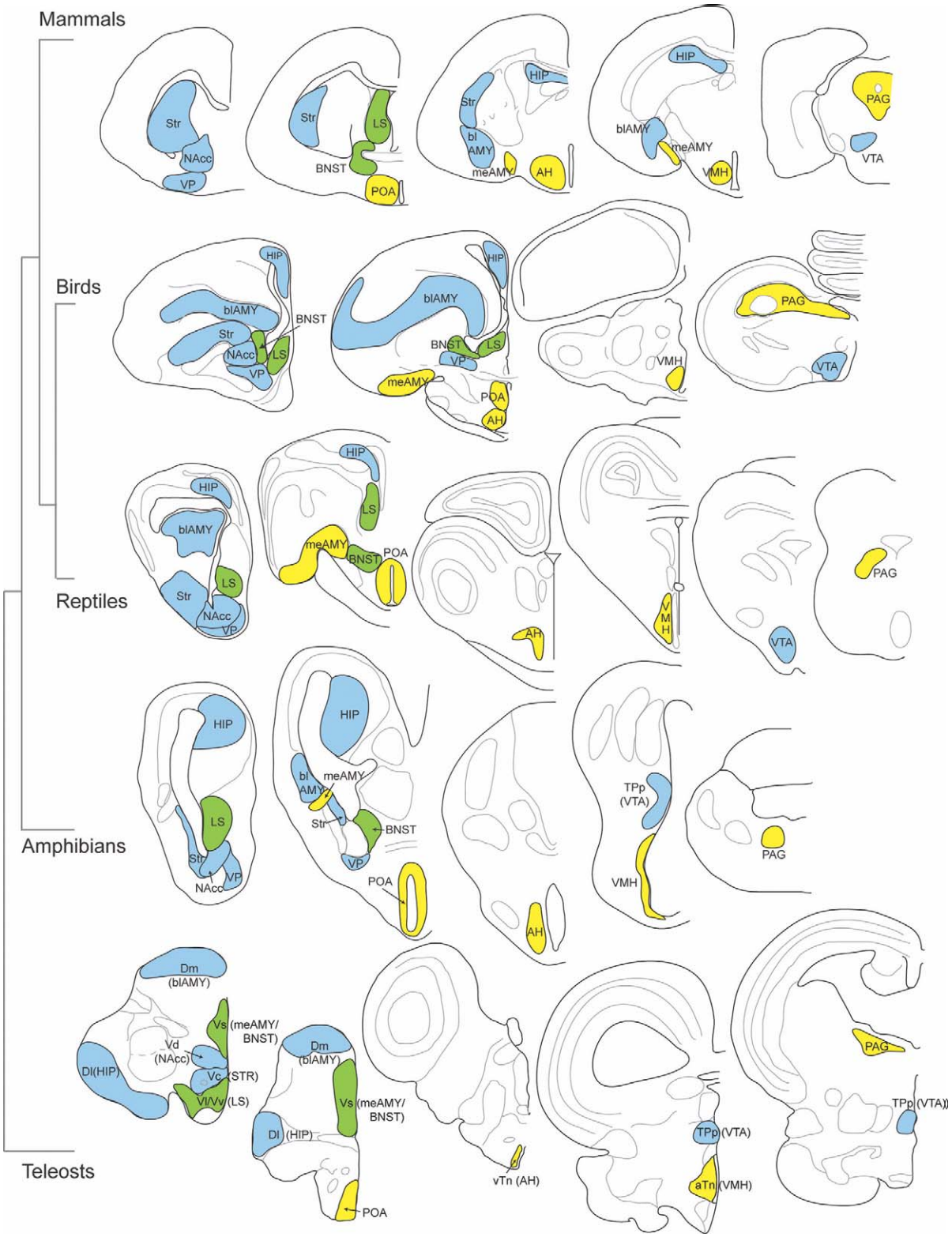

Figure 2. Putative homologies of the social decision-making circuit across vertebrates. Brain regions in the coronal plane within the social behavior network are colored yellow, brain regions in the mesolimbic reward system are colored blue, and brain regions shared by both networks are colored green. Left to right represents rostral to caudal sections. See list for abbreviations. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

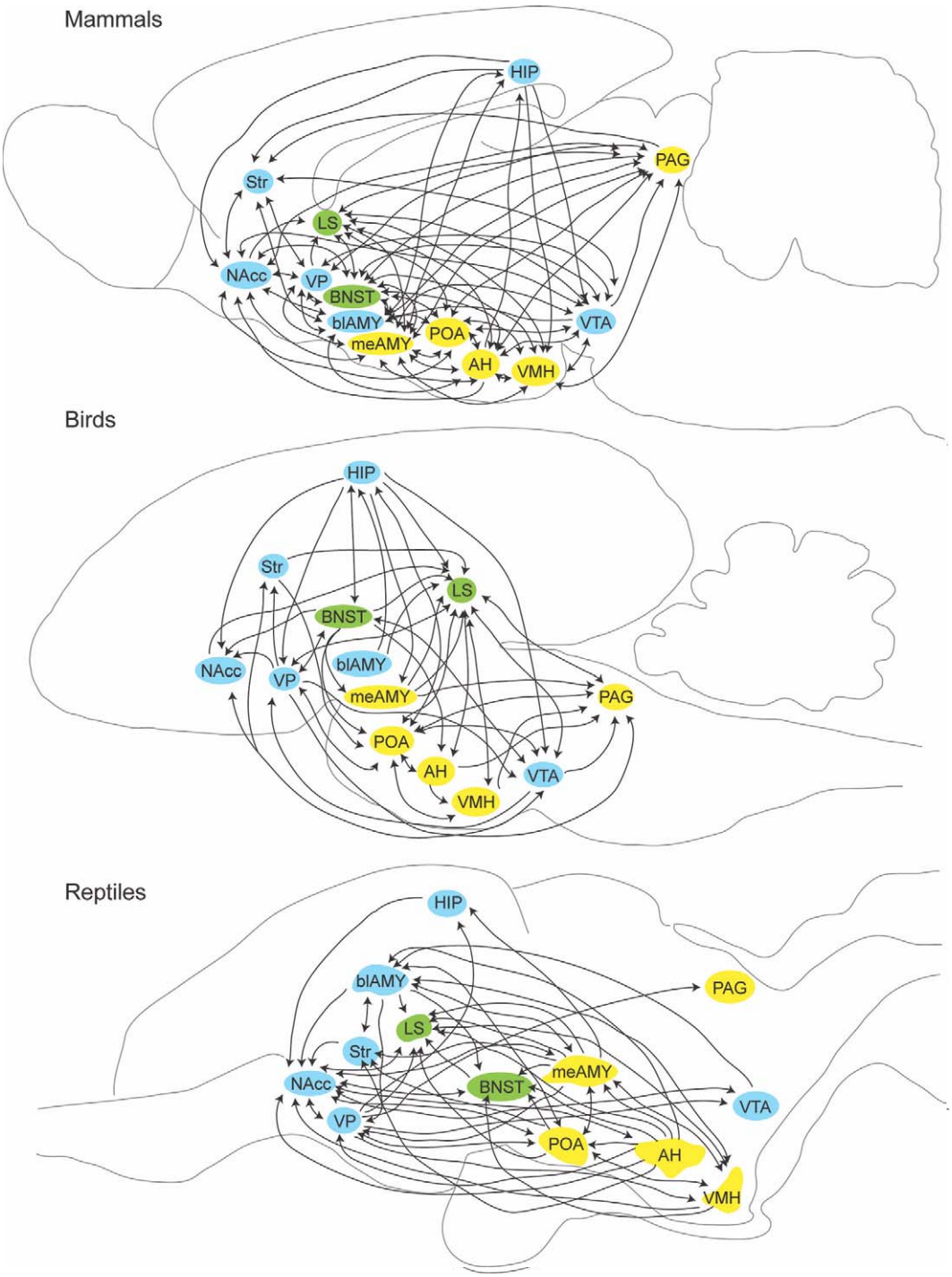

Figure 3. Evidence for homologies by hodology. Sagittal view of the projection patterns of a social decision-making circuit are presented for each major vertebrate lineage. Arrows imply directionality of the connection. Brain regions within the social behavior network are colored yellow, brain regions in the mesolimbic reward system are colored blue, and brain regions shared by both networks are colored green. Mammals: Siegel et al., 1971; Ungerstedt, 1971; Conrad and Pfaff, 1975; Saper et al., 1976; Meibach and Siegel, 1977; Krettek and Price, 1978; Phillipson, 1979; Swanson and Cowan, 1977, 1979; Berk and Finkelstein, 1981; Kelley et al., 1982; Eberhart et al., 1985; Haber et al., 1985; Yang and Mogenson, 1985; Caffe et al., 1987; Domesick, 1988; Groenewegen et al., 1993; Canteras et al., 1994; Napier et al., 1995; Numan and Numan, 1996; Pikkarainen et al., 1999; Carr and Sesack, 2000; Morgane et al., 2005. Birds: Berk and Butler, 1981; Cheng et al., 1987; Wild, 1987; Berk, 1991; Balthazart and Absil, 1997; Medina and Reiner, 1997; Absil et al., 2002; Atoji et al., 2002, 2006; Atoji and Wild, 2004; Montagnese et al., 2008. Reptiles: Russchen and Jonker, 1988; Bruce and Neary, 1995a; Smeets and Medina, 1995; Font et al., 1997; Lanuza et al., 1997; Lanuza and Halpern, 1997; Perez-Santana et al., 1997; Novejarque et al., 2004. Amphibians: Allison and Wilczynski, 1991; Wilczynski and Northcutt 1983a,b; Marin et al., 1995, 1997a; Roth and Westoff, 1999; Sanchez-Camancho et al., 2003; Endepols et al., 2005; Roden et al., 2005. Teleosts: Murakami et al., 1983; Shiga et al., 1985a,b; Wong, 1997; Goodson and Bass, 2002; Rink and Wullimann, 2002; Folgueira et al., 2004a,b; Northcutt, 2006. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

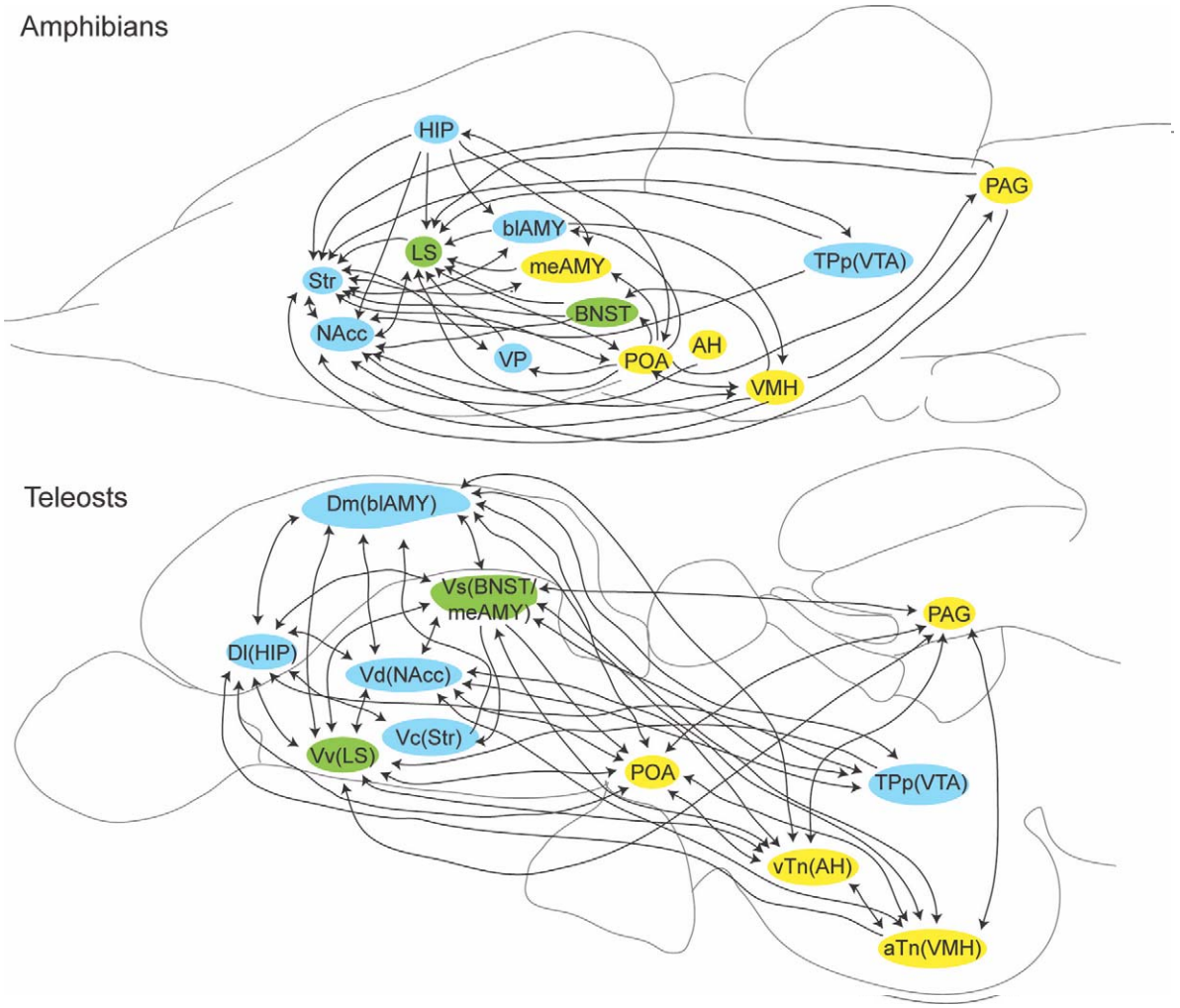

Figure 3. (Continued)

steroid hormone receptors. The nodes that make up this network are the lateral septum (LS), preoptic area (POA), ventromedial hypothalamus (VMH), anterior hypothalamus (AH), the periaqueductal gray/central gray (PAG/CG), the medial amygdala (meAMY), and bed nucleus of the stria terminalis (BNST), as each of these brain regions has been shown in mammals to be important in regulating both reproductive and aggressive behavior.

Reproductive behaviors, such as male- and female-typical sexual behavior as well as parental care, are well established within the SBN framework due to decades of work investigating the contributions of sex steroids to behavior. Male sexual behavior is well defined within this network (Newman, 1999), with a more central role for the POA (Heimer and Larsson, 1967; Hull and Dominguez, 2006). Similarly, thanks to the pioneering work by Pfaff and Sakuma (1979) delineating the lordosis circuit, in females this network also mediates sexual behavior, with a central role for the VMH (Malsbury et al., 1977). In addition to sexual behavior, many of these regions also mediate parental care, which in most mammalian species is only exhibited by females (Miceli and Malsbury, 1982; Lee and Brown, 2007), although a few studies have investigated the neural basis of paternal care in biparental species (Parker et al., 2001; de Jong et al., 2009) within this framework.

Several studies have established that the SBN functions as an integrated circuit in regulating aggressive behavior. For example, hypothalamic stimulation elicits a stronger aggressive response when SBN nodes located in the forebrain (e.g., the BNST, LS, and meAMY) are activated at the same time (Halász et al., 2002). Similarly, the PAG is another node of the SBN that regulates aggressive behavior (Bandler et al., 1986; Siegel and Shaikh, 1997) in concert with the remainder of the circuit. In general, regions of the SBN form an interactive

TABLE 1.
Functional Roles of Brain Regions Regulating Behavior Across Vertebrates

	Mammals	Birds	Reptiles	Amphibians	Teleosts
AH	aggression, reproduction, parental care	n.a.	reproduction	n.a.	n.a.
blAMY	aggression, emotional learning, parental care	n.a.	aggression, emotional learning	emotional learning	emotional learning
BNST	motivation, parental care, reproduction, stress response	reproduction	social affiliation, stress response	n.a.	aggression, reproduction
HIP	spatial learning	spatial, learning	spatial learning	learning	spatial learning
LS	emotional learning, social affiliation/recognition, reproduction, parental care	aggression, reproduction stress response	n.a.	reproduction	reproduction
meAMY	aggression, reproduction, parental care, social recognition	aggression, motivation, reproduction	aggression, reproduction	n.a.	aggression, reproduction
NAcc	emotional learning, impulsivity, motivation, parental care	impulsivity, motivation	n.a.	n.a.	aggression, reproduction
PAG/CG	reproduction, vocalization	vocalization	n.a.	vocalization	vocalization
POA	aggression, reproduction, parental care	aggression, reproduction, parental care	aggression, reproduction	reproduction	aggression, reproduction, parental care
STR	compulsive behavior	learning, motivation	aggression	reproduction	reproduction
VMH	aggression, reproduction, parental care	reproduction, parental care	reproduction	n.a.	n.a.
VP	emotional learning, parental care	n.a.	n.a.	n.a.	n.a.
VTA	motivation, reproduction, parental care	motivation, reproduction	n.a.	motivation?, reproduction	n.a.

Functional roles for each brain region are inferred from lesion and stimulation studies (see Supplementary Table for individual studies and supplementary references). See text for lineage-specific nomenclature for putative homologies. n.a., data not available.

network, and a single node can be involved in mediating many behaviors, such as various forms of aggression (Hayden-Hixon and Ferris, 1991; Delville et al., 2000; Nelson and Trainor, 2007; Fuxjager et al., 2010). For instance, the POA mediates male–male aggression (Albert et al., 1986), male sexual behavior (Heimer and Larsson, 1967; Hull and Dominguez, 2006), and maternal care (Miceli and Malsbury, 1982; Lee and Brown, 2007). As many of the hypothalamic and midbrain nodes of the SBN are downstream of sensory processing areas, and thus associative in nature, it should come as no surprise that this circuit is also considered fundamental to more complex tasks such as social cognition (Ferguson et al., 2002).

Social behavior—especially aggression, sexual behavior, and parental care—is a fundamental and evolutionarily ancient property of most animals, and as such is a major determinant of an individual's fitness. Brain regions regulating these behaviors are thus expected to be highly conserved, at least across vertebrates. Over the past decade, behavioral neuroendocrinologists have extended the SBN framework from mammals to other vertebrate classes including reptiles, birds, and teleosts (for an in-depth discussion, see Crews, 2003; Goodson, 2005). Behavior patterns considered in this context have been reproduction (Sakata et al., 2005; Balthazart and Ball, 2007), aggression (Nelson and Trainor, 2007), and parental care (Ruscio and Adkins-Regan, 2004), and—more generally—variation of sociality (e.g., gregarious vs. solitary) across species (Goodson and Kabelik, 2009). The homologies of hypothalamic regions across vertebrates are far less contentious than regions of the telencephalon, and thus we do not discuss developmental studies here in depth, with the exception of evidence for homologies of the medial amygdala. In the following we focus on neurochemistry, especially the presence of steroid hormone receptors, as a defining criterion of SBN (Newman, 1999), as well as hodology (Fig. 3) to discuss homology relationships. We also address the question as to whether these homologies are functionally similar (e.g., regulate similar behaviors across vertebrates).

Medial amygdala (meAMY)

Mammals.

Across vertebrates, the amygdalar complex is perhaps the most challenging forebrain area to homologize. There is a general consensus that the amygdalar complex is derived from both pallial (roof) and subpallial regions during development (Puelles et al., 2000), and that it is intimately involved with sensory integration (LeDoux, 1995; Moreno and González, 2007a). Developmentally, the meAMY is derived from the subpallium (specifically the entopeduncular region), along with the BNST (Moreno

TABLE 2.

Conserved Neurochemical Patterns in the Telencephalon Support Brain Region Homologies Across Vertebrates

	TH	SP	NA/DBH	ENK	NADPHd	ChAT	SOM	NPY	GABA	CR
blAMY										
Mammals	Δ	Δ	Δ	+/Δ	+/Δ	+/Δ	+/Δ	+/Δ	+	+/Δ
Birds	Δ	-	Δ	-	+/Δ	+/Δ	+/Δ	+	+	n.a.
Reptiles	Δ	-	Δ	+/Δ	+/Δ	+/Δ	+/Δ	+/Δ	+	+
Amphibians	Δ	Δ	Δ	-	+/Δ	Δ	-	Δ	+	-
Teleosts	Δ	-	Δ	Δ	+	-	Δ	Δ	+	Δ
BNST										
Mammals	Δ	Δ	Δ	+/Δ	+/Δ	+/Δ	+/Δ	+/Δ	+	+/Δ
Birds	Δ	+/Δ	Δ	+/Δ	+/Δ	+	+/Δ	+/Δ	+	+/Δ
Reptiles	Δ	-	Δ	+/Δ	+/Δ	+/Δ	+/Δ	+/Δ	+	n.a.
Amphibians	Δ	Δ	Δ	Δ	+/Δ	+/Δ	Δ	Δ	+	-
Teleosts	+/Δ	Δ	Δ	Δ	+	-	+/Δ	Δ	+	+/Δ
LS										
Mammals	Δ	+/Δ	Δ	+/Δ	Δ	+/Δ	+/Δ	+/Δ	+	+/Δ
Birds	Δ	+/Δ	Δ	+/Δ	Δ	+/Δ	Δ	Δ	+	+/Δ
Reptiles	Δ	Δ	Δ	+/Δ	+/Δ	+/Δ	+/Δ	Δ	+	+/Δ
Amphibians	Δ	Δ	-	Δ	Δ	Δ	Δ	Δ	+	-
Teleosts	Δ	+/Δ	Δ	Δ	+	+	+/Δ	+/Δ	+	+/Δ
meAMY										
Mammals	Δ	Δ	Δ	+/Δ	+/Δ	-	+/Δ	+/Δ	+	+/Δ
Birds	+/Δ	-	Δ	+/Δ	+/Δ	Δ	+/Δ	+/Δ	+	n.a.
Reptiles	Δ	Δ	Δ	+/Δ	+/Δ	-	+/Δ	Δ	+	n.a.
Amphibians	Δ	+/Δ	-	+/Δ	+/Δ	+/Δ	+/Δ	Δ	+	-
Teleosts	+/Δ	Δ	Δ	Δ	+	-	+/Δ	Δ	+	+/Δ
NAcc										
Mammals	Δ	+/Δ	Δ	+/Δ	+/Δ	+	+/Δ	+/Δ	+	Δ
Birds	Δ	+/Δ	Δ	+/Δ	+/Δ	+	+/Δ	+	+	+
Reptiles	Δ	+/Δ	Δ	+/Δ	+/Δ	+/Δ	+/Δ	+/Δ	+	Δ
Amphibians	Δ	Δ	Δ	Δ	+	Δ	Δ	Δ	-	+
Teleosts	+/Δ	+	Δ	Δ	+	-	Δ	+/Δ	+	+
STR										
Mammals	Δ	+/Δ	Δ	+/Δ	+/Δ	+	+/Δ	+/Δ	+	Δ
Birds	Δ	+/Δ	Δ	+/Δ	+/Δ	+	+/Δ	+	+	+
Reptiles	Δ	+/Δ	Δ	+/Δ	+/Δ	+/Δ	+/Δ	+	+	Δ
Amphibians	Δ	+/Δ	Δ	+/Δ	+/Δ	+/Δ	+/Δ	Δ	-	-
Teleosts	Δ	+/Δ	Δ	Δ	+	+/Δ	+/Δ	Δ	+	+
VP										
Mammals	Δ	+/Δ	Δ	+/Δ	+/Δ	+	+/Δ	+/Δ	+	-
Birds	Δ	+/Δ	Δ	+/Δ	+/Δ	+	Δ	+	-	Δ
Reptiles	Δ	+/Δ	Δ	+/Δ	+/Δ	+/Δ	Δ	+/Δ	+	+/Δ
Amphibians	Δ	Δ	Δ	Δ	Δ	+/Δ	Δ	Δ	-	-
Teleosts	Homology unknown									

Cell bodies (+); Fibers (Δ); Absent (-); Data not available (n.a.).

blAMY: basolateral amygdala; BNST: bed nucleus of the stria terminalis; ChAT: choline acetyltransferase; CR: calretinin; DBH: dopamine beta hydroxylase; ENK: enkephalin; LS: lateral septum; meAMY: medial amygdala; NA: noradrenaline; NAcc: nucleus accumbens; NADPHd: nicotinamide adenine dinucleotide phosphate diaphorase histochemistry; NPY: neuropeptide Y; SOM: somatostatin; SP: substance P; STR: striatum; TH: tyrosine hydroxylase; VP: ventral pallidum.

References: Mammals: Armstrong et al., 1983; Khachaturian et al., 1983; Hökfelt et al., 1984; Johansson et al., 1984; McDonald, 1984; Ottersen and Storm-Mathisen, 1984; Shults et al., 1984; Wainer et al., 1984; Nakagawa et al., 1985; Onteniente et al., 1986; Resibois and Rogers, 1992; Sun and Cassell, 1993; Gotti et al., 2005; Flames et al., 2007; Birds: Takatsuki et al., 1981; Domenici et al., 1988; Anderson and Reiner, 1990a; Medina and Reiner, 1994; Veenman and Reiner, 1994; Moons et al., 1995; Atoji et al., 2001; den Boer-Visser and Dubbeldam, 2002; Roberts et al., 2002; Goodson et al., 2004; Husband and Shimizu, 2011; Reptiles: Brauth, 1984; Weindl et al., 1984; Bennis et al., 1991a,b; Medina et al., 1993; Smeets, 1994; Smeets et al., 1997; Bennis et al., 2001; O'Connell et al., 2011d; Amphibians: Franzoni and Morino, 1989; Gonzalez et al., 1993; Gonzalez and Smeets, 1993; Marin et al., 1997b, 1998b; Teleosts: Roberts et al., 1989; Sas and Maler, 1991; Vecino et al., 1992; Weld and Maler, 1992; Perez et al., 2000; Castro et al., 2003; Giraldez-Perez et al., 2008; O'Connell et al., 2011b.

et al., 2009), which together form the extended amygdala. Developmental and transmitter gene markers for the subpallial medial ganglionic eminence, from which the meAMY is derived, include Dlx1/2, GAD67, Nkx2.1, Lhx6/7, whereas Shh is absent (Table 3; reviewed in Moreno et al., 2009). Inputs from the vomeronasal system are processed by the mammalian medial and cortical posteromedial amygdala via massive unidirectional projections (Scalia and Winans, 1975; Swanson and Petrovich, 1998) (Fig. 3). The meAMY also receives input from

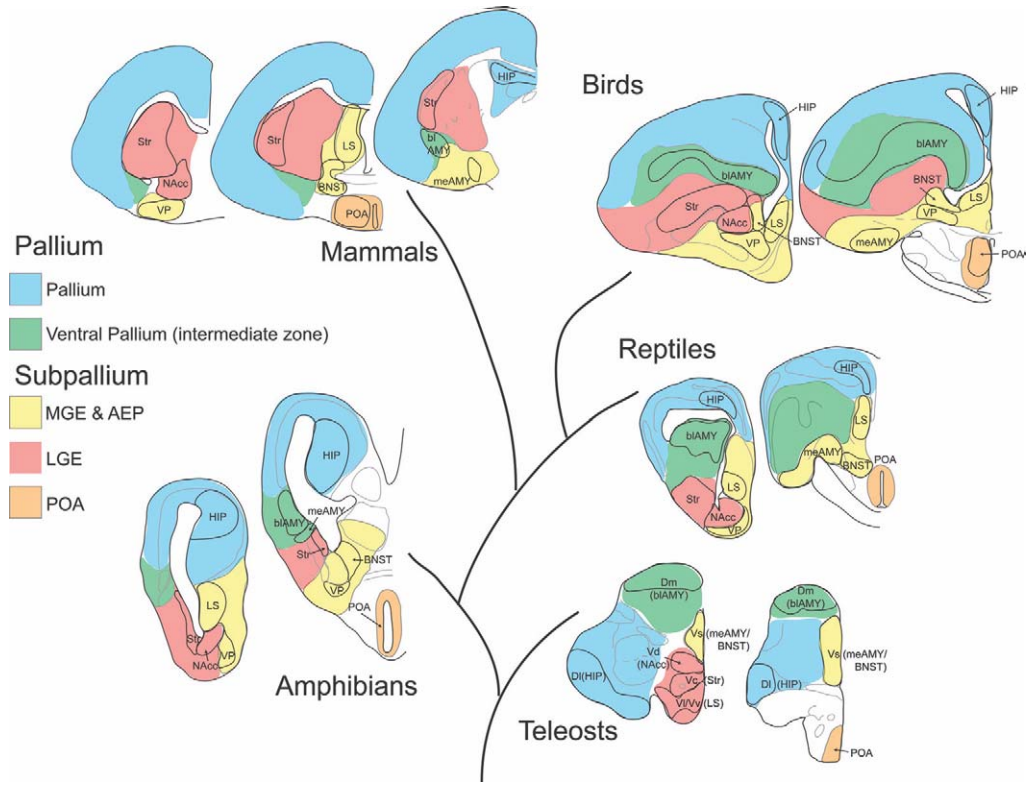

Figure 4. Developmental evidence for neural homologies across vertebrates. Homeobox genes specifying pallial and subpallial telencephalon regions are shown in different colors on a schematic of transverse sections. The pallium is shaded in blue, the ventral pallium (intermediate zone) is shaded in green, medial ganglion eminence (MGE) and peduncular region (AEP) is shaded in yellow, lateral ganglionic eminence (LGE) is shaded in red, and the POA is shaded in orange. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the main olfactory bulb (Kang et al., 2009). The meAMY, in turn, projects mainly to the hypothalamus through the stria terminalis to modulate reproductive, aggressive, and parental behaviors (Canteras et al., 1994; Risold et al., 1997; Swanson and Petrovich, 1998; Sheehan et al., 2001; Choi et al., 2005). Specifically, the meAMY seems to be crucial for social odor recognition in hamsters (reviewed in Petrulis, 2009). In addition to many other neurochemical markers (Table 2), the meAMY is rich with steroid hormone receptors (Cooke et al., 2003), a defining characteristic of nodes in the social behavior network.

Birds

The homology of the meAMY in birds is complicated by the lack of a vomeronasal organ, similar to the situation in teleosts discussed below (Martinez-Garcia et al., 2006). However, based on olfactory input and efferent projections, the nucleus taeniae region has been proposed to be the homolog of the mammalian meAMY (Reiner and Karten, 1985; Yamamoto et al., 2005; Martinez-Garcia et al., 2006). This region projects to the VMH through the putative avian stria terminalis (Fig. 3) (Zeier and Karten, 1971; Reiner and Karten, 1985; Cheng et al., 1999; Reiner et al., 2004), and is subpallial in origin (Fig. 4; see Table 3 for developmental markers), similar to the situation in mammals (Yamamoto et al., 2005). The putative avian meAMY contains sex steroid hormone receptors (Gahr, 2001) and is neurochemically very similar to the mammalian meAMY except that the avian meAMY contains choline acetyltransferase-positive fibers and lacks substance P fibers (Table 3). This region in birds is also functionally similar to the mammalian meAMY. When the nucleus taeniae is electrically stimulated in chicken, the animals become more aggressive (Putkonen, 1966). In a choice paradigm, female zebra finch (*Taeniopygia guttata*) never choose males with lesions to the nucleus taeniae, as they display less sexually motivated behavior (Ikebuchi et al., 2009).

Reptiles

A region similar to the mammalian meAMY has been reported in reptiles based on hodological evidence (Table 2) (Lanuza and Halpern, 1998) in species that have a vomeronasal system (as some reptiles do not, e.g., turtles and crocodilians), as well as neurochemical and developmental evidence. Reptilian vomeronasal information is

TABLE 3.

Conserved Expression Patterns of Developmental or Transmitter Genes Support Brain Region Homologies in the Telencephalon Across Vertebrates

	Emx1/2	Pax6	Tbr1	Dlx1/2	Nkx2.1/2.2	GAD67	Lhx6/7	Shh
Pallium (HIP)								
Mammals	+	+	+	–	–	–	–	–
Birds	+	+	+	–	–	n.a.	n.a.	–
Reptiles	+	+	+	–	–	–	n.a.	n.a.
Amphibians	+	+	+	–	–	–	–	n.a.
Teleosts	n.a.	?	n.a.	–	–	–	–	–
Ventral pallium or intermediate zone (blAMY)								
Mammals	–	+	+	–	–	–	–	–
Birds	–	+	+	–	–	n.a.	n.a.	–
Reptiles	–	+	+	–	–	–	n.a.	n.a.
Amphibians	–	+	+	–	–	–	+	n.a.
Teleosts	n.a.	?	n.a.	–	–	–	–	–
Lateral ganglionic eminence (STR)								
Mammals	–	+	–	+	–	+	–	–
Birds	–	+	–	+	–	n.a.	n.a.	–
Reptiles	–	+	–	+	–	+	n.a.	n.a.
Amphibians	–	+	–	+	–	+	–	n.a.
Teleosts	n.a.	+	n.a.	+	– (Vl) + (Vv)	+	+	–
Medial ganglionic eminence (BNST/meAMY)								
Mammals	–	–	–	+	+	+	+	–
Birds	–	–	–	+	+	n.a.	+	–
Reptiles	–	–	–	+	+	+	n.a.	n.a.
Amphibians	–	–	–	+	+	+	+	n.a.
Teleosts	n.a.	–	n.a.	+	+	+	+	–
POA								
Mammals	–	–	–	+	+	+	–	+
Birds	–	–	–	+	+	n.a.	+	+
Reptiles	n.a.	–	–	n.a.	+	+	n.a.	n.a.
Amphibians	–	–	–	+	+	+	+	n.a.
Teleosts	n.a.	–	n.a.	+	+	+	+	+

Present: (+); Absent: (–); Data not available: (n.a.); Uncertain expression pattern: (?).

blAMY: basolateral amygdala; BNST: bed nucleus of the stria terminalis; HIP: hippocampus; meAMY: medial amygdala; POA: preoptic area; STR: striatum.

References: Mammals: Stoykova and Gruss, 1994; Gao and Moore, 1996; Fernandez et al., 1998; Eisenstat et al., 1999; Puelles et al., 2000; Tamamaki et al., 2003; Flames et al., 2007; Garcia-Lopez et al., 2008; Bird: Fernandez et al., 1998; Puelles et al., 2000; Yamamoto et al., 2005; Bardet et al., 2010; Reptile: Fernandez et al., 1998; Metin et al., 2007; Moreno et al., 2010; Amphibians: Brox et al., 2003, 2004; Moreno et al., 2004; Moreno and Gonzalez, 2007c, Moreno et al., 2008; Teleosts: Mueller et al., 2008; Alunni et al., 2004; Menuet et al., 2007; Mueller and Guo, 2009.

relayed to the pallial nucleus sphericus and subpallial medial amygdala (Lanuza et al., 1998), and these regions send projections through the stria terminalis to the hypothalamus, as is characteristic of the mammalian meAMY (Lanuza et al., 1997; Martinez-Marcos et al., 1999). This reptilian homolog is neurochemically similar to the mammalian meAMY (Table 3) and contains sex steroid hormone receptors (Young et al., 1994; O'Connell et al., 2011c). Additionally, neurochemical evidence supports the subpallial origin of the reptilian meAMY (Table 3) (Moreno et al., 2010). Several functional studies into the role of the reptilian meAMY suggest that this region is also functionally similar to the mammalian meAMY and plays a conserved role in mediating aggression and courtship behavior. Lesions of the nucleus sphericus increase courtship behavior in male red-sided garter snakes (*Thamnophis sirtalis parietalis*; Krohmer and Crews, 1987) and decrease aggression in some lizards (Tarr, 1977). However, in anole lizards (*Anolis carolinensis*), lesions of the medial amygdala decrease both aggressive and courtship displays (Greenberg, 1984).

Amphibians

Vomeronasal information in amphibians is processed by a region in the subpallial telencephalon, the medial amygdala, which has been proposed to be homologous to the mammalian meAMY (Moreno and González 2003, 2005; Moreno et al., 2005) based on hodological, developmental, and neurochemical evidence, although this region is thought to be the cortical amygdala by Laberge et al. (2006). The anuran meAMY also sends massive projections to the VMH (Moreno and González, 2003) and is developmentally derived from the subpallium, but also contains some cells originating from the ventral telencephalon (Moreno and González, 2007b). To our knowledge no lesion or stimulation studies have been done

specifically in this nucleus. However, female salamanders exposed to male pheromones show increased c-fos expression in this region (Laberge et al., 2008), suggesting a conserved role for this region in processing social olfactory information.

Teleosts

Describing homologies between the teleost telencephalon and other vertebrates is especially difficult due to the eversion, rather than invagination, of the neural tube during development (Wullimann and Mueller, 2004; Yamamoto et al., 2007; Braford, 2009; Nieuwenhuys, 2011). However, we are now gaining insight into potential teleost homologies to tetrapod brains from recent neurochemical, hodology, and developmental evidence instead of relying on topography alone (Wullimann and Mueller, 2004).

Similar to the situation in birds (and some reptiles), teleosts lack a vomeronasal organ, which has impeded progress on determining the homolog of the mammalian meAMY. However, developmental studies have pointed to the supracommissural part of the ventral pallium (Vs) as the putative homolog of the extended amygdala (the meAMY and BNST), as this region contains the gene markers Dlx2, Lhx7, Nkx2.1b (Table 3) (Alunni et al., 2004). Vs also projects to several hypothalamic regions (Folgueira et al., 2004a), including the anterior tuberal nucleus (putative homolog of the VMH, see subsection for discussion). This region may also be functionally similar to the mammalian meAMY, as stimulation of Vs increases aggression in male bluegill fish (*Lepomis macrochirus*; Demski and Knigge, 1971), and increases spawning in both male and female sockeye salmon (*Oncorhynchus nerka*; Satou et al., 1984).

Preoptic Area (POA)

Mammals

The POA is widely studied in the context of vertebrate social behavior and is important for regulating many social behaviors in males and females as well as other basic physiological functions such as energy homeostasis (Saper et al., 2001) and thermoregulation (Romanovsky, 2007). It is located in the hypothalamus conspicuously along the third ventricle and ventral to the anterior commissure. It mediates aggression, sexual behavior, and parental care (Table 1) (Heimer and Larsson, 1967; Malsbury, 1971; Hull and Dominguez, 2006; Lee and Brown, 2007), and contains tyrosine hydroxylase (TH)- and neuropeptide-expressing cells as well as sex steroid receptors (Wang et al., 1996; Rosen et al., 2007; Holmes et al., 2008). It is reciprocally connected to many limbic brain regions, especially those in the SBN (Conrad and Pfaff, 1975). The developmental profile of the POA is unique in the subpallium with expression of Shh, Nkx2.1/2.2 and no Gsh2, Lhx7, Olig2 (Table 3) (Flames et al., 2007).

The POA mediates sexual behavior, aggression, and parental care in mammals. Stimulation of the POA in male rats will increase sexual behavior (van Dis and Larsson, 1970; Malsbury, 1971) and lesions will impair ejaculation in both male rodents and monkeys (Slimp et al., 1978; Powers et al., 1987), although chemoinvestigative behaviors are still intact (Powers et al., 1987). Similarly, c-fos immunoreactivity increases in the POA after a single mating trial in male hamsters (Kollack and Newman, 1992). The POA also regulates female sexual behavior, as lesions decrease vaginal marking in female hamsters (Malsbury et al., 1977). Parental care is also mediated by the POA in rodents, as lesions disrupt parental behavior in both males and females (Jacobson et al., 1980; Miceli and Malsbury, 1982; Rosenblatt et al., 1996; Lee and Brown, 2007), and c-fos induction increases with parental care in males (Lee and Brown, 2007). Finally, the POA also mediates aggression, as lesion of the POA in male rats decreases male–male aggression (Albert et al., 1986).

Birds

The avian POA is similar to the mammalian POA in neurochemistry, hodology, development, and topography. The POA is positioned in the hypothalamus along the third ventricle in the subpallium and contains dopamine- and neuropeptide-producing cells (Viglietti-Panzica, 1986; Bailhache and Balthazart, 1993) as well as sex steroid receptors (Balthazart et al., 1998b; Gahr, 2001). The avian POA is also sexually dimorphic in volume (Panzica et al., 1987), and is highly interconnected with the amygdaloid complex and hypothalamus (Berk and Butler, 1981). The development of the POA in the subpallium of birds is similar to mammals (Abellan and Medina, 2008). Furthermore, this region is also functionally similar to the mammalian POA, as the avian POA plays a conserved role in aggression and parental care (Table 1). Electrical stimulation of the POA increases aggression (Akerman et al., 1960) in males and immediate early gene labeling in the POA is decreased in nonmaternal female quail (Ruscio and Adkins-Regan, 2004). Chemical lesions of the POA also disrupt parental care in ring doves (*Streptopelia risoria*; Slawski and Buntin, 1995).

The POA also regulates copulatory behavior in male birds (Balthazart and Surlemont, 1990), similar to mammals. Implants of testosterone directly into the POA of castrated male Japanese quail (*Coturnix japonica*) will fully reinstate male sexual behavior (Riters et al., 1998), although aromatization of testosterone into estrogens is also necessary for the full behavioral rescue (Watson and Adkins-Regan, 1989). However, different subregions of the avian POA seem to differentially regulate appetitive

and consummatory behavior in male quail as shown by lesion and immediate early gene studies (Balthazart et al., 1998a; Taziaux et al., 2006). Interestingly, c-fos immunoreactivity is markedly decreased in the region when olfactory cues are blocked (Taziaux et al., 2008), suggesting not only that sensory integration is important for neuronal activation in the POA, but also that olfactory information plays an important role in avian behavior. In male zebra finch, the dopaminergic cells within the POA exhibit increased c-fos induction after sexual encounters, but not after agonistic encounters (Bharati and Goodson, 2006), suggesting that dopamine plays an important role in regulating male sexual behavior, similar to mammals (Hull and Dominguez, 2006).

Reptiles

The reptilian POA is also conspicuously located in the hypothalamus along the rostral part of the third ventricle and is similar to the mammalian POA in neurochemistry and hodology. The POA contains sex steroid hormone receptors (Young et al., 1994; O'Connell et al., 2011c) and is a central integration point for telencephalic regions and the hypothalamus (Russchen and Jonker, 1988; Smeets et al., 1995). This region is also functionally similar to the mammalian POA, as implants into the POA of either testosterone or DHT in castrated male lizards increase sexual behavior (Morgantaler and Crews, 1978; Rozendaal and Crews, 1989), while lesions of the POA decrease courtship behavior (Kingston and Crews, 1994). In addition to its conserved role in regulating male sexual behavior, the POA in reptiles also plays a role in aggression, as electrical stimulation will increase aggression in both male and female iguanas (*Iguana iguana*; Distel, 1978).

Amphibians

The amphibian POA is similar to the mammalian POA in neurochemistry, hodology, and topography, as this hypothalamic region lies along the third ventricle and contains sex steroid hormone receptors (Kelley et al., 1975; Roy et al., 1986; di Meglio et al., 1987; Chakraborty and Burmeister, 2010; O'Connell et al., 2011a). The amphibian POA has several subregions based on cell size (Northcutt and Kicliter, 1980), although the homology of these subpopulations to the mammalian POA is uncertain. Functionally, the POA plays a conserved role in the regulation of sexual behavior in both male and female amphibians. Lesions of the POA in male frogs (*Rana pipiens*) decrease calling behavior, while testosterone implants into the POA of castrated males increase calling behavior (Wada and Gorbman, 1977a,b). In female toads, POA lesions decrease phonotactic responses, whereas implantation of prostaglandin into the POA increases phonotaxis (Schmidt, 1985, 1989). In female salamanders (*Plethodon shermani*), which rely on pheromone information from the male for mate choice (Houck et al., 1998), c-fos expression is induced in the POA when exposed to male pheromones (Laberge et al., 2008).

Teleosts

The teleost POA also lies in the hypothalamus along the third ventricle, dorsal to the optic tract, and is similar to the mammalian POA in neurochemistry and hodology. This conserved region contains sex steroid hormone receptors (Forlano et al., 2005, 2010; Munchrath and Hofmann, 2010), and receives fibers from and projects to the telencephalon and hypothalamus (Folgueira et al., 2004b). There are three subdivisions of the teleost POA based on cell size: parvocellular, magnocellular, and gigantocellular (Braford and Northcutt, 1983). The gigantocellular and magnocellular cell groups are considered homologous to the supraoptic nucleus of the mammalian POA, while the parvocellular cell group is the putative homolog of the paraventricular nucleus of the mammalian POA (Moore and Lowry, 1998). This region is also functionally similar to the mammalian POA (Table 1), as the teleost POA also plays an important role in the regulation of sexual behavior, aggression, and parental care, providing strong evidence that its role in mediating social behavior is highly conserved throughout vertebrate evolution. Electrical stimulation of the POA in males increases courtship and aggression (Demski and Knigge, 1971; Satou et al., 1984), while lesions decrease spawning behavior (Macey et al., 1974). Interestingly, stimulation of the POA in electric fish (*Eigenmannia virescens*) evokes (electrical) courtship signals (Wong, 2000), presumably through a connection between the POA and the prepacemaker nucleus that regulates electric organ discharge. In females, stimulation of the POA also increases spawning behavior (Satou et al., 1984). Similar to mammals, the teleost POA also regulates parental care as stimulation of the POA also increases nesting in male bluegill sunfish (Demski and Knigge, 1971).

Anterior hypothalamus (AH)

Mammals

The AH is perhaps one of the least understood regions of the SBN. The mammalian AH lies caudal to the POA along the third ventricle and is sensitive to sex steroids (Hayden-Hixon and Ferris, 1991). It appears to play an important role in aggression, especially in the context of neuropeptide modulation, as injections of the AVP V1a receptor antagonist into the AH of hamsters will inhibit aggression (Ferris and Potegal, 1988). In addition to modulating aggression in males, lesions of the AH in female rats facilitates maternal behavior (Bridges et al., 1999),

suggesting a role in regulating parental care as well. Sexual behavior in both males and females seems to also impinge on the AH, as lesions of the AH in female cats inhibit receptivity and prevents pregnant cats from progressing to parturition (Fisher and Ingram, 1936).

Birds

In birds the AH is located ventral to the POA and is similar to the mammalian AH in neurochemistry, as this region is positive for sex steroid hormone receptors (Balthazart et al., 1998b; Gahr, 2001). Functionally, there is evidence that the AH plays a role in both aggression and sexual behavior, similar to the mammalian AH. In male song sparrows (*Melospiza melodia*), c-fos immunoreactivity increases in the AH in response to territorial intrusion (Goodson et al., 2005), similar to the role of AH in resident intruder paradigms in hamsters. c-fos induction also increases in the AH of male European starlings (*Sturnus vulgaris*) when singing courtship songs compared to noncourtship songs (Heimovics and Riters, 2006).

Reptiles and amphibians

The AH is rarely discussed in reptiles and amphibians. In both lineages it is located caudal to the POA along the third ventricle, but rostral to the VMH, and contains sex steroid hormone receptors (Young et al., 1994; Beck and Wade, 2009). There have been many lesion studies that have included the AH that support its role in sexual behavior and aggression (Morgantaler and Crews, 1978); however, these are usually combined lesions of both POA and AH, making it difficult to dissect the functional mechanisms of the AH alone.

Teleosts

Due to its topographical location as the transition zone between the POA and ventral hypothalamic region, the ventral tuberal region is thought to be homologous to the mammalian AH (Goodson and Bass, 2000; Goodson, 2005). This region contains sex steroid hormone receptors (Forlano et al., 2005, 2010; Munchrath and Hofmann, 2010) and is connected to many other hypothalamic nuclei as well as the proposed meAMY homolog (Folguiera et al., 2004a,b). Unfortunately, no functional (lesion or stimulation) studies have exclusively manipulated this region, although POA-AH neuropeptide manipulations have suggested a role for modulating reproductive vocalizations in the plainfin midshipman (*Porichthys notatus*; Goodson and Bass, 2000).

Ventromedial hypothalamus (VMH)

Mammals

The VMH is topographically located in the caudal hypothalamus along the third ventricle, is rich with sex steroid receptors (Zhang et al., 2002; Lonstein and Blaustein, 2004; Holmes et al., 2008), and is highly interconnected with the amygdala and other regions of the hypothalamus (Saper et al., 1976). The best understood function of the VMH in social behavior is its central role in regulating female receptivity. Lesions will decrease receptivity in females (Malbury et al., 1977; Mathews and Edwards, 1977; Pfaff and Sukuma, 1979; Leedy and Hart, 1985; Robarts and Baum, 2007), while stimulation will facilitate lordosis (Pfaff and Sakuma, 1979). The VMH also regulates nonsexual behavior, as lesions will increase aggressive behavior and feeding (Panksepp et al., 1970; Malsbury et al., 1977). Lesions of the VMH also facilitate maternal behavior (Bridges et al., 1999; Sheehan et al., 2001), suggesting that under normal conditions this region inhibits parental care. The VMH also contributes to male-typical behavior, as c-fos induction increases in male hamsters after both sexual and aggressive encounters (Kollack-Walker and Newman, 1995).

Birds

The avian VMH is located in the ventrocaudal hypothalamus, contains sex steroid receptors (Balthazart et al., 1998b; Gahr, 2001), and is highly interconnected with other regions of the hypothalamus and lateral septum (Balthazart and Absil, 1997; Atoji and Wild, 2004). Lesion and stimulation studies, as well as immediate early gene activation, suggest that this region is also functionally similar to the mammalian VMH. In females, induction of c-fos increases in the avian VMH with sexual behavior in Japanese quail (Meddle et al., 1999), and lesions prevent egg incubation behavior (Youngren et al., 1989). Furthermore, the VMH seems to play a role in male sexual behavior, as neural activity in the VMH increases when male European starlings sing courtship songs compared to noncourtship songs (Heimovics and Riters, 2006). Finally, the avian VMH plays a role in feeding behavior (Kuenzel, 1974), similar to mammals.

Reptiles

The reptilian VMH homolog is topographically located along the third ventricle in the ventrocaudal hypothalamus and contains sex steroid hormone receptors (Young et al., 1994; O'Connell et al., 2011c). This region is also highly interconnected with the hypothalamus and amygdaloid nuclei (Bruce and Neary, 1995a,b), and appears to also be functionally similar to the mammalian VMH, as lesions decrease receptivity in female dessert grassland lizards (*Cnemidophorus uniparens*; Kendrick et al., 1995).

Amphibians

The VMH in amphibians is located in the ventrocaudal hypothalamus along the third ventricle and ventral to

the putative ventral tegmental area (VTA) homolog. It contains sex steroid hormone receptors (Davis and Moore, 1996; Chakraborty and Burmeister, 2010; O'Connell et al., 2011a) and has a hodological profile similar to the mammalian VMH (Allison and Wilczynski, 1991). Given how much research has focused on the neural basis of female mate choice in anurans, it is surprising that no functional studies have been done to describe its role in female receptivity. However, female salamanders exposed to male pheromones have increased c-fos induction in the VMH (Laberge et al., 2008), suggesting that, at least in non-anuran amphibians, this region plays a role in female receptivity as well.

Teleosts

The anterior tuberal nucleus is the putative teleostean homolog of the mammalian VMH (Forlano et al., 2005; Goodson, 2005; Forlano and Bass, 2011). It is located in the ventrocaudal part of the hypothalamus, contains sex steroid hormone receptors, and has a similar hodological profile (Folgueira et al., 2004a,b) in that it connects to the POA as well as several regions of the telencephalon. However, this region is regarded by some as more of an octavolateral structure (Yamamoto and Ito, 2005; Giassi et al., 2007). When stimulated, this region induces vocalizations in male midshipman fish (Goodson and Bass, 2000); however, more lesion/stimulation studies in female teleosts need to be conducted within this brain region to further establish its functional similarity to the mammalian VMH.

Periaqueductal gray/central gray (PAG/CG)

Mammals

The PAG plays an important role in social behavior in both males and females, including reproduction, aggression, and especially in the context of vocal communication (see below). It is highly interconnected with the hypothalamus and telencephalon (Eberhart et al., 1985), and contains sex steroid receptors (Murphy et al., 1999). The PAG is activated after sexual experience, but not by aggressive encounters, in male hamsters (Kollack-Walker and Newman, 1995). In lactating female rats the PAG appears to modulate nursing as well as aggression (Lonstein and Stern, 1997). Similarly, PAG stimulation elicits aggressive behavior in rats and cats (Mos et al., 1982; Bandler and Carrive, 1988). The PAG also plays a role in receptivity, as lesions lead to deficits in lordosis (Floody and O'Donohue, 1980). Finally, the PAG has a distinctive role in vocalizations, specifically call initiation (Jürgens, 2002). The PAG is active during speech in humans (Schulz et al., 2005), and lesions of the PAG can lead to mutism (Esposito et al., 1999).

Birds

The putative avian homolog of the mammalian PAG is the dorsomedial intercollicular nucleus and central gray, based on neurochemistry and connectivity (Dubbeldam and den Boer-Visser, 2002; Kingsbury et al., 2011). Androgen (Balthazart et al., 1998a) and estrogen (Gahr, 2001) receptors are present in this region, further supporting this node as part of the SBN, although the progesterone receptor has not been reported here. This region is also functionally similar to the mammalian PAG. In quail and zebra finch, males displaying courtship or sexual behavior exhibit activation of dopaminergic neurons in the PAG compared with noncopulating males (Charlier et al., 2005; Bharati and Goodson, 2006), suggesting a conserved role in mediating sexual behavior. The PAG appears to play an important role in birdsong, as singing male zebra finches show greater activation of dopaminergic PAG neurons than silent individuals (Lynch et al., 2008; Goodson et al., 2009). Further, this region is also required for female courtship vocalizations in ring doves (Cohen and Cheng, 1981).

Reptiles

The identification of the PAG homolog in the reptilian midbrain is based on the presence of sex steroid hormone receptors, hodology, and topography (ten Donkelaar, 1976a,b; Morrell et al., 1979). However, to our knowledge no functional studies have investigated the role of this region in regulating reptilian social behavior.

Amphibians

The PAG in amphibians also resides in the midbrain and contains sex steroid hormone receptors (O'Connell et al., 2011a). Furthermore, this region has a connectivity profile similar to the mammalian PAG/CG (Sánchez-Camacho et al., 2001). In anurans, stimulation of this region elicits vocalizations (Schmidt, 1966), whereas lesioned animals cease calling (Schmidt, 1971), suggesting this region is also functionally similar to the mammalian PAG.

Teleosts

Much of the work on the role of the PAG in regulating behavior in teleosts comes from the midshipman fish, which relies on sound production for social communication (reviewed in Bass, 2008). The PAG is topographically located near the torus semicircularis (inferior colliculus homolog; Bass et al., 2005), displays a connectivity profile very similar to the mammalian PAG (Goodson and Bass, 2002; Kittelberger et al., 2006), and contains sex

steroid hormone receptors (Forlano et al., 2005, 2010; Munchrath and Hofmann, 2010). It also is functionally similar to the mammalian PAG with a role in call initiation and duration (Kittelberger et al., 2006).

INTERSECTION OF THE SBN AND REWARD SYSTEMS

It has become clear that the SBN and reward system are functionally linked, as both circuits play fundamental roles in the regulation of behavior (see discussion above). Additionally, these networks are widely interconnected in each vertebrate class (Fig. 3), suggesting that information can be readily transferred between these two systems. Since we propose here that both circuits should be considered together as the SDM network, it is important to discuss to what extent they are also structurally integrated. Notably, the SBN and mesolimbic reward system share two nodes: the LS and BNST. Both regions play a role in social behavior as well as reward processing, and they are thus well positioned to serve as relay stations that mediate information about the salience of a social stimulus into an adaptive behavioral output, such as showing aggression toward an intruder or sexual behavior to a potential mate. These regions appear to be involved in the regulation of many social and, more generally, reward-related behaviors (see below for discussion). However, it is important to note that just because they are commonly considered to be part of either circuit there is no reason to believe that the LS and BNST are the only nodes engaged in information exchange between the two systems, as both the SBN and reward system are highly interconnected (Fig. 3) and may mediate related aspects of many of the same social actions. A more careful dissociation of appetitive and consummatory aspects of social behavior especially in studies of nonmammalian vertebrates will greatly improve our understanding of the interrelationships between the various SBN and reward system nodes.

Lateral septum (LS)

Mammals

The mammalian LS is located medial to the lateral ventricles and its connectivity is characterized by a massive unidirectional input from the hippocampus (HIP) (Swanson and Cowan, 1977) and projections to the hypothalamus (Meibach and Siegel, 1977; Swanson and Cowan, 1979) and midbrain (Risold and Swanson, 1997). The LS also receives many projections from the hypothalamus, including the AH, POA, and VMH (Staiger and Nürnberger, 1989). There are also dopaminergic projections from the VTA to the LS (Swanson, 1982) and stimulation of LS leads to increased firing of dopaminergic neurons in the VTA, potentially modulating goal-directed behaviors (Maeda and Mogenson, 1981).

There is behavioral evidence that the LS mediates social behavior as well as the evaluation of stimulus novelty. In male rats, lesions of the LS facilitate male sexual behavior while inhibiting female sexual behavior (Kondo et al., 1990). LS lesions also lead to a deficit in resident aggression in territorial intruder tests (Blanchard et al., 1977). Finally, the role of LS in social recognition comes from work with neuropeptides. In monogamous male voles, septal AVP is necessary and sufficient for pair-bond behavior and also increases paternal behavior (Wang et al., 1994; Liu et al., 2001). Infusions of an AVP antagonist or antisense oligonucleotides to the AVP V1a receptor decrease exploration of a novel environment and impair social recognition (Landgraf et al., 1995; Liebsch et al., 1996), whereas infusions of AVP into the LS facilitates social memory (Dantzer et al., 1988). Furthermore, expression of the V1a receptor solely in the LS rescues social recognition in V1a receptor knockout mice (Bielsky et al., 2005).

Birds

The avian LS is also located medial to the lateral ventricles and shares the connectivity profile of the mammalian LS in unidirectional input from the HIP and projections to the hypothalamus and midbrain (Krayniak and Siegel, 1978a,b; Atoji and Wild, 2004). There are dense dopaminergic fibers in this region (Bailhache and Balthazart, 1993), similar to mammals. This region is neurochemically very similar to the mammalian LS (Caffe et al., 1987; Montagnese et al., 2004; discussed in detail in Goodson et al., 2004).

The avian LS homolog is also functionally similar to the LS in mammals, as bilateral lesions of the LS in pigeons (*Columba livia*) decrease resident aggression toward an intruder (Ramirez et al., 1988). The avian LS also plays a conserved role in reproduction, as both appetitive and consummatory sexual behavior in male quail increase c-fos induction in this region (Taziaux et al., 2006). The role of the LS in avian social behavior also seems to vary with social organization. Lesions of the septal region in field sparrows (*Spizella pusilla*; a territorial species) increase aggression, while both courtship and aggression are reduced by septal lesions in gregarious male zebra finches (Goodson and Adkins-Regan, 1999). The modulation of aggression in the LS may impinge on neuropeptide receptors as infusion of AVT into the septum of male zebra finches increases aggression, but has no effect on courtship displays; and infusions of an AVT antagonist decreases aggression (Goodson and Adkins-Regan, 1999). Similarly, territorial intrusions elicit immediate early gene activity in the LS in male song sparrows (*Melospiza melodia*; Goodson et al., 2005).

Reptiles

The reptilian LS shares the mammalian LS trait of unidirectional input from the HIP (Font et al., 1997), contains sex steroid hormone receptors (Young et al., 1994; Beck and Wade, 2009; O'Connell et al., 2011c), and is located medial to the lateral ventricles. Importantly, in reptiles the LS also receives input from the nucleus accumbens (NAcc) and dopaminergic projections from the VTA (Font et al., 1997) and sends massive projections to the hypothalamus, providing a functional link between the reward system and the hypothalamic SBN. The LS in reptiles also seems to be functionally similar to the mammalian LS (Font et al., 1998), as it plays a role in mediating both courtship and aggressive behavior. Lesions of the septal region in the male red-sided garter snake increases courtship behavior (Krohmer and Crews, 1987). In male anoles, observing aggressive encounters is associated with higher activity in the LS, indicating that social experience can modulate the activity of the LS of this region (Yang and Wilczynski, 2007).

Amphibians

The amphibian LS is located medial to the lateral ventricles and has been identified by neurochemical means where cholinergic neurons are abundant in this region and sparse in other regions of the telencephalon (Marin et al., 1997b; Sánchez-Camacho et al., 2003). Furthermore, there are TH-immunoreactive fiber nests in this region (González et al., 1993; González and Smeets, 1994), a feature that is conserved across vertebrates. This region also receives projections from the HIP and projects widely to the hypothalamus (Endepols et al., 2005), indicative of the mammalian LS. Unfortunately, there is little functional evidence for the role of the lateral septum, in particular in regulating social behavior in amphibians. Lesions of the entire septal region in female gray tree frogs lead to a deficit in phonotaxis response (Walkowiak et al., 1999). However, steroid hormone receptors have been indentified in this region in frogs and newts (Davis and Moore, 1998; Chakraborty and Burmeister, 2010; O'Connell et al., 2011a), suggesting that sex steroid hormones could potentially modulate behavior through action in this nucleus.

Teleosts

The ventral (Vv) and lateral (Vl) parts of the ventral teleost telencephalon are putatively homologous to the septal formation in mammals based on neurochemical and hodological evidence (Wullimann and Mueller, 2004). Telencephalic cholinergic neurons have only been detected in Vv and Vl (Ekström, 1987; Brantley and Bass, 1988; Pérez et al., 2000), and these regions also contain androgen-, estrogen-, and progestin-receptors (Munchrath and Hofmann, 2010), similar to other vertebrates. Hodological evidence that supports this homology includes the projections of Vl to the pallial telencephalon (Murakami et al., 1983) and efferent projections of Vv to the hypothalamus (Rink and Wullimann, 2002). Importantly, Dl (the putative HIP homolog) projects to both Vl and Vv (Northcutt, 2006). Finally, Vv has strong bidirectional connections to the hypothalamus and POA (Wong, 1997). This region may also be functionally similar to the mammalian LS, as lesions of Vv decrease spawning in males while stimulation increases courtship behavior (Kyle and Peter, 1982), although part of the supracommissural region (Vs, putative extended amygdala homolog) was included in these lesions. Furthermore, Vv/Vl stimulation in females increases proceptive (digging) and spawning behavior (Satou et al., 1984). This suggests not only a conserved role for the LS in reproduction in both teleosts and tetrapods, but also that it plays an important role in both males and females.

Bed nucleus of the stria terminalis (BNST)

Mammals

The BNST is topographically located dorsolateral to the POA along the anterior commissure, and is developmentally derived from the subpallial medial ganglionic eminence (reviewed in Moreno et al., 2009). The BNST shows sexual dimorphism in volume (Allen and Gorski, 1990; Hines et al., 1992) and the number of neuropeptide-producing cells (De Vries and al-Shamma, 1990). This region also shares many connections with the amygdala and hypothalamus (Alheid and Heimer, 1988; Dong et al., 2001). It is well established that the BNST plays a role in aggression and reproductive behavior (Valcourt and Sachs, 1979; Shaikh et al., 1986; Powers et al., 1987). Male hamsters with lesions of the BNST will still mount a female, but will fail to display chemoinvestigatory behavior (Powers et al., 1987), although c-fos induction increases within the BNST after one mating trial (Kollack and Newman, 1992). Lesions of the BNST in rats increase the number of intromissions and thus ejaculation latency in both experienced and inexperienced males (Claro et al., 1995). Agonistic encounters also increase c-fos induction in the BNST of male hamsters (Kollack-Walker and Newman, 1995). Finally, the BNST also plays an important role in maternal retrieval behavior in rats (Numan and Numan, 1996).

While the basal ganglia and midbrain dopaminergic regions have long been implicated in mediating motivational behavior, much recent attention has been directed toward the BNST, as this region plays a role in the motivational aspects of drug abuse (Delfs et al., 2000) and can generate long-lasting excitatory effects on dopaminergic neurons in the VTA (Georges and Aston-Jones, 2001). A

functional lesion study of the BNST in rats induces depression in forced-swim tests suggesting that motivation or goal-directed behavior is impaired (Schulz and Canbeyli, 2000; Pezük et al., 2006, 2008). During pair-bond formation in monogamous female voles (*Microtus ochrogaster*), a process involving the mesolimbic reward system (Young and Wang, 2004), neuronal activity as measured by c-fos induction increases in the BNST (Curtis and Wang, 2003).

Birds

The avian BNST lies medial to the NAcc, positioned between the LS and ventral pallidum (VP), and its neurochemical, developmental, and hodological profile are very similar to the mammalian BNST (Fig. 3, Table 2). This region was first identified by Aste et al. (1998) as sexually dimorphic in aromatase- and AVT-positive neurons (Aste et al., 1998; Jurkevich et al., 1999), similar to mammals. Developmentally, the BNST of birds and mammals seems to have a similar subpallial origin, as indicated by expression of subpallial markers Lhx6 and Lhx7/8 (Abellan and Medina, 2008).

The avian BNST is also functionally similar to the mammalian BNST. In male Japanese quail the BNST is important for consummatory—but not appetitive—aspects of sexual behavior (Balthazart et al., 1998a). Neuronal activity, as measured by c-fos induction, is increased in the BNST after copulation, but not with appetitive behavior toward a female in male quail (Taziaux et al., 2006). However, this increase was not seen when the cloacal gland was anesthetized (Taziaux et al., 2008), suggesting that somatosensory information is important for this neuronal response to copulation. Further, the BNST also plays a role in reproduction in songbirds, as c-fos induction increases during courtship songs compared to noncourtship songs in male European starlings (Heimovics and Riters, 2006). Finally, the avian BNST may play a role in parental care, as immediate early gene labeling in the BNST is increased in brooding female quail (Ruscio and Adkins-Regan, 2004).

Reptiles

Neurochemical, developmental, and hodological evidence points to a region dorsolateral to the POA as the reptilian BNST homolog, consistent with its topographical location. Neurochemically, this region is similar to the mammalian BNST with the exception that no substance P fibers have been observed there (Table 2). The reptilian BNST also contains neuropeptide-producing cells (Smeets et al., 1990), similar to mammals and birds. This region also has a similar developmental origin to the mammalian BNST, marked by Tbr-1, Dlx, Nkx2.1, and GAD67 expression (Table 3; Moreno et al., 2010). The BNST shares connections with the amygdala and hypothalamus, as well as many regions of the reward system (Lanuza et al., 1997). Unfortunately, there are no reported functional studies regarding the role of the reptilian BNST on motivation or reproductive behavior to determine if these regions are functionally similar.

Amphibians

The BNST is situated dorsolateral to the POA, similar to other tetrapods, and homology is supported by developmental, neurochemical, and hodological evidence. This region is marked by Lhx1/5, Lhx 2/9, Lhx5, and Lhx7 expression during development (Moreno et al., 2004). This region also contains substance P and enkephalin fibers (Table 2) (Marin et al., 1998b) as well as a group of sexually dimorphic AVT neurons (González and Smeets, 1992; Moore et al., 2000), but only sparse neuropeptide Y immunoreactivity (Marin et al., 1998b). The amphibian BNST shares many similar hodological characteristics with the mammalian BNST, including reciprocal connections to the hypothalamus and HIP (Neary and Wilczynski, 1977; Allison and Wilczynski, 1991; Northcutt and Ronan, 1992; Neary, 1995).

Teleosts

Developmental, neurochemical, and hodological evidence point to the supracommissural part of the ventral pallium (Vs) as the putative partial homolog of the mammalian extended amygdala (BNST and meAMY). Vs contains the gene markers Dlx2, Lhx7, Nkx2.1b (Alunni et al., 2004), which mark the medial ganglionic eminence in mammals that gives rise to the meAMY and BNST (reviewed in Moreno et al., 2009). The neurochemical profile is similar to that of mammals except for the apparent absence of choline acetyltransferase-positive or AVT-positive cells (Table 2). Also in support of this homology, this region shares connections with the putative basolateral amygdala (blAMY) homolog as well as many projections to the hypothalamus (Folgueira et al., 2004a).

MESOLIMBIC REWARD SYSTEM

Animals must evaluate the relative importance and implications of an environmental stimulus in order to generate the appropriate behavioral response. Many studies indicate that the mesolimbic reward system (including but not limited to the midbrain dopaminergic system) is the neural network where the salience of such stimuli is evaluated (Deco and Rolls, 2005; Wickens et al., 2007). Central to this network is the dopaminergic innervation of the NAcc that originates from the VTA. The conventional reward system also includes the blAMY, LS, VP, striatum (STR), HIP, and the BNST. Although most treatments of

the reward system in mammals also include the prefrontal cortex (Zilles and Wree, 1995; Cardinal et al., 2002), we do not consider this structure here, as its evolutionary antecedents in other vertebrates are unclear (Reiner, 1986). Note, however, that the avian neostriatum caudolaterale has been proposed as a functionally similar region (Hartmann and Güntürkün, 1998).

The mesolimbic dopamine system is best studied in mammals in the context of addiction, depression, and schizophrenia (Groenewegen and Uylings, 2000; Joseph et al., 2003; Koob and Volkow, 2010). However, these mental disorders can be considered deviations of a potentially ancient network that encodes the salience and positive reinforcement effects of behavior (Northcutt, 1981; Everitt and Robbins, 2000; Schultz, 2000; Jackson and Moghaddam, 2001). Seeking physiological rewards or sensory stimulation is not limited to mammals, but pleasure-seeking is also seen in reptiles and fish (Campbell, 1972) as well as birds (Delius and Pellander, 1982), and may potentially be modulated by similar neural circuits. As the functional contexts in which animals behave (i.e., mate choice, male-male aggression, foraging, etc.) are ancient, it is reasonable to hypothesize that, in vertebrates, the mesolimbic dopamine system plays a conserved role in reinforcing them.

Describing vertebrate homologies of the mesolimbic reward system is more difficult than the SBN, as most regions of this circuit are located in the telencephalon, which shows much more divergence in topography across vertebrates than the midbrain and spinal cord (Northcutt and Kaas, 1995). The most contentious region is the pallium, which includes the basolateral amygdala, where developmental studies have been especially useful in shedding light on these homologies. The basal ganglia constitute another area of contention, at least as far as anamniotes are concerned. These structures appear to be conserved at least across tetrapods (for review, see Smeets et al., 2000) and consist of a ventral and dorsal striatopallidal system (Heimer et al., 1995). The dorsal portion consists of the STR (caudate putamen in most mammals) and the dorsal pallidum, while the ventral portion consists of the NAcc and VP. It was previously thought that the basal ganglia were only present in amniotes (MacLean, 1990), but many studies in the past decade have shown that amphibians clearly possess the basal ganglia regions (Smeets et al., 2000) and teleosts likely do so as well (Wullimann and Mueller, 2004). In the following, we focus mainly on neurochemical, developmental, and hodological studies to support homologies across vertebrates, although we discuss lesion or stimulation studies where available in order to comment on whether these homologous structures are functionally similar.

Ventral tegmental area (VTA)

Mammals

The connection between the VTA and forebrain regions is widely considered the core of the dopaminergic reward system (Phillipson, 1979; Domesick, 1988; Spanagel and Weiss, 1999). Dopaminergic neurons in the VTA (A10 group) play an important role in evaluating the salience of environmental stimuli and signaling motivating events (Schultz, 1998). The VTA is located in the midbrain and sends dopaminergic projections to the NAcc and releases dopamine in response to certain stimuli such as sex, food, or drugs of abuse (Fallon and Moore, 1978; Le Moal and Simon, 1991). Functional studies have also shown that the VTA is important for regulating reproductive behavior, pain sensitivity, and parental behavior (Table 1) (Brackett and Edwards, 1984; Sirinathsinghji et al., 1986; Hansen et al., 1991; Hasegawa, 1991; Sotres-Bayon, 2001). Specification and maintenance of the midbrain dopaminergic neurons have received much attention due to the involvement of the substantia nigra (A9 group) in the development of Parkinson's disease (reviewed in Smidt and Burbach, 2007), and the genes underlying the specification of the substantia nigra and the VTA are remarkably similar. Developmentally, many transcription factors mediate the specification and maintenance of midbrain VTA and substantia nigra dopamine neurons including Nurr1 and Lmx1b, and their electrophysiological properties are also similar (Grenhoff et al., 1998). However, the hodological profiles are quite different; for example, the VTA, but not the SN, projects to the NAcc, although both project to the striatum.

Birds

The avian mesolimbic reward system has received much less attention than the SBN (Goodson, 2005) or the well-known song circuitry (Nottebohm et al., 1976), although investigations into the role of dopamine in song production and evaluation have recently become a popular area of research (Jarvis et al., 1998; Hessler and Doupe, 1999; Heimovics and Riters, 2008). The avian VTA is similar to the mammalian VTA in topography and neurochemical profiles, as it is located in the ventral midbrain and contains a dense cluster of dopamine neurons (Lewis et al., 1981; Kitt and Brauth, 1986; Reiner et al., 1994), and also has comparable electrophysiological properties (Gale and Perkel, 2006). The avian VTA projects not only to the basal ganglia as in mammals (Kitt and Brauth, 1986; Parent, 1986; Mezey and Csillag, 2002), but also to the song nuclei (Lewis et al., 1981), providing evidence that song production may be facilitated by the reward system in certain contexts. Exposure to a social opportunity, such as a reproductive female, increases both immediate early gene expression and neuronal

activity in the VTA of male songbirds (Heimovics and Riters, 2005; Yanagihara and Hessler, 2006; Huang and Hessler, 2008). Lesions of midbrain dopaminergic neurons (both VTA and substantia nigra) decrease courtship songs directed at a female, but do not alter song structure or nonfemale-directed singing in male zebra finch (Hara et al., 2007).

Investigations into the role of dopamine in regulating behavior patterns other than singing have also been carried out in Japanese quail and estrillid finches, mainly in the context of sexual behavior and sociality, respectively. Dopaminergic neurons in the VTA of Japanese quail are activated, as measured by immediate early gene induction, during sexual behavior (Charlier et al., 2005). In estrillid finches, the activation of the VTA reflects not only social motivation to court a female with song, but also different sociality phenotypes, as highly social species have more dopaminergic cells in the VTA than solitary territorial species (Goodson et al., 2009). Furthermore, Bharati and Goodson (2006) showed in male zebra finches that the number of VTA neurons that coexpress c-fos and TH increases during both sexual and agonistic encounters, suggesting a general response to interactions with any conspecific individual in this gregarious species. These neurochemical and hodological studies indicate that the avian and mammalian VTA are indeed homologous and the behavioral studies indicate they are also functionally similar.

Reptiles

Although reptiles do have an ascending dopaminergic system, its role in behavior is poorly understood. The reptilian VTA is topographically and neurochemically similar to the mammalian VTA, given its dense cluster of dopaminergic neurons in the midbrain (Parent and Poirier, 1971; Smeets et al., 1986, 1987; Smeets, 1994). The reptilian VTA sends massive projections to the telencephalon, including the NAcc and LS (González et al., 1990; Perez-Santana et al., 1997), and thus has hodological characteristics similar to the mammalian VTA. Regrettably, there have been no studies on the role of the VTA in modulating reptilian responses to social stimuli, even though this is a promising area of research that will provide an important link in understanding the evolution of dopamine's role in modulating social decision-making.

Amphibians and teleosts

Given its important role in regulating behavior, much attention has been directed toward finding the anamniote homolog to the mammalian VTA (Rink and Wullimann, 2001; Luo et al., 2008). Although both amphibians and teleosts lack a midbrain dopaminergic cell group (Smeets et al., 2000), multiple lines of evidence point to the posterior tuberculum, located in the ventral diencephalon, as the putative anamniote VTA homolog. Rink and Wullimann (2001, 2002) found that the posterior tuberculum is the teleost dopaminergic system ascending to the striatum, similar to mammals (Fallon and Moore, 1978), and suggested that this region in teleosts might be functionally similar and possibly homologous to the mammalian VTA/substantia nigra pars compacta. In amphibians, the posterior tuberculum also sends dopaminergic projections to the putative NAcc, characteristic of the mammalian VTA (Marin et al., 1995). More recently, neurochemical evidence from developing zebrafish (*Danio rerio*) in conjunction with morpholino knockout studies have provided support for the notion that the posterior tuberculum is in fact homologous to the VTA/substantia nigra. Morpholino knockouts targeting the transcription factor Nr4a2, which is essential for both development and terminal differentiation of ventral mesencephalic DA neurons in mammals (Zetterström et al., 1997; Saucedo-Cardenas et al., 1998; Le et al., 1999), results in the absence of the posterior tuberculum dopaminergic group (Luo et al., 2008).

It is unclear at this point whether the posterior tuberculum represents the mammalian substantia nigra, VTA, or both, as it is possible that the separation of midbrain dopaminergic cell populations into the distinct substantia nigra and VTA happened after the anamniote–amniote transition (Yamamoto and Vernier, 2011). Interesting in this context is the finding that a Pitx3 morpholino knockdown in zebrafish results in a partial ablation of the posterior tuberculum (Filippi et al., 2007). This result corresponds with the observation by Smidt et al. (2004), who showed that in Pitx3 knockout mice only the substantia nigra fails to develop, but not the VTA, which suggests that there may be subregions of the posterior tuberculum that are homologous to either the VTA or substantia nigra, although it is unclear which dopaminergic neurons in the adult brain arise from these surviving cells. Clearly, more experimentation is needed to resolve the putative homology relationship between the anamniote posterior tuberculum and the VTA/substantia nigra. In frogs, neurotoxic lesions of dopaminergic neurons in the posterior tuberculum disrupt female phonotaxis behavior such that its expression is correlated with the number of TH neurons remaining in this region (Endepols et al., 2004). However, this result is difficult to interpret, since either the motor patterns underlying phonotaxis may be disrupted by loss of substantia nigra-like neurons or the motivation to respond to a previously rewarding stimulus has decreased due to loss of dopaminergic VTA-like neurons, or both. Once neurochemical markers become available that differentiate the substantia nigra from the VTA, many of these questions can be answered.

Nucleus accumbens (NAcc)

Mammals

Decades of research have established the NAcc as a central integrator of sensorimotor information that facilitates a favorable behavioral output of either approach or avoidance of a stimulus (Ikemoto and Panksepp, 1999). The NAcc is the recipient of massive dopaminergic input from the VTA (Fallon and Moore, 1978; Beckstead et al., 1979), which releases dopamine in response to many social stimuli as well as motivated behaviors (Morgane et al., 2005). Additionally, the NAcc receives input from the blAMY and HIP and projects to the VP (Heimer et al., 1997), a defining characteristic. Based on neurochemical and developmental evidence, the NAcc is considered part of the ventral striatopallidal system (Heimer et al., 1995) along with the VP. In addition to its unique hodological characteristics, the NAcc can be readily identified in the ventral telencephalon by the massive fibers that show immunoreactivity to TH and dopamine (Fallen and Moore, 1978) as well as substance P and enkephalin (Table 2), as these fibers are very dense compared to neighboring regions. The mammalian NAcc has two subregions (the core and shell) that are distinguishable by hodology (Meredith et al., 1992) and neurochemical profiles (Záborszky et al., 1985; Zahm and Brog, 1992; Jongen-Rêlo et al., 1994; Heimer et al., 1997; Riedel et al., 2002), as the core contains higher calbindin-, TH-, and neuropeptide Y-immunoreactivity than the shell. Furthermore, it seems that the shell portion contributes more to the effects of dopamine and behavioral reinforcement than the core (reviewed in Zahm et al., 1999). When the NAcc is depleted of dopamine, reinforcement behaviors decrease while appetitive behaviors remain intact, suggesting that the NAcc modulates the "wanting" (i.e., the appetitive effort of seeking a reinforcer) as opposed to the "liking" (act of consuming a reinforcer) of relevant stimuli (reviewed in Salamone and Correa, 2002). Lesions to the NAcc result in impulsive choice in mammals (Cardinal et al., 2001).

Birds

The avian NAcc shares similar neurochemical and hodological characteristics of the mammalian NAcc (Reiner et al., 1983, 1994; Berk, 1991; Medina and Reiner, 1997; Husband and Shimizu, 2011). The avian NAcc receives input from the VP, HIP, and LS (Székely and Krebs, 1996) and projects to the VP (Medina and Reiner, 1997). Several studies have suggested the avian NAcc can also be divided into core and shell subregions similar to mammals based on hodology and neurochemistry (see Husband and Shimizu, 2011, for detailed discussion). TH- and neuropeptide Y-immunohistochemistry is higher in the putative shell (Roberts et al., 2002; Balint and Csillag, 2007), similar to mammals. However, calretinin immunoreactivity is higher in the putative shell region (Balint and Csillag, 2007), opposite of the mammalian NAcc. Most of our understanding of the avian NAcc function comes from studies on feeding behavior in chicken (*Gallus domesticus*) and pigeon. This body of literature supports the functional analogy of the avian and mammalian NAcc, as lesions of the NAcc result in impulsive choices (Izawa et al., 2003), similar to mammals (Cardinal et al., 2001). Further, food-deprived pigeons will self-stimulate the NAcc (Delius and Pellander, 1982), suggesting that its role in motivation is conserved.

Reptiles

The reptilian NAcc is very similar to the mammalian NAcc based on location, neurochemistry, connectivity, and development (Smeets et al., 1986, 1987; Russchen et al., 1987; Russchen and Jonker, 1988; González et al., 1990; Smeets and Medina, 1995; Guirado et al., 1999). Similar to the situation in mammals, the reptilian NAcc receives input from the VTA, VP, amygdala, thalamic nuclei, and hypothalamus (González et al., 1990; Perez-Santana et al., 1997), and sends projections to the septum, VP, BNST, POA, thalamic regions, VTA, and some hypothalamic regions (Smeets and Medina, 1995). Similar to mammals and birds, the reptilian NAcc can also be divided into two subregions, putatively representing the shell and core, based on neurochemistry and connectivity (Guirado et al., 1999).

Functionally, the reptilian NAcc also modulates behavior patterns in a way similar to the mammalian homolog, as variation in dopamine levels in the NAcc influences the approach behavior to a potentially rewarding stimulus. Leopard geckos (*Eublepharis macularius*) have different behavioral phenotypes based on the temperature of the embryonic environment and individual differences in sexual behavior of male adults of different embryonic environments has been partially attributed to differences in dopamine in the NAcc (Dias et al., 2007), although this study did not distinguish between the core and shell subregions. More studies on the integration of sensorimotor information in the reptilian NAcc would yield insightful information on the role of the NAcc in reptiles.

Amphibians

The amphibian NAcc shares many characteristics of the mammalian NAcc in neurochemistry and hodology. Similar to mammals, the amphibian NAcc homolog receives massive inputs of TH- and dopamine-immunoreactive fibers (González and Smeets, 1991; González et al., 1994). This region also contains many cells immunoreactive for DARPP-32, a marker for dopaminoreceptive cells (López et al., 2010; O'Connell et al., 2010). The

NAcc lies on the rostral telencephalic wall and can be distinguished from the striatum by differences in neurochemistry (Marin et al., 1998b), as the NAcc has more dense TH-, SP-, and ENK-positive fibers and lacks NADPH-positive cells compared to the STR. Similar to the situation in mammals, the anuran NAcc also receives inputs from the VP, HIP, STR, and VTA-like homologs (Marin et al., 1997a, 1998a).

Unfortunately, functional studies of the NAcc in amphibians are largely lacking. However, studies in female túngara frogs (*Physalaemus pustulosus*) utilizing immediate early gene expression have demonstrated that the NAcc activation is correlated with both phonotaxis behavior and the type of mating call that is used as a stimulus (Hoke et al., 2007). This work suggests that the NAcc may play an important role in the decision to approach a potentially rewarding stimulus, such as the attractive call of a conspecific.

Teleosts

The dorsal (Vd) and central (Vc) parts of the ventral telencephalon is thought to be homologous to the striatal formation in mammals based on the presence of substance P-immunoreactive cells (Sharma et al., 1989; Batten et al., 1990; Weld and Maler, 1992). Other neurochemical and hodology evidence points to Vd as the partial putative homolog to the mammalian NAcc. Vd is rich in GABA immunoreactivity (Medina et al., 1994) and dopamine receptors (Kapsimali et al., 2000; Vacher et al., 2003; O'Connell et al., 2011b). Vd also receives ascending dopaminergic input from the putative VTA-like homolog (Rink and Wullimann, 2001a), although more research is needed to confirm the identity of a VTA homolog in teleosts, which will then facilitate a more confident identification of the NAcc as well. The ventral part of the ventral telencephalon (Vv) also receives projections from the VTA-like nucleus in zebrafish (Rink and Wullimann, 2001); however, this region is not considered a potential homolog due to its septal-like cholinergic immunoreactivity (Brantley and Bass, 1988).

Basolateral amygdala (blAMY)

Mammals

The pallial blAMY in particular integrates inputs from many sensory modalities and is sometimes referred to as the "multimodal amygdala" involved in emotional behavior (LeDoux, 2000; Moreno and González, 2007a). The blAMY as a whole generally refers to three subregions: the basolateral, lateral, and basomedial amygdala (Swanson and Petrovich, 1998). The mammalian blAMY projects to the hypothalamus through the stria terminalis (LeDoux et al., 1987; Turner and Herkenham, 1991; Risold et al., 1997), a connection that appears to be conserved across tetrapods (Bruce and Neary, 1995c), and also projects to the striatum and NAcc (Russchen and Price, 1984; Petrovich et al., 1996, Wright et al., 1996). Further, neuronal activity in the blAMY can modulate the firing rate of dopaminergic VTA neurons (Maeda and Mogenson, 1981), providing a mechanistic basis for the role of the blAMY in modulating goal-directed behaviors. Lesions of the blAMY result in a loss of emotional learning, including fear conditioning (LeDoux, 2000; Cardinal et al., 2002).

Developmentally, the blAMY is derived from the lateral and ventral pallium (Table 3). In particular, the basolateral subregion is derived from the lateral pallium and can be identified in development by Emx-1 and Tbr-1 (Medina et al., 2004; Remedios et al., 2004; Garcia-López et al., 2008). However, gene markers for the ventral pallium can identify the lateral and basomedial subregions of the blAMY: Tbr-1 Dbx-1, Lhx2/9, and Lmo3 (Remedios et al., 2004), although some cells express the lateral pallial marker emx1 (Gorski et al., 2002), which may represent migrated cells. These regional differences in developmental origin add to the complexity of establishing blAMY homology in other vertebrates (see reviews, Martinez-Garcia et al., 2002; Moreno and González, 2007a; Bruce and Braford, 2009). We therefore discuss the lateral and ventral pallial amygdala in reptiles and birds, but there are not enough data at present to determine the corresponding developmental subregions in amphibians and teleosts.

Birds

The identification of the avian blAMY is difficult due to a poorly developed olfactory system and the presence of a large dorsal ventricular ridge, which is also present in reptiles but absent in mammals. However, developmental, neurochemical, and hodological studies, as well as comparative studies in reptiles, have illuminated the potential avian blAMY as the caudal (dorsocaudal and caudomedial) nidopallium and the ventral part of the intermediate arcopallium (including the posterior pallial amygdala) as the ventral pallial homolog (discussed in detail in Martínez-García et al., 2002). Whereas the dorsal and posterior arcopallium and tempero-parieto-occipital area (TPO) represents the lateral pallial homolog (discussed in detail in Puelles et al., 2000; Martínez-García et al., 2002) based on Tbr-1 and Emx-1 expression (Puelles et al., 2000). Interestingly, Wang et al. (2010) recently suggested that the nidopallium shares similarities with the mammalian neocortex based on cell morphology in addition to its multimodal connectivity. However, pallial markers Lmo3 and Lhx2/9 are expressed in the caudal nidopallium during development (Abellán and Medina, 2009; Abellán et al., 2009), which provides

additional support for the ventral pallial homology. The TPO and dorsal arcopallium receives dopaminergic and cholinergic innervation similar to the mammalian blAMY (Waldmann and Güntürkün, 1993; Medina and Reiner, 1994; Balthazart and Absil, 1997). Importantly, the dorsocaudal and caudomedial nidopallium receives auditory, visual, and somatosensory information from the thalamus (Wild, 1987; Martínez-García et al., 2002), supporting the homology of these structures with the lateral nucleus of the mammalian blAMY. Furthermore, this region projects to the ventral hypothalamus via the stria terminalis (Zeier and Karten, 1997; Davies et al., 1997; Dubbeldam et al., 1997), a characteristic hodological signature of the blAMY.

Reptiles

A multimodal information processing area equivalent to the blAMY has also been identified in the reptilian pallium (Martínez-García et al., 1991, 2002; Lanuza et al., 1998; Lanuza and Halpern, 1998) that includes the posterodorsal ventricular ridge and lateral amygdaloid nucleus as well as the dorsolateral amygdala (discussed in detail in Martínez-García et al., 2002). The dorsal ventricular ridge (DVR) represents one of the most striking changes in the transition between amphibians and amniotes (ten Donkelaar, 1999), although mammals do not have this region (Northcutt and Kaas, 1995). Bruce and Neary (1995c) first proposed that the reptilian posterodorsal dorsal ventricular ridge/dorsolateral amygdala is comparable to the mammalian blAMY based on hodological evidence, as this region receives massive projections from the main olfactory bulb as well as other nonchemosensory regions like the thalamus (Lanuza et al., 1998). This region also projects to the striatum and VMH through the stria terminalis (Hoogland and Vermeulen-Vanderzee, 1995; Lanuza et al., 1997, 1998; Lanuza and Halpern, 1997; Martinez-Marcos et al., 1999), similar to the mammalian blAMY. Although some have proposed that the reptilian DVR is similar to the mammalian isocortex (Aboitiz, 1999), developmental studies have shown that the posterior DVR may be ventral pallial in origin (Fernandez et al., 1998; Puelles et al., 2000), whereas the mammalian isocortex is dorsal pallial in origin (Aboitiz et al., 2002). The posterodorsal DVR is positive for pallial markers Tbr-1 and Lhx9, while the dorsolateral amygdala is positive for the pallial markers Emx-1 and Tbr-1 (Fernandez et al., 1998; Moreno et al., 2010), further supporting the homology of these two reptilian regions to the mammalian blAMY. Finally, the dorsolateral amygdala has both dopaminergic and cholinergic innervation (Medina et al., 1993; Smeets, 1994), similar to the lateral pallial part of the mammalian blAMY (Loughlin and Fallon, 1984; Carlsen et al., 1985).

Functional studies in male Western fence lizards (*Sceloporus occidentalis*) have shown that the blAMY homolog facilitates responsiveness to social stimuli, as lesions to this region reduce aggressive displays to conspecific males (Tarr, 1982). Similarly, lesions of the blAMY in caiman disrupt the appropriate behavioral output to relevant social stimuli such that the animals no longer attacked or retreated from a specific stimulus (Keating et al., 1970). Complementary stimulation studies of the reptilian blAMY increased agonistic escape responses (Distel, 1978; Sugar and Demski, 1978), suggesting that this region plays an important role in integrating social stimuli into an adaptive behavioral response.

Amphibians

Due to neurochemical, developmental, and hodological characteristics, the brain region corresponding to the multimodal mammalian blAMY is the lateral amygdala (discussed in detail in Moreno et al., 2004; Moreno and González, 2004), which receives both olfactory and nonchemosensory information (Moreno and González, 2007c), although the homology status of this region is still under debate (Laberge et al., 2006). The integration of chemical (olfactory, including pheromonal) cues with nonchemical stimuli from the thalamus, such as species-specific calls, may aid in labeling particular stimuli as attractive or noxious (Moreno and González, 2007a). The amphibian lateral amygdala is ventropallial in origin, marked by Lhx-2/9 and tbr1 expression (Bachy et al., 2001; Brox et al., 2004; Moreno et al., 2004), similar to lateral and basomedial portions of the mammalian blAMY. However, Lhx-2/9 is also expressed in the adult subpallium (Bachy et al., 2001; Brox et al., 2004; Moreno et al., 2004), although Moreno et al. (2004) suggested that these Lhx-2/9 cells originate in the ventral pallium and then migrate to the subpallium, as is sometimes seen in mice. Much more work on the developmental origins and connectivity of this region is needed to firmly establish homology. From a function viewpoint, this region is similar to the mammalian blAMY, as lesions disrupt emotional learning in the newt *Triturus alpestris* (Wenz and Himstedt, 1990).

Teleosts

Given that the mammalian amygdala is derived from both pallial and subpallial regions, finding the homologous region in teleosts is complicated by the eversion of the teleost forebrain during development. Even though the pallial and subpallial regions are topographically in close proximity in tetrapods, the teleost homologs are situated in completely different regions of the telencephalon. The medial part of the dorsal telencephalon (Dm) is currently thought to be the putative blAMY homolog. This

region receives olfactory input (Folgueira et al., 2004a) as well as other nonchemosensory inputs (Folgueira et al., 2004b), similar to the mammalian blAMY. However, it should be noted that there are subregions of Dm about which little is known in terms of their function. For example, lateral line and auditory information are integrated in different subregions of Dm (Yamamoto and Ito, 2005, 2008). There is also developmental evidence available for this putative homology from both Medaka (*Oryzias latipes*) and cavefish (*Astyanax mexicanus*), where the pallial marker Lhx-9 is expressed in Dm (Alunni et al., 2004; Menuet et al., 2007), similar to the mammalian blAMY. Dm is also functionally similar to the mammalian blAMY, as lesions impair emotional learning similar to mammals (Portavella et al., 2002), consistent with the Dm being homologous to the lateral pallium (Nieuwenhuys, 2009).

Striatum (STR)

Mammals

The STR is thought to play an important role in reinforcement learning and selecting previously reinforced actions (Wickens et al., 2007). Based on developmental, hodology, and neurochemical evidence, the mammalian STR is located in the dorsal striatopallidal system (Heimer et al., 1995) and receives massive inputs of TH- and dopamine-immunoreactive fibers (Fallen and Moore, 1978) from the midbrain (Shults et al., 1984). It also contains neurons that express substance P, nitric oxide synthase, somatostatin, and neuropeptide Y (Tepper and Bolam, 2004), and both D_1 and D_2 dopamine receptor families are expressed in this region (Matamales et al., 2009). The STR develops as part of the subpallium (the lateral ganglionic eminence) and is characterized by several gene markers (reviewed in Moreno et al., 2009), including GAD67, Dlx, and Isl1 (Table 3). Functional studies indicate that the STR mediates learning and expression of goal-directed actions (reviewed in Wickens et al., 2007).

Birds

Based on neurochemical profile and hodological data, the dorsolateral part of the avian medial striatum (previously the lobus parolfactorius) is comparable to the mammalian STR (Karten and Dubbeldam, 1973; Reiner et al., 1983; Medina and Reiner 1995, 1997). Based on strong enkephalin staining (Galatioto et al., 1998), Reiner et al. (1998) first suggested a homology between the lobus parolfactorius and the mammalian STR. The avian STR developmentally arises from the molecularly inferred homolog of the lateral ganglionic eminence, marked by expression of Dlx2 and lack of Nkx2.1 (Puelles et al., 1999). Furthermore, the electrophysiological properties of the neurons in this region are very similar to those of cells in the mammalian STR (Farries and Perkel, 2000). Consistent with functional studies in mammals, the avian STR seems to play a role in learning goal-directed behaviors, as pigeons with STR lesions were unable to change goals in a discrimination task (Watanabe, 2001).

Reptiles

The reptilian STR is similar to the mammalian and avian STR in hodology, neurochemistry, and developmental gene markers (Smeets et al., 1986, 1987; Russchen et al., 1987; Russchen and Jonker, 1988; González et al., 1990; Smeets, 1994; Moreno et al., 2010). A feature unique to the reptilian STR is dopaminergic input subfunctionalization (Marín et al., 1998c), as the ventral STR receives dopaminergic input exclusively from the VTA, while the dorsal striatum receives dopaminergic input from the substantia nigra (González and Russchen, 1988; González et al., 1990; Perez-Santana et al., 1997). In mammals and birds, the dopaminergic innervation is more overlapping (Fallon and Moore, 1978; Nauta et al., 1978). Developmental gene markers (presence of Pax6 and absence Nkx2.1 and others) are similar between the reptilian STR and the mammalian STR (Table 3) (Moreno et al., 2010). An STR lesion in male anole lizards leads to deficits in a male-typical assertion display (Greenberg, 1977) while stimulation promotes this behavior (Tarr, 1982).

Amphibians

The STR is situated along the ventrolateral wall of the telencephalon and homology is supported by neurochemical and developmental studies. This region contains many TH- and dopamine-immunoreactive fibers as well as many cells immunoreactive for GABA, substance P, enkephalin, and DARPP-32 (Table 2) (Inagaki et al., 1981; González and Smeets, 1991, 1994; O'Connell et al., 2010). Developmentally, the anuran STR also has similar gene markers including GAD67, Dlx, and Isl1 (Table 3) (Bachy et al., 2002; Moreno et al., 2008). In anurans, the STR is sensitive to auditory cues (Mudry and Capranica et al., 1980). Functionally, lesions of the striatum in female gray tree frogs (*Hyla versicolor*) abolish phonotactic responses to mating calls (Walkowiak et al., 1999), suggesting that expression of goal-directed behaviors (i.e., finding the source of the attractive call) is disrupted.

Teleosts

It is generally accepted that the dorsal (Vd) and central (Vc) part of the ventral telencephalon are striatal-like (Wullimann and Mueller, 2004) based on neurochemical evidence. This homolog was suggested based on the presence of substance P-immunoreactive cells (Sharma et al., 1989; Batten et al., 1990; Weld and Maler, 1992), as well as GABA-immunoreactive fibers in the Vd (Martinoli et al., 1990; Medina et al., 1994). Further, there is

selective enkephalin staining within Vd (Vecino et al., 1992) that is also indicative of the striatal-like regions of the mammalian basal ganglia. It is, however, important to mention here that neurochemically Vd shows both striatal-like and NAcc-like (see above) properties, suggesting that homology relationships can be nested within each other. It is thus possible that Vd functions in ways similar to both the STR and the NAcc, although further functional and developmental studies are needed to fully dissect any subfunctionalization of this region.

Ventral pallidum (VP)

Mammals

The VP mediates the motor output of motivated or goal-directed behaviors (Mogenson et al., 1980). The mammalian VP is part of the ventral striatopallidal system (Heimer et al., 1995), along with the NAcc, and largely receives input from the STR and NAcc and projects to regions outside the basal ganglia circuit, including limbic areas in the hypothalamus and the VTA (Haber et al., 1985; Groenewegen et al., 1993; Ikemoto, 2007). Neurochemically, it is characterized by high levels of substance P and enkephalin (Zahm and Heimer, 1990; Napier et al., 1995), and most of the catecholaminergic innervation here is noradrenergic (Reiner et al., 1994). Developmentally, the VP arises from the medial ganglionic eminence, marked by expression of Dlx1/2/5, Nkx2.1, and Lhx6 (reviewed in Moreno et al., 2009). The VP not only regulates the motor output of behaviors, but also plays an important role in reward processing. Functional studies have shown that the VP is necessary and sufficient for reward and mediates both the "liking" and "wanting" components of reward (reviewed in Smith et al., 2009).

Birds

The avian VP is similar to the mammalian homolog in topography, hodology, and neurochemistry (Medina and Reiner, 1997). As in mammals, the avian VP also projects to limbic areas, the hypothalamus, and the VTA (Medina and Reiner, 1997), and receives catecholaminergic innervation that is primarily noradrenergic (Balthazart and Absil, 1997). Neurochemically, the VP can be distinguished by a strong staining for substance P and enkephalin (Reiner et al., 1983; Anderson and Reiner, 1990b; den Boer-Visser and Dubbeldam, 2002). During development, the avian VP also expresses Dlx2, Nkx2.1, yet no Pax6, similar to the situation in the mammalian VP (Puelles et al., 2000). Functionally, the VP constitutes an integral link between the dopaminergic reward system and song nuclei (Gale et al., 2008). The dopaminergic reinforcement of a bird's own song involves the disinhibition of the dopaminergic neurons by inhibition of VP, suggesting that the reward system and song nuclei compose a functional pathway for vocal learning and reinforcement of song production (Gale and Perkel, 2010).

Reptiles

The reptilian VP is very similar to both the mammalian and avian VP in neurochemistry, hodology, and topography (Russchen and Jonker, 1988; Smeets and Medina, 1995). It has a bidirectional connection with the NAcc that seems to be conserved across tetrapods (Russchen and Jonker, 1988; González et al., 1990), and projects to the hypothalamus and VTA (Russchen and Jonker, 1988). Developmentally, the reptilian VP also arises from the medial ganglionic eminence, as marked by Nkx2.1 expression (Moreno et al., 2010). Unfortunately, functional studies that test the reptilian VP's role in the regulation of reward have yet to be conducted.

Amphibians

The VP has been identified based mostly on neurochemical studies utilizing antibodies specific to the basal ganglia. It can be recognized by strong immunoreactivity to substance P and moderate enkephalin presence as well noradrenergic innervation (Merchenthaler et al., 1989; González and Smeets, 1993; Marin et al., 1998b). It also shares a bidirectional connection with the NAcc (Marin et al., 1997a, 1998a) and projects to the hypothalamus and the SN/VTA-like region (Marin et al., 1997a, 1998a). Developmentally, the amphibian VP also is marked by Nkx2.1 expression (van den Akker et al., 2008). Although there are no functional studies targeting specifically the VP in amphibians, this would be an interesting avenue of research due to its role in regulating motor output of goal-directed behavior and the rich literature on female phonotaxis and mate choice in anurans.

Teleosts

To our knowledge, a teleost homolog of the mammalian VP has not yet been identified. There is a region in the developing teleost brain that is neurochemically similar to the mammalian medial ganglionic eminence (Rohr et al., 2001), although where this region is topographically located in the adult brain is not entirely clear, in part due to the eversion of the developing telencephalon. Furthermore, only one of the paralogs of the developmental gene marker Nkx2.1 is expressed in the telencephalon of developing zebrafish (Rohr et al., 2001), thus making it difficult to interpret if this is an ancestral vertebrate trait or if this paralog has been recruited for a new function after the teleost genome duplication. Identification of this brain region would provide an excellent foundation for deepening our understanding of the evolution of the teleost basal ganglia and their contributions to behavioral regulation. A recent study by Ganz et al. (2011) provides evidence that the

caudal portion of Vv is homologous with the pallidum/pallidal septum of mammals.

Hippocampus (HIP)

Mammals

The HIP in mammals plays an important role in the formation of episodic memories and is thus crucial for relational memory representations of the environment and/or experiences (O'Keefe and Nadel, 1978; Anderson et al., 2007; Humphries and Prescott, 2010). The HIP's role in mediating reward stems from its ability to encode environmental information into navigational maps that the animal can recall. For example, if an animal were to find a mate or a particularly enriched food source while foraging, remembering the location of this rewarding stimulus in space and time is clearly adaptive. In development, the HIP is derived from the medial pallium and is thus relatively easy to identify across vertebrates (Sherry and Duff, 1996; Eichenbaum et al., 1999; Rodriguez et al., 2002a). Functional studies in mammals suggest that the HIP is not only involved in spatial memory, but more generally in the storage of repeated experiences (Eichenbaum et al., 1999). HIP lesions produce a selective deficit in spatial learning based on multiple environmental features, but not cue learning, which relies on a single cue or nonspatial discrimination (Morris et al., 1982). Additionally, natural space use can predict HIP volume in small rodents, including species variation in territory size food-caching (reviewed in Sherry et al., 1992).

Birds

The HIP avian homology is supported by developmental and hodological (Fig. 3) studies. The avian HIP is of medial pallial origin with characteristic Lhx2 expression, just as in mammals (Moreno et al., 2004), and exhibits a similar hodological profile (Krayniak and Siegel, 1978b; Atoji et al., 2002; Atoji and Wild, 2004). This region is also functionally similar to the mammalian HIP, with the strongest evidence coming from studies investigating spatial learning in birds, which has been especially well examined in the context of homing behavior in pigeons (Bingman, 1993) and food caching (Sherry and Duff, 1996). Lesion of the HIP in pigeons impairs place learning but not cue learning (Fremouw et al., 1997), similar to HIP lesions in mammals. Importantly, the avian HIP plays a critical role in landmark navigational learning in a natural setting (Gagliardo et al., 1999), and is important in processing spatial rather than visual information (Colombo et al., 1997). HIP lesions in Eurasian nutcrackers (*Nucifraga caryocatactes*), a food caching species, render them unable to find their food stores (Krushinskaya, 1966). Interestingly, bilateral HIP lesions disrupt the memory of the food cache location without disrupting food cache searching in chickadees (Sherry et al., 1989), suggesting that the HIP plays an important role in spatial memory but not motivation. Comparative studies have also shown that food-storing birds have larger HIP volumes than nonfood-storing birds within the same taxonomic group (Krebs et al., 1989; Sherry et al., 1989; Hampton et al., 1995).

Reptiles

Developmental evidence in reptiles points to the medial cortex as the reptilian homolog of the mammalian HIP (Fernandez et al., 1998), as it is derived from the medial pallium (Moreno et al., 2010). There is also much evidence suggesting this region is functionally similar to the mammalian HIP, as a behavioral dimorphism in the size of the HIP is found in lizards: those species that forage for food have a larger medial cortex than other species that have adopted a sit-and-wait strategy (Day et al., 1999). Additionally, lesions of the medial cortex in both lizards and turtles also lead to deficits in spatial learning but not in cue learning (Day et al., 2001; Rodriguez et al., 2002b; López et al., 2003).

Amphibians

The medial pallium in amphibians is generally accepted as the HIP homolog, due to its developmental origin (Brox et al., 2003, 2004) and connectivity (Westhoff and Roth, 2002). The HIP is also sensitive to auditory cues (Mudry and Capranica, 1980), which may be important in encoding the acoustic information into spatial maps that anurans utilize during phonotaxis. Toads (*Bufo arenarum*) with lesions in the medial pallium show deficits in response inhibition to a nonrewarding stimulus (Muzio et al., 1994), similar to HIP lesions in rats (Jarrard and Isaacson, 1965).

Teleosts

The lateral part of the dorsal telencephalon (Dl) is currently thought to be the homolog of the mammalian HIP based on connectivity to the POA and hypothalamus (Folgueira et al., 2004b), and cell mass criteria (Nieuwenhuys, 2009). There is also support for this region being functionally similar to the mammalian HIP, as lesions lead to deficits in spatial learning, but not emotional or cue learning (Portavella et al., 2002; Rodriguez et al., 2002b).

INTEGRATION OF SOCIAL BRAIN CIRCUITS

Although the SBN and mesolimbic reward system have traditionally been studied as separate circuits, they are anatomically linked by bidirectional connections between several brain regions as well as the two shared nodes, LS and BNST. These two circuits complement each other by regulating both the evaluation of stimulus salience and the behavioral output. By integrating them into the SDM

network, we can build a strong foundation for studying the neural basis and evolution of social behavior. Numerous studies have greatly increased our understanding of complex social behaviors within this framework. For example, work in monogamous voles has integrated the rewarding basis of being with a mate in the mesolimbic reward system with reproductive behaviors of the SBN (Young and Wang, 2004). Additionally, work in túngara frogs has lead to important insights into the neural response to conspecific calls in females, where both hypothalamic and dopaminergic regions, such as the putative VTA homolog, respond to an attractive call as measured by immediate early genes (Hoke et al., 2007).

Another brain node that participates in both the mesolimbic reward system and SBN is the amygdala, where the meAMY is considered part of the SBN, whereas the blAMY is generally associated with reward processing. These two regions of the amygdala are highly interconnected and play an important role in regulating adaptive behavior. Lanuza et al. (2008) proposed that the meAMY detects pheromonal cues in the environment and this information is sent to the blAMY where information is tagged with a negative or positive emotional value. Further, in mammals the central amygdala is the main integration point for amygdalar information, as it processes information from the blAMY and meAMY and relays this information to the thalamus and brainstem (Moreno and González, 2007a). Although the central amygdala is not classically considered part of the mesolimbic reward system and SBN, it plays an important role in implementing motor responses to stimuli resulting in approach or avoidance (Gonzales and Chesselet, 1990; Saha et al., 2000; Finn et al., 2003). Thus, the central amygdala can also be considered a structural link between these two circuits. Studies in mammals, snakes, and amphibians show that emotional learning can occur with both a negative-associated pheromonal cue (i.e., a predator pheromone) or a positive-associated pheromone, like potential mate (Dielenberg and McGregor, 2001; Lanuza et al., 2008). Associating sensory information with emotional memory allows an animal to produce a behaviorally appropriate response to a social stimulus, such as withdrawing from a noxious stimulus or approaching a potentially rewarding stimulus.

EVOLUTION OF THE SOCIAL DECISION-MAKING NETWORK

Our analysis of homologies based on topography, neurochemistry, hodology, and developmental gene markers suggest that many of the nodes of the mesolimbic reward system and SBN were already present in early vertebrates. This is in a way expected, as brain regions that regulate adaptive behaviors should be highly conserved. Across vertebrate classes, the developmental gene profiles that mark the progenitor domains of the pallium and subpallium are highly conserved (Table 3), further supporting the conservation of these developmental brain modules (Redies and Puelles, 2001), although many more genes and species need to be added to this analysis. Given the available data across vertebrates on neurochemical markers (Table 2) as well as developmental markers for progenitor domains (Table 3), there appears to be more variation between vertebrate lineages in neurochemical profiles (in terms of the presence or absence of cell bodies or fibers immunoreactive for particular neurochemicals), although the overall pattern is still highly conserved.

We have discussed all nodes of the SDM network across vertebrates for which the available data suggest putative homologies, although much more work is clearly needed to firmly establish these homologies in nonmammalian vertebrates. The brain regions that currently do not have any putative homologies with their mammalian counterparts is the VP and the extended amygdala (the mammalian meAMY and BNST) in teleosts, and the hypothesized VTA/substantia nigra-like subdivisions of the posterior tuberculum in anamniotes. The homology of the extended amygdala (meAMY and BNST) in teleosts is mostly based on developmental evidence for gene markers of the mammalian medial ganglionic eminence, whereas the homology of the posterior tuberculum as the homolog to the VTA/substantia nigra in anamniotes is mostly based on neurochemistry and hodology. There are two alternative explanations for the dual homology of these regions. First, it is possible that the meAMY and BNST differentiated into distinct brain regions after tetrapods diverged from fish, although testing this hypothesis would require investigating developmental marker profiles of a non-teleost fish, such as lungfish (a sarcopterygian, like all tetrapods) or cartilaginous fish in order to determine when this trait diverged. Similarly, the VTA and substantia nigra possibly diverged into anatomically and functionally distinct regions in amniotes. The other possibility is that subregions of these nuclei may correspond to the meAMY or BNST in the case of the teleost Vs and the VTA and substantia nigra in the case of the anamniote posterior tuberculum. However, not enough is known about these nuclei to distinguish subpopulations. In teleosts, the neurochemical profiles of the putative extended amygdala (meAMY and BNST) are nearly identical, with the exception of choline acetyltransferase immunoreactivity, and from this one protein it could be proposed that the teleost Vs is more like the meAMY than the BNST, which is also supported by lack of AVT-producing cells in this region. Similarly, the neurochemical profiles of the VTA and substantia nigra are remarkably similar and more studies need to be done in frogs and fish to better elucidate whether functionally distinct subpopulations within

the posterior tuberculum exist. However, developmental studies have indicated that the diencephalic posterior tuberculum is the likely ancestor of the midbrain dopaminergic cells due to longitudinal expression of lmx1b during zebrafish development (Filippi et al., 2007), although why these cells began to migrate in amniotes is a mystery.

By studying behavior within a network framework rather than specific brain regions, we will be able to better understand how the brain integrates external and internal information into a behavioral response (Newman, 1999; Crews 2003; Goodson and Kabelik, 2009). More work in nonmammalian systems in this context will help us better understand brain homologies as well as how information is processed into a meaningful output. Specifically, neuroanatomical and functional studies are severely lacking in reptiles, although they represent an important group for understanding the evolution of birds and mammals. The need for more information of patterns of homeobox genes during brain development, regional connections, chemoarchitecture, and more functional lesion/stimulation studies in behaving animals would greatly improve our understanding of not only the evolution of these neural networks that regulate behavior, but also improve our capacity to better understand mental disorders that arise from deviations in these circuits.

The neuroanatomical framework we have proposed here provides an important foundation for future experiments and analyses that will greatly increase our understanding of the neural evolution of adaptive decision-making. With putative homologies established across vertebrates, neurochemical or gene expression analyses will shed light on how evolutionary changes on the molecular level within these brain regions might be associated with variation in ecology or life-history strategies of animals. Furthermore, a network view of decision-making, such as proposed here, provides the theoretical framework in which to ask how neural nodes within a network act in concert to produce context-appropriate behavior patterns or how changes in sensory cues (e.g., as a consequence of specialization on certain sensory modalities) might shift neural network activity. Finally, the comparative analysis of the SDM network allows us to identify homologous brain regions and thus provides the basis necessary for testing the hypothesis that brain region-specific neural or molecular responses to environmental stimuli in challenge or opportunity contexts are conserved across animals (Robinson et al., 2008; O'Connell and Hofmann, 2011a).

CONCLUSIONS

Here we have synthesized topographical, neurochemical, developmental, and hodological evidence in support of putative homologies of the mesolimbic reward system and SBN, two circuits important in behavioral regulation that together constitute the social decision-making network. We have also discussed whether these regions are functionally similar, given the data available. These complementary lines of evidence all converge on the basic insight that the brain regions in question are indeed conserved across vertebrates, can—for the most part—be reliably identified, and play similar roles in the regulation of adaptive social behavior. Thus, our analysis suggests that these neural circuits regulating behavior are evolutionary ancient and were already present in early vertebrates. Our synthesis provides a comprehensive framework for comparative studies that will increase our understanding of the evolution of the neural and molecular mechanisms that govern social behavior across vertebrates.

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