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The vertebrate social behavior network: Evolutionary themes and variations ☆

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Abstract

Based on a wide variety of data, it is now clear that birds and teleost (bony) fish possess a core "social behavior network" within the basal forebrain and midbrain that is homologous to the social behavior network of mammals. The nodes of this network are reciprocally connected, contain receptors for sex steroid hormones, and are involved in multiple forms of social behavior. Other hodological features and neuropeptide distributions are likewise very similar across taxa. This evolutionary conservation represents a boon for experiments on phenotypic behavioral variation, as the extraordinary social diversity of teleost fish and songbirds can now be used to generate broadly relevant insights into issues of brain function that are not particularly tractable in other vertebrate groups. Two such lines of research are presented here, each of which addresses functional variation within the network as it relates to divergent patterns of social behavior. In the first set of experiments, we have used a sexually polymorphic fish to demonstrate that natural selection can operate independently on hypothalamic neuroendocrine functions that are relevant for (1) gonadal regulation and (2) sex-typical behavioral modulation. In the second set of experiments, we have exploited the diversity of avian social organizations and ecologies to isolate species-typical group size as a quasi-independent variable. These experiments have shown that specific areas and peptidergic components of the social behavior network possess functional properties that evolve in parallel with divergence and convergence in sociality.
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The research program described below is designed to address two major goals. The first of these goals is to elucidate evolutionary themes in the neuroendocrine, functional, and connectional organization of brain circuits that regulate social behavior. This will provide a phylogenetically broad framework for examining the neural and neuroendocrine mechanisms of behavior and will allow detailed and meaningful comparisons to be made across the major vertebrate classes. Building upon this foundation, the second primary goal is to capitalize on the extraordinary behavioral diversity of birds and teleost (bony) fish to elucidate the ways that

neural and neuroendocrine mechanisms are adjusted over evolutionary time to produce intraspecific and interspecific variation in behavior. If conducted within a well-characterized, comparative framework, these findings obtained in birds and fish should yield solid predictions for other vertebrates as well. Thus, our work addresses evolutionary *themes*, as described in the first section below, and *variations* on those themes, as presented in the second section.

Evolutionary themes and the concept of a vertebrate social behavior network

As originally suggested for mammals (Newman, 1999), the brain's social behavior network is comprised of six nodes—the extended medial amygdala (i.e., the medial

amygdala and the medial bed nucleus of stria terminalis, BSTm), the lateral septum (LS), the preoptic area (POA), the anterior hypothalamus (AH), the ventromedial hypothalamus (VMH), and the midbrain (Fig. 1 and Table 1). The relevant midbrain areas include the periaqueductal gray (PAG) and various areas of the tegmentum that link forebrain regions with motoneuron pools of the hindbrain. The other five nodes lie within the basal ("limbic") forebrain. Newman (1999) proposed that these areas comprise a social behavior network based upon a few important criteria. First, each of the nodes has been implicated in the control of multiple forms of social behavior. These include aggression, appetitive and consummatory sexual behavior, various forms of communication, social recognition, affiliation, bonding, parental behavior, and responses to social stressors (Bamshad and Albers, 1996; Coolen et al., 1997; Cushing et al., 2003; Delville et al., 2000; Ferguson et al., 2002; Gammie and Nelson, 2001; Heeb and Yahr, 2001; Kalinichev et al., 2000; Kirkpatrick et al., 1994; Kollack-Walker and Newman, 1995; Kollack-Walker et al., 1997; Lim and Young, 2004; Lonstein et al., 1998; Morgan et al., 1999; Sheehan et al., 2001; Wang et al., 1997). The nodes are also bidirectionally connected (Coolen and Wood, 1998; Coolen et al., 1998; Dong and Swanson, 2004; Risold and Swanson, 1997b), and each area contains sex steroid receptors that are

essential for the sexual differentiation and temporal coordination of social behavior (Commins and Yahr, 1985; Morrell and Pfaff, 1978; Simerly et al., 1990; Wood and Newman, 1995). The mammalian brain obviously contains a large number of other areas that are relevant for social behavior (e.g., other basal forebrain areas that regulate stress and reward processes, and cortical areas that serve executive functions); thus Newman's network should be regarded as the "core" of the social brain, not the social brain in toto.

Newman (1999) proposes that this network of brain areas does not contain segregated, linear systems for the regulation of each kind of social behavior. Rather, each node of the network responds to a variety of stimuli, with each social context and behavioral response being associated with a distinct *pattern* of response across the nodes. For instance, some of the same areas show increases in immediate early gene (IEG) activity during male sexual behavior, female sexual behavior, and male aggression, but the overall pattern is distinct for each behavioral context (Fig. 1). Although this model is in some ways very simplified (e.g., each area may have distinct neuronal populations with different response profiles), the idea is nonetheless compelling and supported by a good body of data (see references above).

Increasing evidence suggests that this network is present in all vertebrates. While most relevant findings have come from birds, consistent data are also available for amphibians, fish, and reptiles (see Table 1 and the following two sections), and Newman's model has been explicitly applied as a conceptual framework for data in geckos (*Eublepharis macularius*) (Crews, 2003). Interestingly, data from geckos demonstrate that behavioral variations are correlated with distinct patterns of functional connectivity within the network (Sakata and Crews, 2004; Sakata et al., 2000), a finding that lends good empirical support to Newman's (1999) ideas about the significance of distributed activation patterns.

Our own research expands upon these studies in two important respects: First, our work on the vocal circuitry of the plainfin midshipman fish (*Porichthys notatus*) provides the first comprehensive mapping of the network's connections in a non-mammal and has yielded strong evidence that the social behavior network arose in the earliest vertebrates (Goodson and Bass, 2002). As detailed below, the vocal system of the midshipman offers opportunities for systems-level experiments on the network that are not possible in most other animals (i.e., the whole brain can be exposed during analyses of social behavior patterning), thus understanding the comparative organization of the relevant circuitry in fish is particularly valuable. Secondly, our anatomical and behavioral experiments in both fish and birds demonstrate that many functional, structural, and neuroendocrine features are exceptionally similar to those in mammals, thereby rendering detailed comparisons across classes much more feasible than we initially anticipated.
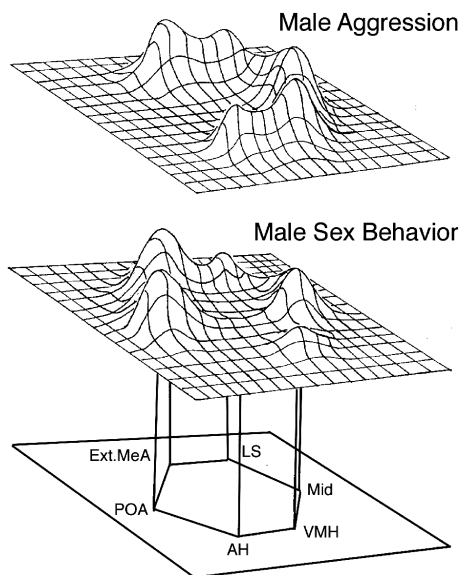

Fig. 1. The social behavior network as originally suggested for mammals (schematics modified from Newman, 1999). The network is comprised of six nodes—the extended medial amygdala (i.e., the medial amygdala and the medial bed nucleus of stria terminalis), the lateral septum (LS), the preoptic area (POA), the anterior hypothalamus (AH), the ventromedial hypothalamus (VMH), and various areas of the midbrain, including the periaqueductal gray. Each of the nodes binds sex steroid hormones and has been implicated in the control of multiple forms of social behavior. Newman (1999) proposes that this network does not contain segregated, linear systems for each kind of behavior. Rather, as shown in these schematic representations of immediate early gene data, each behavioral context is associated with a distinct pattern of activation across the nodes.

Table 1
Components of the social behavior network as described for mammals (Newman, 1999) and proposed homologues in other vertebrate classes

Class Mammalia	Class Aves	Class Reptilia	Class Amphibia	Class Osteichthyes (bony fish)
Extended medial amygdala: Medial amygdala (MeA) and medial bed nucleus of the stria terminalis (BSTm)	Nucleus taeniae and BSTm	MeA[a] and BST[b]	MeA (formerly the amygdala pars lateralis) and BST[b]	Supracommissural nucleus of the ventral telencephalon (amygdala homologue; subdivisions not known)
Preoptic area (POA)	POA	POA	POA	POA[c]
Anterior hypothalamus (AH)[d]	AH[d]	AH[d]	AH[d]	AH (includes ventral tuberal region)[d]
Lateral septum (LS)[e]	LS[e]	LS[e]	LS and dorsal septum	Ventral nucleus of the ventral telencephalon (septum homologue; subdivisions not known)
Ventromedial hypothalamus (VMH)	VMH	VMH	VMH	Anterior tuberal nucleus (in part)[f]
Midbrain: Periaqueductal or central gray (PAG/CG)[g]	CG (substantia grisea centralis)	PAG/CG	?	PAG/CG

Classes Chondrichthyes (cartilaginous fish) and Agnatha (jawless vertebrates) are excluded due to insufficient data.

[a] The nucleus sphericus of squamate reptiles has also been compared to the mammalian MeA based upon vomeronasal inputs, but this structure is most likely homologous to the mammalian posteromedial cortical nucleus of the amygdala (Lanuza and Halpern, 1997).

[b] The BST of reptiles and amphibians is not differentiated into medial and lateral subdivisions, but a portion of the nucleus contains AVT neurons (Lowry et al., 1997; Marin et al., 1998; Smeets et al., 1990; Stoll and Voorn, 1985), as found for the medial BST of most mammals and birds (Aste et al., 1998; Caffe et al., 1989; De Vries et al., 1985).

[c] The POA of fish incorporates peptidergic neuron groups that are homologous to anterior hypothalamic populations in tetrapods (supraoptic and paraventricular nuclei) (Moore and Lowry, 1998).

[d] This large area represents a transition zone between the POA and posterior hypothalamic zones and contains multiple subdivisions in each class. Insufficient data are available to allow direct comparisons of these subdivisions.

[e] Detailed comparisons of subdivisions can be made between rodents, songbirds, and lizards (Font et al., 1995, 1998; Goodson et al., 2004a; Risold and Swanson, 1997a,b).

[f] As recently advanced by Forlano et al. (2005), this homology is suggested by connectivity, position, and the distribution of steroid hormone receptors. However, sex steroid receptors are most dense in hypothalamic areas that are caudolaterally adjacent to the anterior tuberal nucleus (Fine et al., 1990, 1996; Forlano et al., 2005). This topography is similar to that observed in tetrapods for the medial and lateral VMH, respectively, with most sex steroid receptors being found in the lateral VMH (e.g., Wood and Newman, 1995); thus much of the anterior tuberal nucleus may be comparable to the medial VMH.

[g] The midbrain also includes a variety of tegmental sites that are important for social behavior. These include a vocally active tegmental field that lies lateral to the PAG and medial to the auditory torus/inferior colliculus (Goodson and Bass, 2002; Jürgens, 1994; Kennedy, 1975; Phillips et al., 1972) in all classes except Amphibia, in which a comparable vocal site is located at isthmal levels (Wetzel et al., 1985).

Other selected references: Balthazart et al. (1996); Beitz, 1995; Bruce and Neary (1995); Coolen and Wood (1998); Coolen et al. (1998); Cheng et al. (1999); Dong and Swanson (2004); Dong et al. (2001); Dubbeldam and den Boer-Visser (2002); Goodson and Bass (2000c); Goodson et al. (2003, 2004a); Lanuza and Halpern (1998); Lanuza et al. (1997); Moreno and Gonzalez, 2003; Nieuwenhuys et al. (1998); Northcutt (1981); Panzica et al. (1996); Petrovich et al. (2001); Rink and Wullimann (2004); Wong (1997); Wullimann and Mueller (2004).

The social behavior network in a vocalizing fish

One difficulty of studying behavioral systems in most vertebrates is that naturalistic social behavior cannot be observed in a neurophysiological preparation that allows access to large amounts of the brain. However, the plainfin midshipman offers such an opportunity. These fish produce social vocalizations that are structurally simple (rhythmic), and the fundamental frequency and duration of actual vocalization relate in a one-to-one manner with the activity of the sonic motor nucleus in the medulla. The sonic motor neurons fire synchronously, thus their output ("fictive vocalizations") can be neurophysiologically recorded to provide a very accurate depiction of patterned social "behavior" in an acute preparation (Fig. 2A; Bass and Baker, 1990; also see Goodson and Bass, 2000b). The vocal-motor system can be driven by low-amplitude electrical stimulation in many areas of the brain (Goodson and Bass, 2000a,b,c, 2002) and therefore offers the opportunity to study socially relevant brain circuits at a level of detail that is not possible in most other animals (but see Kelley, 2004, for a comparable approach in frogs).

In order to determine the afferent and efferent connections of vocally-active brain loci, we injected biotin compound tract tracers into neurophysiologically-identified sites, which were found distributed throughout the basal forebrain, midbrain tegmentum, and hindbrain (Goodson and Bass, 2002). Other tracings were conducted concurrently on ascending auditory circuitry (Bass et al., 2000; Goodson and Bass, 2002), and we confirmed the general
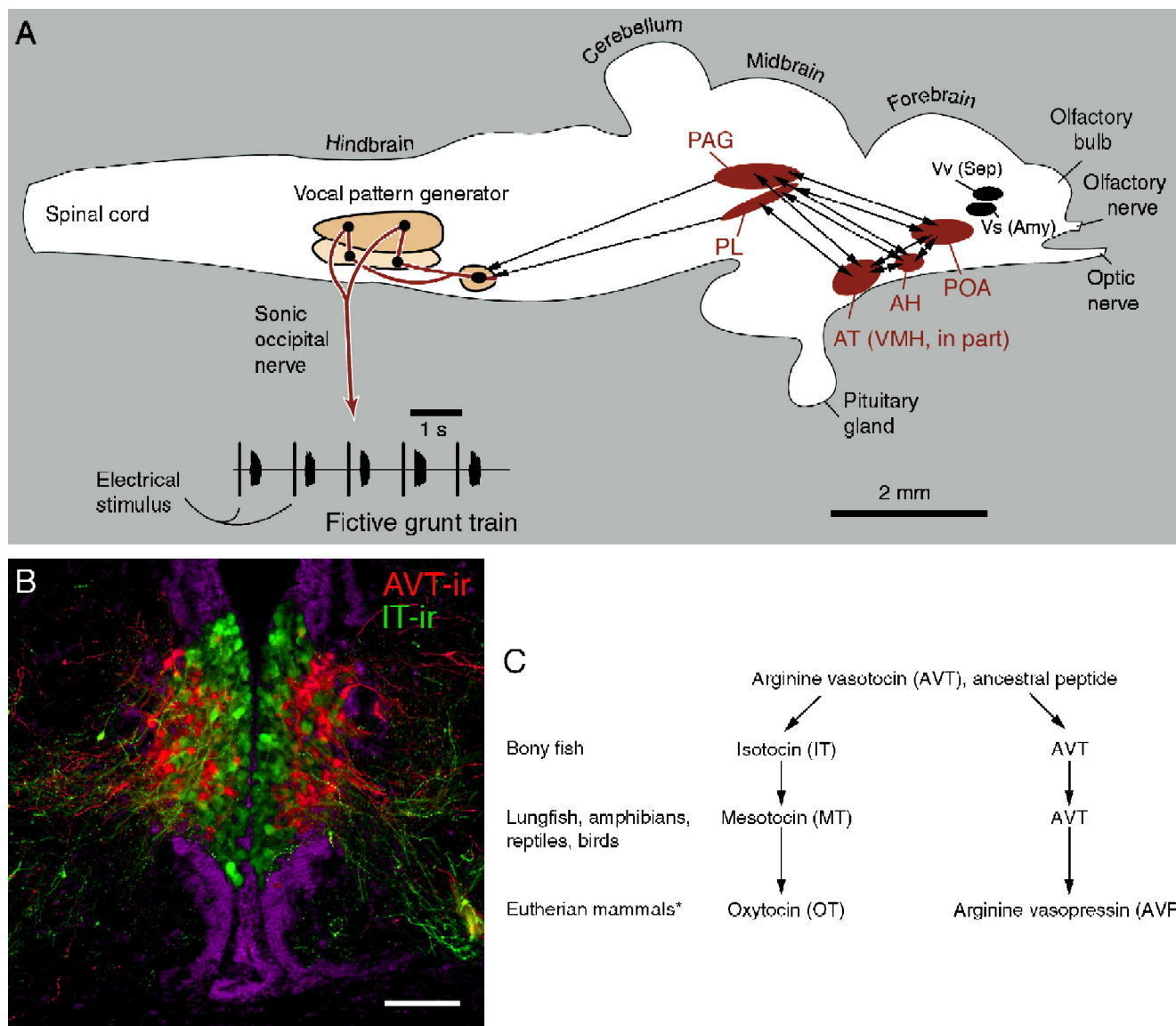
Fig. 2. Connectional, functional, and histochemical features of the social behavior network as exemplified in a vocalizing fish, the plainfin midshipman (*Porichthys notatus*). (A) A schematic sagittal view of the midshipman brain. Electrical stimulation of numerous brain sites activates the hindbrain vocal pattern generator and elicits fictive vocal-motor output that precisely mimics natural vocalizations (shown here are fictive agonistic grunts). Tract tracings of vocally active sites demonstrate that reciprocal connections exist between four areas (shown in red) that are homologous to nodes of the mammalian social behavior network (see Table 1). These areas are also reciprocally connected with nuclei of the basal telencephalon that are homologous to the septum and amygdala (shown in black; for clarity, connections are not shown). As with the six nodes of the mammalian social behavior network, these six areas express sex steroid receptors (e.g., Forlano et al., 2005). (B) Neurons and fibers immunoreactive for arginine vasotocin (red) and isotocin (green) in the parvocellular preoptic area of the midshipman fish (DAPI counterstain is pseudocolored purple). These neurons are the evolutionary precursors of peptidergic neurons in the paraventricular hypothalamus of tetrapods (see panel C for evolution of the vasotocin-like peptide forms; schematic after Acher, 1972; *metatherian mammals retain mesotocin). In all vertebrates, these neurons project to components of the social behavior network, and in the midshipman, these projection systems modulate vocal-motor activity in a sex- and morph-specific manner (see *Blending the sexes* section). Scale bar in B = 200 μm (modified from Goodson et al., 2003). Other abbreviations: AH, anterior hypothalamus; AT, anterior tuberal nucleus of the hypothalamus; PAG, periaqueductal gray; PL, paralemniscal tegmentum; POA, preoptic area; VMH, ventromedial hypothalamus; Vs, supracommissural nucleus of the ventral telencephalon; Vv, ventral nucleus of the ventral telencephalon.

pattern found for midshipman in a related vocal teleost, the gulf toadfish (*Opsanus beta*) (Goodson and Bass, 2002). Once completed, our mapping of vocal-acoustic circuitry in the midshipman and toadfish had outlined a network that is strikingly comparable to the social behavior network of mammals (Fig. 2A).

Forebrain vocal-acoustic sites were found in areas that are homologous to three of Newman's (1999) nodes: the AH, anterior tuberal nucleus (VMH homologue; see Table 1 and Forlano et al., 2005), and POA. Midbrain sites were located within the PAG and adjacent tegmentum (also corresponding to a node in Newman's network). As in the

mammalian social behavior network, all of these forebrain and midbrain areas are reciprocally connected, and all are interconnected with basal forebrain areas that are homologous to the septum and amygdala (Northcutt, 1981). In addition, each of these six areas contains sex steroid receptors (Fine et al., 1990, 1996; Forlano et al., 2005). The topography of these sites is also generally comparable to that in other vertebrates. In fact, the midbrain topography is virtually identical to the topography of vocal sites in mammals (e.g., squirrel monkeys) (Jürgens, 1994), with vocally active sites being found in the portion of the PAG that lies adjacent to the auditory torus (homologue of the inferior colliculus), and in a tegmental band that extends along the medial edge of the torus and lateral lemniscus (paratoral tegmentum and paralemniscal tegmentum). Finally, fish exhibit neuropeptide distributions throughout these areas that are highly similar to neuropeptide distributions in other vertebrate groups (e.g., Batten et al., 1990; Goodson and Bass, 2000c; Goodson et al., 2003; see Figs. 2B–C).

The social behavior network in birds

A wide variety of data have been collected on the neuroendocrine systems of birds, and the avian literature is growing rapidly (Goodson et al., in press). On the whole, the social behavior network in birds exhibits extensive similarities with the mammalian network in its connections, histochemistry, and locations of sex steroid receptors (e.g., Aste et al., 1998; Atoji and Wild, 2004; Balthazart et al., 1994, 1996; Briganti et al., 1996; Cheng et al., 1999; Goodson et al., 2004a; Montagnese et al., 2004; Panzica et al., 1996; Watson and Adkins-Regan, 1989). The pattern of IEG induction that is observed in birds following agonistic interactions is also comparable to that observed in mammals, as are IEG responses to appetitive and consummatory sexual interactions (Ball et al., 1997; Coolen et al., 1996, 1997; Davis and Marler, 2004; Delville et al., 2000; Goodson and Evans, 2004; Goodson et al., submitted for publication; Kollack-Walker and Newman, 1995; Kollack-Walker et al., 1997; Meddle et al., 1997, 1999; Maney and Ball, 2003; Riters et al., 2004; Tlemcani et al., 2000). These similarities in birds and mammals include sex differences in the response to copulation; thus, the POA is more responsive in males whereas the VMH is more responsive in females. Finally, the IEG findings are well corroborated by lesion data on the neural substrates of appetitive and consummatory sexual behavior, as well as aggression (Absil et al., 2002; Balthazart et al., 1998; Goodson et al., 1999; Kondo et al., 1990; Liu et al., 1997; Riters and Ball, 1999; Thompson et al., 1998).

One node of the network that we have focused on extensively is the LS. Septal lesions and neuropeptide infusions influence aggression and social communication in a variety of avian and mammalian species (Fig. 4; Clarke and File, 1982; Ferris et al., 1990; Goodson, 1998a,b; Goodson and Adkins-Regan, 1999; Goodson et al., 1999; Koolhaas et al., 1990), and in birds, the effects of these

manipulations vary in relation to species-typical social structure (see second subsection below). Given that the LS of birds and mammals receives the heaviest hippocampal projection of any structure in the brain, and that this projection is topographically organized (Atoji and Wild, 2004; Risold and Swanson, 1997b), it is not surprising that the effects of septal manipulations are complex and context-dependent (e.g., Goodson, 1998a; Goodson et al., 1999). The organization of the LS is likewise daunting in its complexity, with 20 chemoarchitectonic zones having been described for rats (Risold and Swanson, 1997a). However, this architecture is remarkably conserved: By using antibodies against ten neuropeptides and enzymes, we have recently identified virtually all of these zones (or their conglomerates) in songbirds (Goodson et al., 2004a; see Fig. 3).

These anatomical studies have provided a detailed framework for analyzing IEG data, and we have therefore produced data on LS function that are on a relatively fine spatial scale (Goodson and Evans, 2004; Goodson et al., 2005; Goodson et al., submitted for publication). These recent IEG studies show that the ventrolateral zones of the caudal LS are the most responsive to social stimuli, a finding that matches well to data from mammals. Interestingly, LS responses to agonistic encounters are greater in subordinant male hamsters (*Mesocricetus auratus*) than in dominant animals (Kollack-Walker et al., 1997), and we have likewise found that IEG responses of the LS are negatively correlated with aggressive behavior in male song sparrows (*Melospiza melodia*; Figs. 4A–B). In both hamsters and sparrows, this effect is particularly pronounced in the ventrolateral LS.

Variations on the themes: evolutionary modifications associated with phenotypic diversity

While the network described above appears to be fundamental to the expression of social behavior in all vertebrate species, it must also express functionally labile features that underlie phenotypic variation in behavior. As described below, we have identified several network features that provide some of this functional diversity. For instance, we have demonstrated that various neuropeptides exhibit morph- and species-specific effects on behavior (Goodson, 1998a,b; Goodson and Adkins-Regan, 1999; Goodson and Bass, 2000a) and have additionally shown that network responses to social stimuli are divergently patterned in songbird species that differ selectively in sociality (Goodson et al., 2005). Ongoing work suggests that these species-specific network responses are related to divergence in peptidergic neuron activity and species differences in neuropeptide receptor distributions. That is, peptidergic variables may coordinate the species differences in network response.

A number of these studies have focused on the vasotocin family of neuropeptides, which includes arginine vasotocin (AVT; found in non-mammals), its mammalian homologue
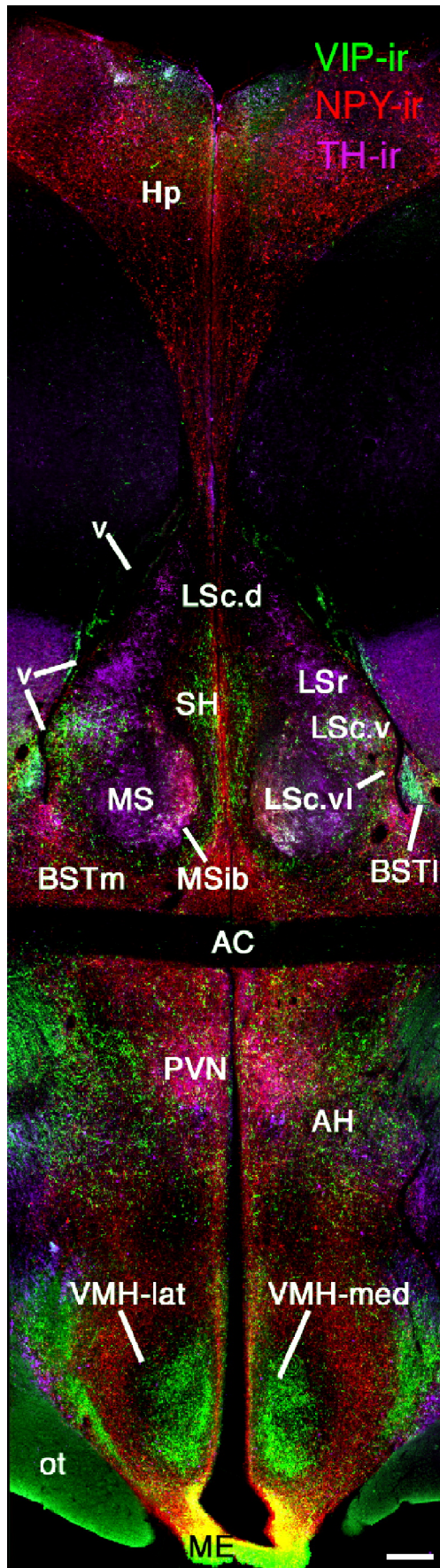
arginine vasopressin (AVP), and the oxytocin-like peptides (isotocin, found in fish; mesotocin, found in lungfish and non-eutherian tetrapods; and oxytocin, found in eutherian mammals) (Acher, 1972; see Figs. 2B–C). More so than any other class of neurochemicals, these peptides have been found to be axes of behavioral plasticity and social diversity, and the features of these systems are associated with seasonal variation, sex differences, and species divergence in behavior (reviews: De Vries and Boyle, 1998; Foran and Bass, 1999; Goodson and Bass, 2001; Insel and Young, 2000; Keverne and Curley, 2004; Lim et al., 2004a; Panzica et al., 2001). Despite these aspects of variation, the locations of AVT/AVP neurons and fibers have been strongly conserved during vertebrate evolution (Moore and Lowry, 1998; Goodson and Bass, 2001), and the AVT/AVP system is an integral component of the social behavior network in all vertebrate groups.

Blending the sexes: peptidergic neuromodulation in a sexually polymorphic fish

Given that (1) the plainfin midshipman exhibits strong sex and morph differences in the contextual use of vocalizations (Brantley and Bass, 1994), (2) peptides of the vasotocin family influence communication behaviors across a wide range of vertebrate taxa (Goodson and Bass, 2001), and (3) peptides of the vasotocin family occasionally exhibit sex-specific effects (see below), we conducted a series of neurophysiological experiments in the midshipman to determine the neuromodulatory effects of isotocin and AVT on fictive social vocalizations in the three reproductive morphs (Goodson and Bass, 2000a). We hypothesized that neuropeptide manipulations would produce sex-specific effects, given that AVT and AVP are more strongly implicated in male-typical behaviors (although this is not ubiquitous), while oxytocin is more strongly associated with a female-typical functions (Bluthe

Fig. 3. Chemoarchitectural themes of the social behavior network as exemplified in songbirds (photomontage of a female zebra finch brain at the level of the anterior commissure; AC). Immunohistochemical triple-labeling for vasoactive intestinal polypeptide (VIP; Alexa Fluor 488, green), neuropeptide Y (NPY; Alexa Fluor 594, red), and tyrosine hydroxylase (TH; Alexa Fluor 350, pseudocolored purple) shows the location of multiple zones of the lateral septum (LS) and bed nucleus of the stria terminalis (BST) that are now known to be extensively comparable to mammals (see Aste et al., 1998; Goodson et al., 2004a; Richard et al., 2004). This labeling also clearly shows the medial and lateral divisions of the ventromedial hypothalamus which exhibit a similar topography across the vertebrate taxa (see Table 1). Scale bar = 200 μm. Modified from Goodson et al., 2004a. Other abbreviations: AH, anterior hypothalamus; BSTm, medial bed nucleus of the stria terminalis; BSTl, lateral bed nucleus of the stria terminalis; Hp, hippocampus; LSc, caudal division of the lateral septum (dorsal, ventrolateral, and ventral zones denoted as LSc.d, LSc.vl, and LSc.v, respectively); LSr, rostral division of the lateral septum; ME, median eminence; MSib, internal band of the medial septum; ot, optic tract; OM, occipitomesencephalic tract; PVN, paraventricular nucleus of the hypothalamus; SH, septohippocampal septum; v, lateral ventricle.
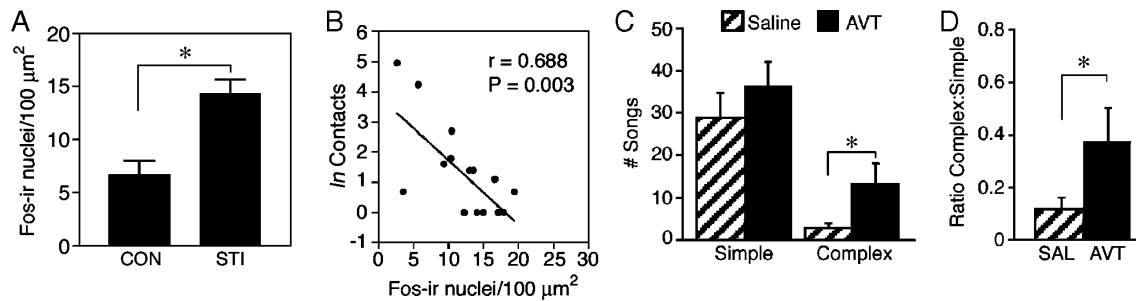
Fig. 4. Functional themes of the lateral septum (LS) as exemplified by findings in wild-caught, territorial male song sparrows (*Melospiza melodia*; A–B) and field sparrows (*Spizella pusilla*; C–D). Similar to rodents, Fos-immunoreactive (-ir) cell counts in the ventrolateral LS are increased by an agonistic encounter (A; simulated territorial intrusion; STI), but the most aggressive animals show virtually no Fos induction (B; cf. Kollack-Walker et al., 1997). The aggression measure shown in B is based on contacts with the wire barrier that separated the subject from the intruder (A–B; Goodson et al., submitted for publication). Also similar to rodents, septal infusions of arginine vasotocin (AVT; homologue of arginine vasopressin) facilitate agonistic communication (C–D; cf. Irvin et al., 1990). Data shown in C–D are from field sparrows housed on semi-natural territories (field-based flight cages placed in natural habitat; modified from Goodson, 1998a). (C) The number of simple and complex songs given spontaneously during the dawn singing period; these song types are multipurpose and strictly agonistic, respectively (see Nelson and Croner, 1991). (D) The ratio of complex to simple songs, showing an increase in the agonistic content of song following intraseptal infusion of 100 ng AVT. *$P < 0.05$, unpaired t test (A) or Wilcoxon signed ranks (C–D).

and Dantzer, 1990; Carter and Altemus, 1997; Francis et al., 2002; Goodson et al., 2004b; Insel and Hulihan, 1995; Keverne and Curley, 2004).

The plainfin midshipman exhibits three reproductive phenotypes (type I males, type II males and females) and this species therefore offers a relatively novel system for the examination of sex-specific peptide functions. Type I males excavate nests in the intertidal zone and vocally court females with a long-duration hum that can last up to 2 h. These hums are exhibited solely by the type I males, as are territorial growls. Given that females visit nests only to spawn, the type I males are also the sole providers of parental care. Type II males are morphologically feminized and likewise visit nests only to spawn (by sneak spawning or satellite spawning). However, while the type II males are feminized in their appearance and much of their behavior, they are gonadally hypermasculinized and possess gonad: body size ratios that are ~9 times that of the type I males (Brantley and Bass, 1994). All three of the morphs exhibit agonistic grunts–short duration calls (~50 ms) that are distinguished from hums primarily by their duration and contextual use. Grunts are the only vocalization exhibited by females and type II males (for a review of midshipman behavioral biology, see Bass, 1996).

We found that fictive grunting elicited by stimulation of the AH in female midshipman is (1) inhibited by local delivery of isotocin in a dose-dependent manner, (2) dramatically facilitated an oxytocin antagonist, and (3) relatively insensitive to AVT and an AVP antagonist. In contrast, type I males show an opposite pattern of sensitivity, being sensitive to AVT and its antagonist, but not isotocin or its antagonist. Interestingly, the type II males exhibit a pattern of peptide sensitivity that is virtually identical to females (Goodson and Bass, 2000a), despite the fact that the site of peptide delivery is located in a brain region (the POA-AH) that regulates the pituitary-gonadal axis of type II males in a hypermasculine manner. Hence, these data indicate that regulatory mechanisms for sex-typical behavior and gonadal

physiology can be uncoupled from each other within the same general brain areas. Indeed, this uncoupling may occur at the level of individual neurons, as other data from teleosts show that IT and gonadotropin releasing hormone are produced by the same cells (Maejima et al., 1994).

Patterns of peptidergic modulation and network response reflect species-typical group size

AVT also exerts behavioral effects that are species-specific. For instance, AVT inhibits overt aggression when infused into the septum of territorial songbird species but facilitates aggression in a colonial species (Goodson, 1998a,b; Goodson and Adkins-Regan, 1999). These experiments employed two species that independently evolved territoriality and controlled for multiple aspects of behavior, ecology, and phylogeny. However, results in male field sparrows (*Spizella pusilla*) indicate that these effects may not reflect direct effects on agonistic behavior per se, given that AVT facilitates the use of a strictly agonistic song type during spontaneous dawn singing (Figs. 4C–D) but inhibits overt aggression directed at a male intruder (Goodson, 1998a). Such findings suggest that AVT may primarily modulate anxiety or stress-related processes, with subsequent effects on agonistic behavior being context-dependent. Indeed, by combining AVT receptor blockade with presentation of an intense non-social stressor and/or simulated territorial challenge, we have shown that the release of endogenous AVT into the LS primarily modulates responses to stress (as determined by examining immunoreactivity for the IEG Zenk) (Goodson and Evans, 2004). In addition, the effects of AVT on agonistic behavior are generally opposite of those produced by intraseptal infusions of vasoactive intestinal polypeptide (VIP) (Goodson, 1998a,b; Goodson and Adkins-Regan, 1999), and these findings are paralleled by data showing that VIP- and AVT-immunoreactive (-ir) fibers within the LS are differentially sensitive to castration and testosterone replacement in male quail (i.e., castration

produces increases in VIP-ir and decreases in AVT-ir, with effects being reversed by treatments with testosterone) (Aste et al., 1997).

The experiments described above suggest that neuroendocrine processes related to stress may play an important role in differentiating the behavior of animals that live in large groups from those that live as territorial pairs. Data from mammals are consistent with this idea, as neuropeptide manipulations that influence affiliation also modulate anxiety (e.g., Pitkow et al., 2001). However, evolutionary shifts in species-typical group size ("sociality") could reflect natural selection on several motivational processes in addition to anxiety and stress, including social arousal, approach-avoidance, reward, and dominance. In fact, evolutionary divergence in reward processes has been clearly linked to evolution in another aspect of social structure – mating system. Monogamous mammals exhibit higher levels of vasopressin and oxytocin receptors within the ventral pallidum and/or nucleus accumbens than do non-monogamous species, and these species-specific features play an important role in the expression of bonding (Lim and Young, 2004; Lim et al., 2004b; Pitkow et al., 2001). However, while these findings show that reward-related processes are linked to affiliation and bonding, they do not make clear whether reward processes evolve divergently in relation to sociality, when sociality is uncoupled from mating system.
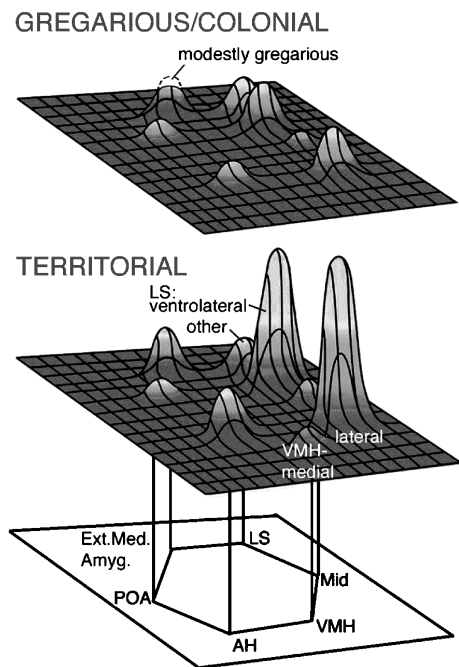

Fig. 5. A schematic representation of immediate early gene responses (Fos and/or Zenk) within the social behavior network following exposure to a same-sex conspecific in four estrildid songbird species that differ selectively in their species-typical group sizes (two colonial species, one modestly gregarious species and one territorial species; both males and females were examined). Exposure was conducted in a paradigm that limits overt behavioral performance; thus, species differences should reflect differences in motivational and/or perceptual processes. Modified from Goodson et al., 2005.

Thus, in order to gain a broader understanding of how neuromotivational systems evolve in relation to species-typical group size, we recently examined Fos and Zenk (egr-1) responses to a same-sex conspecific in songbird species that differ selectively in sociality. Analyses were focused on components of the social behavior network and related structures that are involved in stress and reward processes. In order to isolate sociality as a quasi-independent variable, we used four estrildid species (both sexes) that differ selectively in their species-typical group sizes (Goodson et al., 2005) (Fig. 5). These species are the territorial violet-eared waxbill, *Uraeginthus granatina* (group size = 2, excluding dependent young; i.e., male-female pair), the moderately gregarious Angolan blue waxbill, *Uraeginthus angolensis* (group size = 8–40), and two colonial species, the zebra finch, *Taeniopygia guttata*, and the spice finch, *Lonchura punctulata* (group sizes = 90–300). In choosing these species, we sought to control for multiple aspects of behavior and ecology that may influence how an animal responds to social stimuli. The species that we used are all monogamous (typically pair bonding for life), exhibit biparental care, breed semi-opportunistically dependent upon rainfall, and inhabit arid and/or semi-arid habitat (although the spice finch's range also includes more mesic habitats). These songbirds exhibit only limited conditional variability in grouping behavior such that the species differences in sociality are stable across seasons and contexts (Goodwin, 1982; Skead, 1975; Zann, 1996; also see references within).

Our paradigm for social exposure limited behavioral performance; thus, species differences in IEG response should reflect divergence in motivational and/or perceptual processes. The significant results from this experiment are presented schematically in Fig. 3. Within the extended medial amygdala (which is involved in appetitive approach, social arousal, and avoidance; Absil et al., 2002; Newman, 1999; Sheehan et al., 2000; Thompson et al., 1998), we observed species differences in IEG response that are negatively graded in relation to sociality. In addition, the ventrolateral septum, anterior hypothalamus, and lateral subdivision of the ventromedial hypothalamus exhibited IEG responses that were significantly greater in the territorial species than in the three gregarious species (Goodson et al., 2005). These areas are strongly responsive to social subjugation in hamsters (Kollack-Walker et al., 1997) and are components of a putative aversion network in rats (Sheehan et al., 2000, 2001). Thus, the pattern of IEG response that distinguishes the territorial species may be reflective of social stress. This hypothesis is solidly supported by other IEG data in song sparrows: As shown in Figs. 4A–B, the ventrolateral LS is strongly responsive to agonistic encounters, but Fos and Zenk responses correlate negatively with the subjects' aggressive behavior (similar to the difference between dominant and subordinate hamsters). The AH exhibits a similar profile to the ventrolateral LS (Goodson et al., submitted for publication) and the lateral VMH is responsive to both handling/restraint stress and agonistic challenge (Goodson and Evans, 2004).

Importantly, the responses of other stress-related areas (most zones of the LS, lateral BST, and paraventricular nucleus of the hypothalamus; see Goodson and Evans, 2004) and reward areas (nucleus accumbens and ventral pallidum) do not correlate with sociality. These findings suggest that social evolution has been accompanied by selection on a relatively discrete suite of motivational systems.

We are currently completing multiple studies that are designed to elucidate neuroendocrine mechanisms that underlie these species differences in neural response. These recent experiments have added a second territorial species, the melba finch (*Pytilia melba*), and therefore include two species that have independently evolved territoriality (melba finch and violet-eared waxbill), two species that independently evolved coloniality (spice finch and zebra finch), and one intermediate species (Angolan blue waxbill). We have found that receptor distributions for corticotropin-releasing factor, VIP and AVT are all species-specific, with multiple species differences showing good correspondence to species-typical group size (J. L. Goodson, Y. Wang and A. K. Evans, unpublished observation). In addition, an extensive series of experiments is focused on activation of the AVT neurons in the extended medial amygdala (BSTm). By immunocytochemically double-labeling for AVT and IEGs (Fos and Zenk), we have found that the activity of these AVT neurons reflects both reproductive state and species-typical group size (J. L. Goodson and A. K. Evans, unpublished observation), and we are now more fully characterizing the stimulus parameters that elicit IEG responses within this neuronal population.

Conclusions

Based on a variety of behavioral, connectional, and histochemical findings, it is now clear that the brain circuits that regulate social behavior in non-mammalian vertebrates are extensively similar to those in mammals. These observations strongly support the proposal that the social behavior network (as first described for mammals; Newman, 1999) is a fundamental and evolutionarily conserved feature of the vertebrate brain. Given this, it should be possible to select species for study based upon their behavioral biology, not their taxonomic class, and yet generate insights that are potentially relevant for all vertebrate classes. However, research is often (even typically) conducted within a taxon-specific framework, even when relevant data are available in other vertebrate groups. As our understanding of behavioral neuroendocrinology becomes more advanced, such an approach will unnecessarily limit us as to what we can understand. Studies of sociality provide a good example: Even in the most socially diverse taxa, species differences in group size are typically confounded with other important variables, including mating system, patterns of parental care, habitat preferences, and/or the seasonal expression of behavior. Aggregation in many species is also highly condi-

tional. Thus, for most animals, controlled species comparisons of grouping behavior are virtually impossible to conduct. Fortunately, a limited number of songbird groups exhibit stable patterns of aggregation that can be investigated independently of other important variables. These species therefore offer a unique opportunity to understand how neural, neuroendocrine, and motivational processes evolve in relation to species-typical group size, and in response to ecological variables that ultimately select for relevant behavioral variations.

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