Psychoneuroendocrinology (2013) 38, 465—478

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INVITED REVIEW

Deconstructing sociality, social evolution and relevant nonapeptide functions

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Received 7 August 2012; received in revised form 11 December 2012; accepted 12 December 2012

KEYWORDS
Vasopressin;
Vasotocin;
Oxytocin;
Mesotocin;
Isotocin;
Vole;
Songbird;
Flocking;
Sociality;
Pair bond

Summary Although behavioral neuroendocrinologists often discuss "sociality" as a unitary variable, the term encompasses a wide diversity of behaviors that do not evolve in a linked fashion across species. Thus grouping, monogamy, paternal care, cooperative breeding/alloparental care, and various other forms of social contact are evolutionarily labile and evolve in an almost cafeteria-like fashion, indicating that relevant neural mechanisms are at least partially dissociable. This poses a challenge for the study of the nonapeptides (vasopressin, oxytocin, and homologous neuropeptides), because nonapeptides are known to modulate all of these aspects of sociality in one species or another. Hence, we may expect substantial diversity in the behavioral functions of nonapeptides across species, and indeed this is the case. Further compounding this complexity is the fact that the pleiotropic contributions of nonapeptides to social behavior are matched by pleiotropic contributions to physiology. Given these considerations, single "model systems" approaches to nonapeptide function will likely not have strong predictive validity for humans or other species. Rather, if we are to achieve predictive validity, we must sample a wide diversity of species in an attempt to derive general principles. In the present review, I discuss what is known about functional evolution of nonapeptide systems, and critically evaluate general assumptions about bonding and other functions that are based on the model systems approach. From this analysis I attempt to summarize what can and cannot be generalized across species, and highlight critical gaps in our knowledge about the functional evolution of nonapeptide systems as it relates to dimensions of sociality.

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http://dx.doi.org/10.1016/j.psyneuen.2012.12.005

1. What is sociality?

The term ''sociality'' has its roots in the fields of animal behavior, behavioral ecology and evolutionary biology, where it is most often used explicitly in reference to grouping behavior. In fact, in his classic review of social behavior, Alexander (1974) succinctly states ''Sociality means group-living'' (1974, p. 326). This definition persists in the disciplines just listed; for example, Silk (2007) carefully distinguishes sociality from other social categories such as bonds. However, over the last 20+ years, this definition has been substantially broadened within the behavioral neuroscience community, and is now used to refer to virtually any social behavior that is in some way affiliative (e.g., Carter et al., 2008; Donaldson and Young, 2008). Thus, in addition to group-living, behavioral neuroscientists consider

Table 1 A sample of social behaviors and associated processes that are influenced by OT and OTR activation, or by homologous peptides and receptors.[a]

Behavior	Effect[b]	Species	Reference[c]
Maternal aggression	Decrease	Rat	Giovenardi et al. (1998)
	Increase	Rat	Bosch et al. (2005)
Territorial aggression	Decrease	Syrian hamster	Harmon et al. (2002a)
		Syrian hamster	
Agonistic communication	Decrease	Plainfin midshipman fish	Goodson and Bass (2000)
	Increase	Syrian hamster	Harmon et al. (2002b)
Social contact, approach	No effect	Zebra finch	Goodson et al. (2009b)
	Increase	Goldfish	Thompson and Walton (2004)
	Increase	Common marmoset	Smith et al. (2010)
	Increase	Rat	Lukas et al. (2011)
	Increase	Human	Liu et al. (2012a)
Gregariousness	Increase	Zebra finch	Goodson et al. (2009b)
Outgroup derogation	Increase	Human	De Dreu et al. (2011)
Parochial altruism	Increase	Human	De Dreu et al. (2010)
Trust	Increase	Human	Kosfeld et al. (2005)
	Decrease	Human	Bartz et al. (2011a)
Maternal care	Increase	Rat	Pedersen et al. (1982)
		Prairie vole	Olazabal and Young (2006)
		Sheep	Kendrick et al. (1987)
Alloparental care	Increase	Vole	Keebaugh and Young (2011)
Pair bonding, partner preference	Increase	Prairie vole	Williams et al. (1994)
	No effect	Cichlid (*A. burtoni*)[d]	Oldfield and Hofmann (2011)
	No effect	Common marmoset	Smith et al. (2010)
	No effect	Human	Liu et al. (2012b)
	Increase	Zebra finch	Klatt and Goodson (2013) and Pedersen and Tomaszycki (2012)
Cooperation	Phenotype-specific	Human	Rilling et al. (2012) De Dreu (2012)
Sexual behavior (copulation, receptivity)	Increase	Rabbit	Fjellstrom et al. (1968)
	Decrease	Prairie vole	Mahalati et al. (1991)
	Increase	Rat	Caldwell et al. (1989) and Argiolas and Melis (2004)

[a] Note that in most species, OTRs and homologous receptors mediate effects of oxytocic peptides, VT, and VP, and not oxytocic peptides alone.
[b] Effects may be brain site-specific and/or sex-specific; see references for details.
[c] References are representative and not intended to be exhaustive.
[d] Based on nonselective antagonism of nonapeptide receptors.

sociality to encompass dimensions of behavior such as parental care, alloparental care, pair bonding, allogrooming, and huddling. The descriptor "prosocial behavior" is increasingly being used in much the same way. Nonetheless, these terms are not problematic if the expanded definitions are used by behavioral neuroscientists in a consistent manner that is understood by all. For the most part, this seems to be the case. However, it does *not* appear to be widely appreciated that these terms are now umbrellas for multiple dimensions of behavior. Of greatest concern is the fact that sociality and prosocial behavior are often presented as unitary constructs that are influenced by the nonapeptides; for instance, by stating that nonapeptides such as oxytocin (OT) and vasopressin (VP) promote sociality or prosocial behavior (e.g., Meyer-Lindenberg, 2008; Zak, 2011; Poulin et al., 2012).

The reasons for such generalizations are not hard to identify. First, in the most common model of social monogamy and biparental care, the prairie vole (*Microtus ochrogaster*), nonapeptides promote almost all of the social behaviors listed above (parental care, alloparental care, pair bonding, allogrooming, and huddling) (reviews: Carter et al., 2008; McGraw and Young, 2010; Young et al., 2011). Second, even in nonmonogamous, uniparental species such as rats, nonapeptides promote aspects of affiliation such as maternal care and infant huddling, in addition to sexual behavior (Pedersen et al., 1982; Pedersen and Boccia, 2006; Bosch and Neumann, 2008; Kojima and Alberts, 2011). However, the fact that nonapeptides promote some dimensions of sociality in rats without also promoting social monogamy, male parental care and cooperative breeding is clear evidence that nonapeptides do not influence some unitary dimension of behavior that we can call "sociality." Rather, rats have evolved nonapeptide circuits that promote some social behaviors, whereas other behaviors that now fall under the sociality umbrella do not exist in rats at all. Furthermore, nonapeptides often produce effects that cannot be construed as prosocial (see Tables 1 and 2 for exemplars of nonapeptide effects, and Bos et al., 2012, for a comprehensive review of the human literature). These include the promotion of offensive aggression (Ferris and Delville, 1994), social avoidance (Thompson and Walton, 2004), negative appraisal of neutral social stimuli (Thompson et al., 2006), outgroup derogation (De Dreu et al., 2011; but see Van and Bakermans-Kranenburg, 2012), and aggressive responses to perceived threat (De Dreu et al., 2010). OT also reduces trust in borderline personality patients (Bartz et al., 2011a) and biases memory for aversive stimuli relative to neutral stimuli (Striepens et al.,

Table 2 Social behaviors and associated processes that are influenced by VT/VP and V_{1a}-like receptors.[a]

Behavior	Effect[b]	Species	Reference[c]
Maternal aggression	Decrease	Rat	Nephew and Bridges (2008)
Territorial aggression	Decrease	Violet-eared waxbill	Goodson (1998b)
		Field sparrow	Goodson (1998a)
Aggressive competition for mates	Increase	Zebra finch	Goodson et al. (2004)
		Violet-eared waxbill	Goodson et al. (2009a)
Agonistic communication	Decrease	Plainfin midshipman fish	Goodson and Bass (2000)
	Increase	Syrian hamster (male)	Ferris et al. (1984)
	Decrease	Syrian hamster (female)	Gutzler et al. (2010)
	Species-specific	Frog species	Goodson and Bass (2001)
	Increase	Human	Thompson and Walton (2004)
Social contact, approach	Decrease	Zebra finch	Kelly et al. (2011)
	Increase	Rat	Landgraf et al. (2003)
	Decrease	Goldfish	Thompson and Walton (2004)
Gregariousness	Increase	Zebra finch	Kelly et al. (2011)
Maternal care	Increase	Rat	Bosch and Neumann (2008)
Paternal care	Increase	Prairie vole	Wang et al. (1994)
Pair bonding	Increase	Prairie vole	Winslow et al. (1993)
	No effect	Cichlid (*A. burtoni*)[d]	Oldfield and Hofmann (2011)
	No effect	Zebra finch	Kabelik et al. (2009)
Cooperation	Increase	Human	Rilling et al. (2012)
Sexual behavior (copulation, receptivity)	Decrease	Rabbit	Kihlstrom and Agmo (1974)
	Decrease	Rat	Sodersten et al. (1983)
	Increase	Syrian hamster	Huhman and Albers (1993)
	Increase	Chicken	Kihlstrom and Danninge (1972)
	Increase	Rock dove	Kihlstrom and Danninge (1972)
	Decrease	Japanese quail	Castagna et al. (1998)
	Increase	Rough-skinned newt	Moore and Miller (1983)
	Increase	Northern leopard frog	Diakow (1978)

[a] Note that in many species, V_{1a}-like receptors mediate effects of both VT/VP and oxytocic peptides, and not VT/VP alone.
[b] Effects may be brain site-specific and/or sex-specific; see references for details.
[c] References are representative and not intended to be exhaustive.
[d] Based on nonselective antagonism of nonapeptide receptors.

2012). Finally, even our views of what qualifies as more social or prosocial are sometimes questionable; for instance, perhaps only from a western, anthropocentric view would monogamy be considered more social than having multiple mates.

Consistent with a modular view of nonapeptide function and evolution, there is abundant evidence spanning all vertebrate classes to underscore the point that components of sociality evolve independently of each other. For instance, bonobos (*Pan paniscus*) are in many ways highly sexual, gregarious and affiliative, but at the same time highly promiscuous (Stanford, 1998). Similarly, many other primates exhibit a high paternal investment in offspring, despite being nonmonogamous (Smuts and Gubernick, 1992). The socially monogamous superb fairy-wren (*Malurus cyaneus*) exhibits strong pair bonds and cooperative breeding, yet is also highly promiscuous, with the vast majority of nestlings being sired through cuckoldry (Mulder et al., 1994). Many such examples can be provided in which behaviors that are often lumped under the descriptor of "sociality" are clearly dissociable. Hence, it is inaccurate at best to state that any neural system promotes "sociality," unless the term is being used in the more restricted sense of grouping. This is not to say that we must return to the historical use of the term (as still employed in other disciplines), but rather that we should be specific about what we are talking about, and discuss "sociality" as a general category comprised of many dissociable dimensions, much as we might use the term "behavior" more broadly.

2. Model systems, evolutionary diversity and translation

2.1. Functional constraints and pleiotropy

As described above, dimensions of sociality that are known to be influenced by the nonapeptides are also dissociable over evolutionary time. The implications of this for the "model systems" approach are truly profound. This is because the model systems *modus operandi* is to delve deeply into the biology of one or two tractable species and then generalize to others — hence the descriptor "model," which is defined as a representation of some other person or thing. But if nonapeptides exert pleiotropic effects on multiple dimensions of behavior and physiology, and if natural selection pushes those aspects of behavior and physiology in different directions, then something will need to change in the pleiotropic relationship between a given nonapeptide circuit and its multiple targets and functions. For instance, if an OT circuit promotes both gregariousness and monogamous behavior in the ancestral state, and natural selection begins to favor promiscuity but not solitary living, then something has to give. If OT is more important for the modulation of one behavioral function than the other, perhaps the less important function may be lost, but only if it is mechanistically possible to drop one function while augmenting another. If not, then the evolutionary process may be constrained, or the evolution of behavior and brain systems may be canalized to some extent.

Given these considerations, it is clear that nonapeptide systems will tend to evolve in very species-specific ways, depending upon the evolutionary background of the species. Relevant aspects of evolutionary background will include anything that is influenced by nonapeptides — social behaviors, nonsocial behaviors, various aspects of physiology, sensory processing, etc., in addition to the ecological variables to which they relate, such as resource availability, seasonal variation, and temperature. All of those things may guide or constrain the evolutionary process.

This is particularly relevant when weighing evidence from model systems, because we cannot assume that nonapeptide systems will evolve in similar ways in all taxa, or even in closely related species. This produces a conundrum for translation that can only be dealt with by (1) broadening the study of sociality and nonapeptide functions to a much larger number of species, (2) conducting work in an explicitly evolutionary framework that considers phylogeny and ancestral states, and (3) looking for themes amongst the diversity. This does not mean that common lab animals such as mice, rats, and voles need to take a back seat. To the contrary — the tools that are available for the study of those animals virtually assure that they will be at the cutting edge of discovery. Nonetheless, when it comes to translational insights into sociality and underlying nonapeptide mechanisms, it must be appreciated that laboratory rodents cannot be viewed as models for humans. Rather, predictive validity for humans and other species can only be achieved by examining how nonapeptide functions evolve on different backgrounds of social life history and physiology.

2.2. The vertebrate nonapeptides

Nonapeptides are an ancient family of neuropeptides found in both vertebrates and invertebrates. The vertebrate nonapeptides are all derived from arginine vasotocin (VT), and the separate clades (evolutionary lineages) of OT- and VP-like peptides are derived from a duplication of the VT gene in early jawed fishes. VT is present in all nonmammalian species examined to date, and a single amino acid substitution was made in mammals, giving rise to arginine VP. Some mammals, such as pigs and hippos, express lysine VP instead of arginine VP, and some marsupials express phenypressin. A variety of other taxonomically restricted variants also exist (Acher, 1972; Hoyle, 1998).

The gene duplication event in early fish is temporally associated with two amino acid substitutions in the duplicated gene product, giving rise to the oxytocic peptide lineage. The form found in all extant bony fish is Ser^{4}, Ile^{8}-OT, or isotocin. Lungfish, amphibians, reptiles and birds all possess another form, Ile^{8}-OT, or mesotocin (MT). MT is also found in some marsupial mammal species. Another amino acid substitution was made in mammals, which mostly express Leu^{8}-OT, although recent findings show that New World monkeys exhibit Pro^{8}-OT (Acher, 1972; Hoyle, 1998; Lee et al., 2011). Finally, cartilaginous fish (e.g., sharks, skates and rays) have evolved at least six oxytocic peptide forms, including the common mammalian form, Leu^{8}-OT (Acher et al., 1999). Despite this diversity, Leu^{8}-OT and VT differ in only one amino acid.

Athough there is currently an intense focus on the social functions of nonapeptides, these peptides also play important and evolutionarily conserved roles in numerous physiological and nonsocial functions such as cardiovascular tone, hydromineral balance, secretion of adrenocorticotropin,

anxiety modulation, and smooth muscle contractions (Sawyer, 1977; Robinzon et al., 1988; Baker et al., 1996; Engelmann et al., 2000; Kelly et al., 2011). In addition, other functions have been described in mammals (which may exist in other taxa, as well), including grooming, appetite modulation, and thermoregulation (Banet and Wieland, 1985; Van Wimersma Greidanus et al., 1990; Leng et al., 2008). Finally, in all taxa, including humans, nonapeptides interact with sex steroids to influence behavior in a context-appropriate manner (Goodson and Bass, 2001; Bos et al., 2012).

2.3. Nonapeptides and bonding: common or uncommon?

To date, very few research programs have placed socially-relevant nonapeptide functions into an evolutionary framework, and the majority of this work has been conducted on the mechanisms of pair bonding. In 1993, Winslow and colleagues published the seminal findings in this field, which showed that in male prairie voles, chronic intracerebroventricular (i.c.v.) infusions of VP promote selective partner preferences in the absence of mating. Mating is normally required for the establishment of pair bonds. This effect is reversed by administration of a V_{1a} receptor (V1aR) antagonist (Winslow et al., 1993). Subsequent experiments demonstrate that V1aRs in the ventral pallidum and lateral septum (LS) are critical for VP's effects on partner preference (Liu et al., 2001; Lim and Young, 2004), and that viral vector-mediated overexpression of V1aRs in the ventral pallidum facilitates preference (Pitkow et al., 2001).

Other findings have further focused attention on the ventral pallidum. First, monogamous prairie voles and monogamous pine voles (*M. pinetorum*) exhibit higher V1aR densities in the ventral pallidum than do nonmonogamous meadow voles (*M. pennsylvanicus*) and nonmonogamous montane voles (*M. montanus*) (Insel et al., 1994; note that the area was originally misidentified; see Young et al., 2001). Second, and quite impressive, is the finding that V1aR overexpression in the ventral pallidum of montane voles promotes the establishment of selective partner preferences (Lim et al., 2004). Similar behavioral results are obtained in transgenic mice expressing the prairie vole V1aR gene (Young et al., 1999).

These findings convincingly demonstrate that the levels of V1aR expression in the ventral pallidum are a critical part of what makes male prairie voles monogamous. The findings also suggest that nonmonogamous species may evolve the ability to form selective partner preferences simply by increasing V1aR density in the ventral pallidum. However, male prairie voles that behave promiscuously in naturalistic outdoor enclosures do not exhibit lower V1aR densities in the ventral pallidum than do males that pair bond, and thus under natural conditions, these receptors may play a permissive role in monogamy, rather than dictating it (Ophir et al., 2008).

Regardless, the question thus becomes, *is this a mechanism that commonly evolves in relation to monogamy?* On the surface, it may seem to be so in microtine voles, given the differences in receptor distributions between the monogamous and nonmonogamous species. However, the monogamous pine and prairie voles are much more closely related to each other than they are to the nonmonogamous montane and meadow voles (Fink et al., 2006). Thus, mechanisms associated with the evolution of monogamy in voles can be stated with certainty for only a single case of independent evolution (i.e., pine/prairie vs. montane/meadow). Furthermore, the nonmonogamous meadow vole facultatively expresses partner preferences under a variety of conditions (Parker et al., 2001), indicating that partner preference is not wholly dependent upon a high level of V1aR expression in the ventral pallidum.

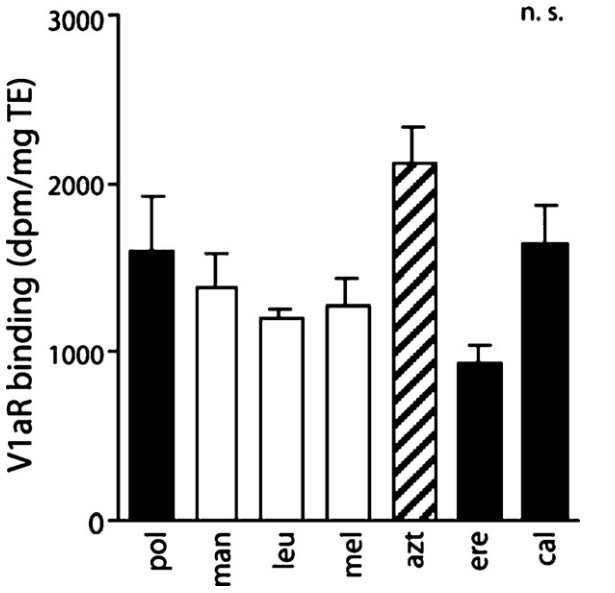

Figure 1 V1aR binding in the ventral pallidum of *Peromyscus* mouse species does not differentiate monogamous and promiscuous species. Binding densities are shown for *P. polionotus* (pol), *P. maniculatus* (man), *P. leucopus* (leu), *P. melanophrys* (mel), *P. aztecus* (azt), *P. eremicus* (ere) and *P. californicus* (cal). Species are ordered by phylogenetic relationship (see Figure 1 of Turner et al., 2010). Monogamous species are in black, promiscuous in white, and unknown are hatched. Data are shown as means $\pm$ SEM.
Modified from Turner et al. (2010).

Of course, taxa other than voles can be examined as well, and if V1aR density in the ventral pallidum is key to the evolution of monogamy, then we would expect to find higher densities in monogamous species than in nonmonogamous species. This hypothesis has been addressed using 8 species of *Peromyscus* mice that differ in their mating systems, with the finding that there is no association between mating system and V1aR density in the ventral pallidum (Turner et al., 2010) (Fig. 1). Similarly, estrildid finch species that pair bond for life have very low densities of V_{1a}-like binding sites in the ventral pallidum (Goodson et al., 2006), and pharmacological findings have also been negative: Chronic, central blockade of V_{1a}-like receptors does not impair pair bonding in male zebra finches (Estrildidae: *Taeniopygia guttata*) (Kabelik et al., 2009) and peripheral injections of a nonapeptide receptor antagonist do not block pair bonding in the monogamous convict cichlid (*Amatitlania nigrofasciata*) (Oldfield and Hofmann, 2011). Nonetheless, these manipulations do alter other behaviors in both species, demonstrating efficacy of the pharmacological agents.

Similar lines of research have been conducted with OT and MT. Endogenous OT acting via OT receptors (OTRs) in the nucleus accumbens is necessary for pair bonding in female prairie voles (Young et al., 2001; Liu and Wang, 2003); exogenous OT promotes pair bonding in the absence of mating (Liu and Wang, 2003); and viral vector-mediated upregulation of OTR expression in the nucleus accumbens promotes selective partner preference (Ross et al., 2009). Similar to the V1aR findings, the monogamous prairie and pine voles exhibit higher OTR expression in the nucleus accumbens than do the nonmonogamous montane and meadow voles (Insel and Shapiro, 1992). Again, however, similar findings were not reported in a study of *Peromyscus* mice (Insel et al., 1991), and monogamous finches and sparrows exhibit no detectable expression of oxytocic receptors (or binding sites) in the nucleus accumbens or surrounding striatum (Leung et al., 2009, 2011).

Relevant pharmacological data from other species is mixed. In common marmosets (*Callithrix penicillatata*), peripheral injections of OT and an OTR antagonist alter some aspects of affiliation, but do not alter pair bond formation or subsequent partner preference behavior (Smith et al., 2010). Similarly, as described above, pair bonding in monogamous convict cichlids is not impaired by injections of a nonselective nonapeptide receptor antagonist (Oldfield and Hofmann, 2011), and intranasal OT administrations in humans do not influence social preferences in a manner consistent with pair bonding (Liu et al., 2012b). However, all of these studies differ substantially in methodology from those in voles (e.g., peripheral vs. central administrations; acute vs. chronic), and in fact romantic attachments in humans are associated with chronic elevations in circulating OT (Schneiderman et al., 2012).

In contrast, both peripheral and i.c.v. administrations of an OTR antagonist impair pair bonding in zebra finches (Klatt and Goodson, 2013; Pedersen and Tomaszycki, 2012) (Fig. 2). However, despite this functional similarity to voles, zebra finches do not express oxytocic receptors in the nucleus accumbens (Leung et al., 2009, 2011), suggesting that there are differences in the underlying mechanisms. Perhaps the most likely site of action is the LS, an area that expresses high levels of oxytocic receptor mRNA and binding sites in both zebra finches and rodents (Insel and Shapiro, 1992; Goodson et al., 2009b; Leung et al., 2009, 2011). Antagonism of either LS OTRs or V1aRs blocks the facilitation of pair bonding by VP in male prairie voles (Liu et al., 2001) (Fig. 3), and thus the LS may be critical for nonapeptide effects on zebra finch pair bonding, as well, although these findings fall short of demonstrating that oxytocic receptors *promote* or *mediate* pair bonding in zebra finches. Because septal VP and OT promote social recognition in rodents (Popik et al., 1992; Engelmann and Landgraf, 1994; Everts and Koolhaas, 1997; Bielsky et al., 2005), antagonism may simply disrupt social recognition rather than pair-bonding per se. Thus, it seems possible that oxytocic receptors in the LS are simply *necessary* but not sufficient to induce pair bonding (although VP actions in the LS are sufficient in male prairie voles; Liu et al., 2001).

Thus, although it is common to read general statements to the effect that nonapeptides are essential for pair bonding, sufficient evidence to make that point is difficult to obtain, and is presently available only for zebra finches and prairie voles. However, there are sufficient data on anatomy and

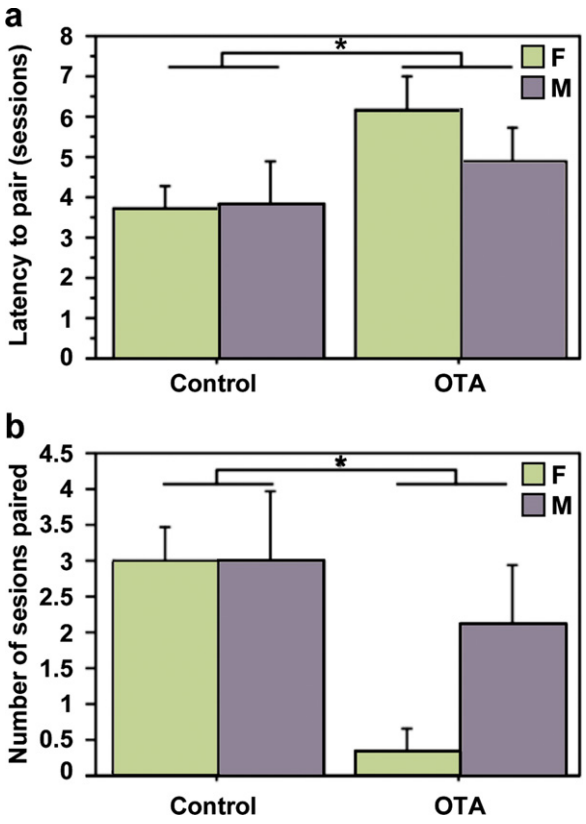

Figure 2 Chronic i.c.v. infusions of an OTR antagonist (OTA) significantly (a) increase the latency to pair and (b) decreases number of sessions paired in male and female zebra finches housed in colony environment. Subjects were observed twice per day for 3 days. Data are shown as means ± SEM; $^*p < 0.05$, two-way ANOVA.
Modified from Klatt and Goodson (2013).

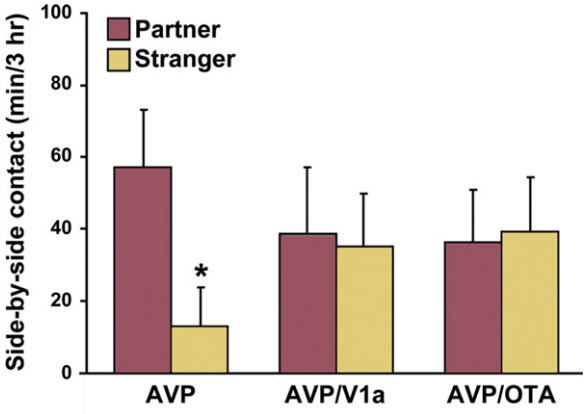

Figure 3 Male prairie voles dialyzed with VP in the septum during 6 h of cohabitation with a female spend more time in contact with the partner than with a stranger in a preference test. However, co-administration of a V1aR antagonist (V1a) or OTR antagonist (OTA) blocks VP-induced partner preferences. Data are shown as means ± SEM; $^*p < 0.05$.
Modified from Liu et al. (2001).

function to suggest that the vole findings do not have high predictive validity for other species. This is particularly the case with regards to the evolution of peptide mechanisms in the nucleus accumbens, and its primary output target, the ventral pallidum.

Pair bonding aside, is it not the case that nonapeptides promote bonding processes more generally, such as mother–infant bonding? Certainly this is commonly stated to be the case, but to address this question more rigorously, it is first necessary to define what is meant by "bonding" and generate an operational definition that can be used to experimentally demonstrate that a neurochemical system actually underlies the bonding process. In terms of definition, bonding has been compared to an associative process that is much like addiction, in that a specific social partner acquires an hedonic, emotional association that other conspecifics do not, which is afterwards sufficient to drive selective affiliation with that individual (Insel, 2003; McGregor and Bowen, 2012). If we accept this as a general definition, then a good operational definition must necessarily address the associative process itself. It is not sufficient to simply show that a given neurochemical increases the amount of time that an animal spends in some aspect of affiliation with another individual (e.g., as in maternal care). *Rather, the experimental evidence must address the necessity of the neurochemical for the establishment of the association to begin with.*

A simple nonsocial example may make this point somewhat more clearly. Some foods are purported to have addictive qualities (e.g., chocolate, various fast foods, etc.), and the processes of food addiction, like other addictive processes that associate the stimulus with an hedonic state, almost certainly rely upon the mesolimbic dopamine system (e.g., nucleus accumbens) or closely related structures (e.g., ventral pallidum) (Grimm et al., 2011). Now, assume that we take a subject that is addicted to a particular food and infuse neuropeptide Y (NPY) into the lateral hypothalamus. As known from a wide range of studies, activation of NPY receptors in the lateral hypothalamus will drive a feeding response (Mercer et al., 2011), and because of the addictive processes that have occurred elsewhere in the brain, the outcome will likely be that the subject will consume more of the addictive food following infusion of NPY. But the observation of that response does not mean that NPY itself is important for the associative process of addiction, only that it drives a general class of behavior (feeding) that gains further selectivity by virtue of the associative processes that have occurred elsewhere in the brain.

If we apply this same logic to nonapeptide functions, it becomes clear that the vast majority of data for nonapeptides fall into the "NPY category." That is, we know that they modulate or promote a variety of social processes, but we have extremely few data to support the assertion that nonapeptides are important for the associative, hedonic processes of bonding. Pair bonding in voles provide the most compelling case, as described above, but beyond voles, only the findings for mother-offspring attachment in sheep come close to demonstrating the direct relevance of nonapeptides to the actual bonding process.

Female sheep learn their offspring's odor soon after parturition and will normally reject all lambs except for their own. Parturition elicits oxytocin release in the brain and promotes maternal acceptance and care, as does vaginocervical stimulation in estradiol-primed, non-pregnant females. These effects are blocked by epidural anesthesia and rescued by central OT administrations (Kendrick et al., 1997; Nowak et al., 2011).

As strong as these findings are, we are again faced with evolutionary lability. That is, although OT promotes maternal care in many (perhaps all) mammalian species, selective mother-offspring attachments do not appear to exist in most species, including rats and other rodents (Nowak et al., 2011). In addition, whereas OT modulation of olfaction appears to be central to attachment in sheep (Kendrick et al., 1997; Nowak et al., 2011), other taxa that have evolved parent-offspring bonds may rely predominantly on other sensory modalities; e.g., vision and audition in humans and other primates. In fact, recent findings in human fathers demonstrate that intranasal OT *dampens* activation of the nucleus accumbens when looking at photos of their own children relative to other familiar children (Wittfoth-Schardt et al., 2012), suggesting that if OT promotes selective, parent-child bonds in humans, it does not do so via actions in the nucleus accumbens.

As suggested by the considerations above, it remains an open question whether nonapeptide systems reliably evolve in relation to bonding behavior. Indeed, the broader view that nonapeptides selectively promote positive social behavior is challenged by an increasingly large number of studies (Ferris and Delville, 1994; Thompson and Walton, 2004; Thompson et al., 2006; De Dreu et al., 2010, 2011; Bartz et al., 2011a,b), as summarized in Section 1, and it is quite clear that the relationships between nonapeptides and behavior cannot be accurately summarized in succinct sound bites, such as those often encountered in the popular press (and not infrequently in the primary literature). In addition, characterizing nonapeptides as "prosocial neuropeptides" (Meyer-Lindenberg, 2008), "social neuropeptides for translational neuroscience" (Meyer-Lindenberg et al., 2011), or describing OT as the "moral molecule" (Zak, 2011), not only ignores numerous nonapeptide functions that are certainly not prosocial, but is also inconsistent with the complexities of nonapeptide action. That is, it is difficult to reconcile the view that nonapeptides exert uniformly prosocial effects with the extensive literature demonstrating that nonapeptides exert effects that are often sex-specific (in taxa ranging from fish to humans) (Insel and Hulihan, 1995; Goodson and Bass, 2000; Goodson et al., 2004; Thompson et al., 2006), dependent upon social phenotype and context (Goodson et al., 2009a; Kabelik et al., 2009; Bartz et al., 2010; De Dreu et al., 2010), or clearly antisocial (see references at the beginning of this paragraph).

Another concern is that many investigators have become convinced that nonapeptides are prosocial molecules (particularly OT) without sufficient data about possible roles in negative or antisocial behaviors. For instance, despite the hundreds of studies on prosocial effects of OT, only one study has examined the effect of central OT manipulations on standard resident-intruder aggression. This experiment showed that OT acts within the medial preoptic area and anterior hypothalamus to decrease resident-intruder aggression in female Syrian hamsters (*Mesocricetus auratus*) (Harmon et al., 2002a). However, generalization from this finding to males, and to other brain areas and species is difficult, because (1) anterior hypothalamic infusions of VP actually

exert opposing effects on aggression in male and female hamsters (Gutzler et al., 2010) (i.e., OT may do the same), and (2) OT *promotes* maternal aggression in brain areas outside of the preoptic area-anterior hypothalamus, including the amygdala (Bosch et al., 2005). Whether amygdalar OT promotes aggression in other contexts is an extremely important question, but not one that has been addressed. However, because OT is important for anxiolysis and stress coping (Quirin et al., 2011; Knobloch et al., 2012; Kubzansky et al., 2012), and because aggressive animals tend to be hyporesponsive to stress (Koolhaas et al., 2007, 2010), we might hypothesize that OTR activation is at a minimum *permissive* for territorial aggression outside of a maternal context, even if it does not actively promote it. Recent findings in the highly aggressive violet-eared waxbill (*Uraeginthus granatina*) strongly support this idea (J. L. Goodson and S. E. Schrock, unpublished observations).

2.4. Evolving nonapeptide functions: the importance of physiological ecology and social life history background

As addressed in the preceding section, nonapeptide circuits and functions do not always evolve in a predictable manner in relation to a given aspect of social behavior. However, it must be emphasized that this work has been conducted without examining (or controlling for) aspects of physiological ecology and social life history that may influence the evolutionary trajectory of nonapeptide circuits and their functions (see Section 2.1 above). Thus, we may yet identify consistent patterns if we take these variables into consideration.

The importance of physiological ecology is perhaps most clear in studies of two isolated populations of Death Valley pupfish (*Cyprinodon nevadensis*), which live in pools of different salinity, and therefore face different osmoregulatory challenges. The two populations also vary in multiple aspects of VT anatomy in the preoptic area and hypothalamus (Lema and Nevitt, 2004; Lema, 2006). Common garden experiments demonstrate that the behavioral differences are heritable. Furthermore, manipulations of temperature and salinity influence VT anatomy differently in fish derived from the two populations, and although aggression correlates with VT anatomy in fish from both, the pattern of effects for each population is different (Lema, 2006). These results suggest that the thermoregulatory and osmoregulatory challenges of the environment play a primary role in shaping VT anatomy, with downstream effects on the relationship between VT and aggression.

The complex results in pupfish strongly underscore the importance of considering physiological ecology in relation to the evolution of nonapeptide behavioral functions, and thus in our own work in finches (family Estrildidae), we have focused our comparisons on species that differ in grouping behavior, but not in aspects of physiological ecology that are likely relevant to nonapeptide function. All five species that we study occupy arid or semi-arid grassland scrub habitat and breed opportunistically or semi-opportunistically in response to rainfall and subsequent food abundance (Goodson and Kingsbury, 2011). Thus, nonapeptide systems in these species must cope with similar thermal and osmoregulatory challenges, and are adapted to similar patterns of reproduction. Like all other estrildids, these species exhibit long-term (typically life-long) pair bonds and biparental care for young. This comparative system includes two estrildid finch species that have independently evolved an extreme level of gregariousness (living in large groups year-round), two species that have independently evolved territoriality and a high level of aggression (living in male–female pairs year-round), and a modestly gregarious species that is closely related to one of the territorial species. Hence, these species allow us to study nonapeptide mechanisms that accompany evolutionary divergence and convergence in grouping behavior while controlling for other relevant aspects of behavior and ecology.

Experiments with these species have shown that the anatomy and functions of multiple peptide systems have evolved divergently and convergently in relation to grouping behavior. For instance, relative to the less gregarious species, the highly gregarious species exhibit significantly more VT-immunoreactive (-ir) neurons in the medial bed nucleus of the stria terminalis (BSTm; a component of the medial extended amygdala) (Goodson and Wang, 2006), and all three flocking species exhibit higher densities of V_{1a}- and oxytocin-like binding sites in the LS, particularly in the pallial (dorsal) LS (Goodson et al., 2006, 2009b) (Fig. 4a–c). Nonapeptide circuitry of the BSTm and LS is therefore hypertrophied in gregarious finch species, and consistent with that observation, simple exposure to a same-sex conspecific through a wire barrier produces a significant *increase* in Fos protein expression (a proxy marker of neural activity) in the VT-ir neurons of the BSTm in gregarious species, but a *decrease* in the territorial species (Goodson and Wang, 2006).

Importantly, the gregarious species normally affiliate with same-sex conspecifics whereas the territorial species do not, and in fact, additional experiments demonstrate that the BSTm VT neurons are sensitive to the valence of social stimuli. Thus, these neurons *increase their activity in response to positive stimuli that normally elicit affiliation*, as observed for the gregarious species exposed to same-sex stimuli, *but decrease their activity (or show no response) to stimuli that normally elicit avoidance or aggression*, as in the territorial species exposed to same-sex stimuli. Consistent with this valence sensitivity, we find that social activation of VT neurons in the highly gregarious zebra finch can be suppressed by subjugation (a negative social stimulus). Conversely, territorial birds will activate their BSTm VT neurons following reunification with their pair bond partner (a positive social stimulus) (Goodson and Wang, 2006). Recent findings in mice and chickens suggest that this valence sensitivity is phylogenetically widespread (Ho et al., 2010; Xie et al., 2011).

Because VT/VP neurons of the BSTm project heavily to the LS (De Vries and Panzica, 2006), the findings described above suggest that BSTm VT neurons and septal nonapeptide receptors may promote grouping behavior. In support of this hypothesis, antisense knockdown of VT production in the BSTm produces a robust (80%) reduction in the percent of social contact time that male zebra finches spend with the larger of two groups (10 vs. 2 males), and a virtually identical effect is obtained following intraseptal infusions of a V1aR antagonist (Kelly et al., 2011). Similarly, i.c.v. infusions of an OTR antagonist significantly reduce gregariousness (preferred group size) in zebra finches of both sexes, albeit more strongly in females, and intraseptal infusions of the OTR

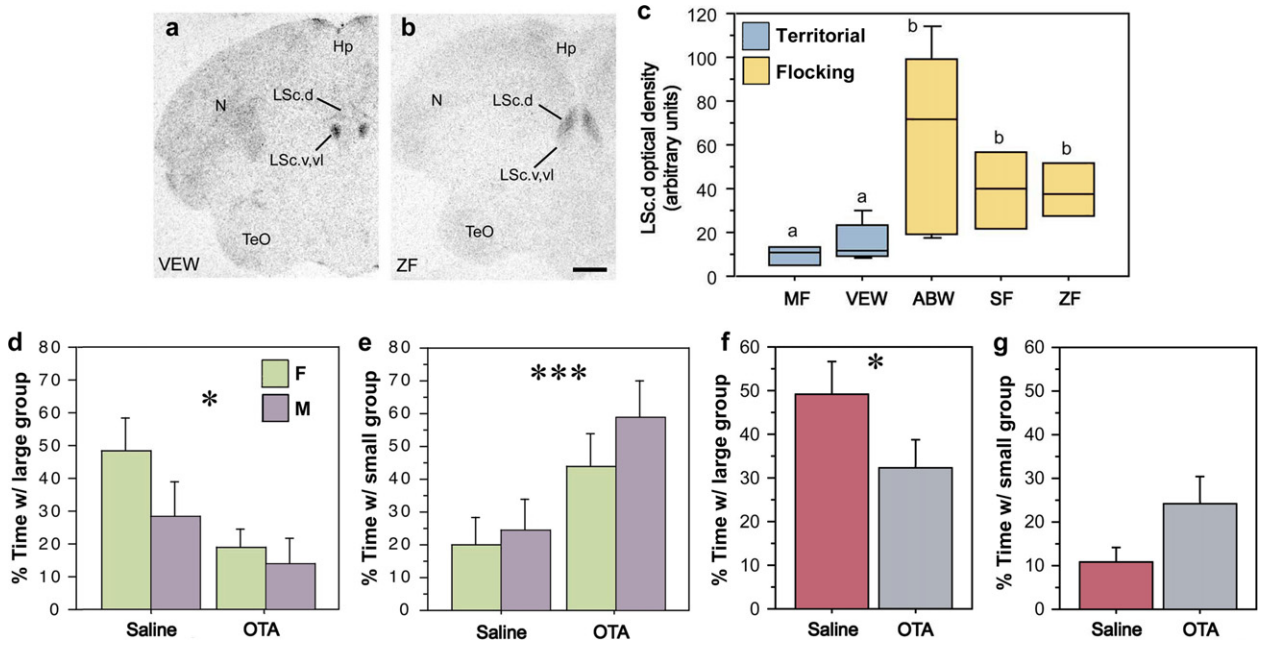

Figure 4 OT-like receptors exhibit differential distributions in the LS of territorial and flocking finch species, and mediate large-group preferences in the highly gregarious zebra finch. (a, b) Representative autoradiograms of ^{125}I-OT antagonist (OTA) binding sites in the caudal LS (LSc) in the territorial violet-eared waxbill (a) and the highly gregarious zebra finch (b). Scale bar = 500 μm. (c) Densities of OTA binding sites in the dorsal (pallial) LSc of two territorial species (Melba finch, MF, and violet-eared waxbill, VEW), a moderately gregarious species (Angolan blue waxbill, ABW), and two highly gregarious species (spice finch, SF, and zebra finch, ZF). No sex differences are observed and sexes were pooled. Different letters above the boxes denote significant species differences (Mann—Whitney $p < 0.05$) following significant Kruskal—Wallis. (d, e) Relative to vehicle treatments, i.c.v. infusions of OTA reduce the amount of time that zebra finches spend in close proximity to the large group (d) and increase time in close proximity to the small group (e). Total time spent in social contact is not altered. *$p < 0.05$, ***$p < 0.001$, main effect of Treatment, repeated-measures ANOVA. (f, g) Comparable effects are observed following OTA infusions into the septum. *$p < 0.05$, paired t-test. Hp, hippocampus; LSc.d, dorsal zone of the LSc; LSc.v,vl, ventral and ventrolateral zones of the LSc; N, nidopallium; PLH, posterolateral hypothalamus; TeO, optic tectum.
Modified from Goodson et al. (2009b).

antagonist produce comparable effects (Goodson et al., 2009b) (Fig. 4d—g).

As emphasized above with respect to the peptide mechanisms of pair bonding, it is important to ask whether our findings in finches are predictive for other taxa, particularly those that have evolved patterns of grouping and territoriality on different backgrounds of physiological ecology and social life history. In this context, it is particularly important to note that the estrildid finches that we study are opportunistic breeders and exhibit stable VT anatomy year-round (Kabelik et al., 2010). This stands in strong contrast to the majority of seasonally breeding mammals, amphibians and birds, which display a dramatic collapse of VT/VP production in the BSTm outside of the breeding season. In addition, the finch species that we study exhibit stable differences in grouping behavior year-round, whereas many other vertebrates form groups only outside of the breeding season (this is very common in birds). Thus, two important questions must be asked: (1) Can our findings about the nonapeptide mechanisms of grouping behavior in opportunistic finch species be extended to species that occupy predictable habitats? This is essentially a question about the relevance of physiological ecology (seasonality) to the evolution of nonapeptide mechanisms underlying behavior. (2) Are the mechanisms of year-round grouping in life-long-monogamous finches predictive for other species that group and pair bond on a strictly seasonal basis? This is essentially a question about the evolution of nonapeptide mechanisms of grouping behavior when grouping evolves on different backgrounds of social life history.

To address these questions, we have recently begun a series of experiments in highly seasonal, temperate zone emberizid sparrows to determine whether the seasonal shift from being territorial while breeding (spring-summer) to flocking in the fall and winter is accompanied by seasonal variation in the same nonapeptide circuits that promote gregariousness in finches. We recently completed a relevant immunohistochemical study in males of four species (described below), and parallel receptor binding and pharmacological experiments are underway.

Because (1) BSTm VT neurons and septal nonapeptides potently promote grouping behavior in finches (Goodson et al., 2009b; Kelly et al., 2011), and (2) most amniote vertebrates regress the VT/VP circuitry of the BSTm and LS outside of the breeding season (Goodson and Bass, 2001; De Vries and Panzica, 2006), we predicted that sparrow species that flock in the winter would *maintain* the VT-ir circuitry of the BSTm in winter (or show less of a decline than

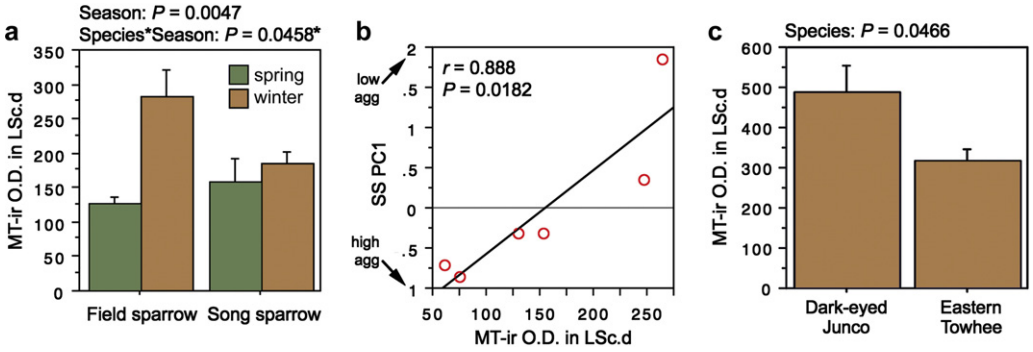

Figure 5 MT innervation of the dorsal LS (LSc.d) differentiates species that flock in winter (field sparrow and dark-eyed junco) from species that do not (song sparrows, which are territorial year-round, and eastern towhees, which are neither territorial or flocking). (a) Optical density (O.D., in arbitrary units) of MT-ir fibers in the LSc.d of field sparrows and song sparrows collected in spring and winter, showing increased innervation density in winter field sparrows. (b) MT-ir fiber densities correlate negatively with song sparrow aggression (SS PC1), suggesting that the increased innervation in winter field sparrows may suppress aggression rather than promote flocking. (c) However, comparisons of two species that are not territorial in winter show that MT-ir fiber densities are greater in the flocking species (dark-eyed junco) than in the non-flocking species (eastern towhee). Note that different fluorophores were used in the field-song and junco-towhee datasets, and thus direct comparison of O.D. across the two datasets is not possible. Data are shown as means $\pm$ SEM. $^*p < 0.05$.
Modified from Goodson et al. (2012).

non-flocking species), whereas non-flocking species would show a winter decrease in VT immunoreactivity. Contrary to these predictions, both flocking and non-flocking species exhibit a massive decrease in VT immunoreactivity during winter (Goodson et al., 2012). Hence, VT circuitry of the BSTm and LS has evolved to promote gregariousness in finch species that flock year-round, but not in species that flock seasonally.

However, our predictions for MT were more accurate. Because flocking finch species exhibit higher densities of nonapeptide receptors in the dorsal LS than do non-flocking species (Goodson et al., 2006, 2009b), and that intraseptal infusions of nonapeptide antagonists reduce gregariousness (Goodson et al., 2009b; Kelly et al., 2011), we predicted that MT-ir fiber density would increase in the dorsal LS of winter flockers. We first conducted a spring and winter comparison of field sparrows (*Spizella pusilla*), which flock in winter, and song sparrows (*Melospiza melodia*), which are territorial year-round, and found that MT-ir innervation did indeed show a large winter increase in field sparrows, but not song sparrows (Fig. 5a). However, MT-ir innervation of the dorsal LS correlates negatively with aggression displayed during the breeding season (Fig. 5b), and thus the winter increase in field sparrows may serve to suppress aggression rather than promote flocking. To address this possibility, we compared two other wintering sparrows — dark-eyed juncos (*Junco hyemalis*), which flock in winter, and eastern towhees (*Pipilo erythropthalmus*), which are neither flocking nor territorial in winter. MT-ir innervation of the dorsal LS is greater in winter juncos than in towhees, even though neither is territorial, suggesting that MT innervation in the dorsal LS is relevant to flocking, and does not simply suppress aggression (Goodson et al., 2012) (Fig. 5c).

Recent findings in humans suggest that the dorsal LS is also an important site for the nonapeptide modulation of cooperation, an aspect of behavior that requires at least some amount of affiliation. Men playing the prisoner's dilemma game exhibit greater cooperation (in response to perceived partner cooperation) following intranasal administration of VP, and this effect is statistically correlated with a locus of neural activation centered over the dorsal LS (Rilling et al., 2012). These results are particularly interesting in light of recent findings from mice, which demonstrate that the dorsal LS plays an important role in linking contextual information received from hippocampal field CA3 to the mesolimbic dopamine system. More specifically, hippocampal projections to the dorsal LS activate GABAergic LS neurons that then project upon inhibitory interneurons of the ventral tegmental area, effectively disinhibiting the mesolimbic dopamine system (Luo et al., 2011). Thus, socially relevant nonapeptide projections to the dorsal LS may drive affiliation by linking social context to incentive and reward.

If nonapeptide actions in the dorsal LS promote social motivation, why would sparrows that flock in winter not maintain their BSTm-LS VT outside of the breeding season? A few observations bear on this question. First, most tetrapod vertebrates (amphibians, mammals, reptiles and birds) exhibit a male-biased dimorphism of this circuit, and like the sparrows, collapse the circuit when not breeding (Goodson and Bass, 2001; De Vries and Panzica, 2006); however, many or most of these species do not group. Thus, the historical functions of the VT/VP circuitry of the BSTm and LS are likely tied to reproductive behavior, particularly in males, and not grouping behavior. Because (1) intraseptal VT infusions suppress territorial aggression in finches and sparrows (Goodson, 1998b,a), (2) BSTm VT content correlates negatively with aggression across sparrow species (Goodson et al., 2012), and (3) antisense knockdown of BSTm VT production dramatically increases male aggression zebra finches (A. M. Kelly and J. L. Goodson, unpublished observations), *we hypothesize that the function of the seasonal expression and dimorphism in this circuit is to offset male aggression during the breeding season, specifically in affiliative contexts that should drive the activity of the VT neurons in the BSTm, such as interactions with mates and young.*

Unlike the seasonally breeding sparrows and most other tetrapods, the opportunistically breeding estrildid finches do not collapse their VT circuitry outside of the breeding period (Kabelik et al., 2010), presumably because of their flexible breeding schedules. Thus, we hypothesize that the importance of the BSTm-LS VT circuitry for flocking in the estrildid finches is an evolutionarily derived condition that arose once the seasonality of the circuit disappeared, opening up the opportunity to modulate behaviors that were not exhibited only during the breeding period. Although this explanation is speculative, the different profiles of VT anatomy and function that are exhibited by estrildid finches and emberizid sparrows strongly underscore the point that evolutionary backgrounds of social life history and physiological ecology are of profound importance for understanding the relationships between nonapeptides and behavior.

3. Frontiers

More than 100 papers are currently being published per year on the topic of nonapeptides and social behavior (Goodson and Thompson, 2010), yet large gaps exist in our knowledge of nonapeptide systems, their functions, and their evolution in relation to behavior. For instance, because human experiments rely entirely upon correlational analyses or intranasal peptide delivery, we do not have a window into the functions of endogenous peptide (which would require receptor antagonism or other disruptions of endogenous peptide circuitry), and we do not yet know whether intranasal OT exerts direct effects on the brain, or whether feedback from the periphery mediates experimental effects (Churchland and Winkielman, 2012). Even invasive studies in lab animals have barely scratched the surface of this latter issue, and thus, although we know that peptides influence peripheral body states, we know very little about the impact of peripheral modulation on central emotional and social processes. In addition, we know very little about the unique contributions of specific cell groups to behavior and the complex patterns of neuromodulation that they give rise to throughout the brain (''neuromodulatory patterning'') (Goodson and Kabelik, 2009). This is because most studies either employ intraventricular delivery of peptides and antagonists, or site-specific manipulations in target zones of interest (e.g., using peptides, antagonists, viral vector, dialysis, etc.). However, only by manipulating specific populations of nonapeptide neurons can we understand their full contributions to behavior, which will be mediated via actions in multiple target areas and by binding to multiple receptor types (see Kelly et al., 2011). Finally, we also know very little about the mechanistic bases for sex and individual differences in nonapeptide function. Although these issues pose some daunting challenges, they are absolutely essential to grapple with if we are to gain a sophisticated understanding of how nonapeptide systems function in coordinated fashion, and how neuromodulatory patterning by those systems contributes to sex-, individual-, and species-specific patterns of behavior.

4. Conclusion

Some of the most fascinating aspects of social behavior have evolved many times (e.g., grouping, selective mother-offspring attachments, various mating systems and patterns of parental care), and based on their phylogenetic distributions, some appear to be extremely labile over evolutionary time. Given this evolutionarily lability, a good understanding of the nonapeptide mechanisms of behavior requires that we explore those mechanisms in multiple species that have independently evolved the behavior of interest. Because nonapeptides make pleiotropic contributions to physiology and behavior, we must also ask whether mechanisms evolve similarly on different backgrounds of physiological ecology and social life history. Based on the evidence discussed above, it appears that we can expect both similarities and differences across species, and only through broadly comparative experimentation can we determine the predictive validity of any given finding. This comparative process is essential for the generation of broadly relevant insights into the functional properties of nonapeptide systems, and is also essential for assessing the potential for translational application to humans.

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Conflict of interest

None declared.

Role of funding source

None declared.

Acknowledgements

I thank Marcy Kingsbury for helpful comments on the manuscript and the authors of Liu et al. (2001) and Turner et al. (2010) for their kind permission to adapt figures.

References

Acher, R., 1972. Chemistry of the neurohypophysial hormones: an example of molecular evolution. In: Endocrinology, American Physiological Society, Washington, DC, pp. 119—130.

Acher, R., Chauvet, J., Chauvet, M.T., Rouille, Y., 1999. Unique evolution of neurohypophysial hormones in cartilaginous fishes: possible implications for urea-based osmoregulation. J. Exp. Zool. 284, 475—484.

Alexander, R.D., 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5, 325—383.

Argiolas, A., Melis, M.R., 2004. The role of oxytocin and the paraventricular nucleus in the sexual behaviour of male mammals. Physiol. Behav. 83, 309—317.

Baker, B.I., Bird, D.J., Buckingham, J.C., 1996. In the trout, CRH and AVT synergize to stimulate ACTH release. Regul. Pept. 67, 207—210.

Banet, M., Wieland, U.E., 1985. The effect of intraseptally applied vasopressin on thermoregulation in the rat. Brain Res. Bull. 14, 113—116.

Bartz, J., Simeon, D., Hamilton, H., Kim, S., Crystal, S., Braun, A., Vicens, V., Hollander, E., 2011a. Oxytocin can hinder trust and cooperation in borderline personality disorder. Soc. Cogn. Affect. Neurosci. 6, 556—563.

Bartz, J.A., Zaki, J., Bolger, N., Ochsner, K.N., 2011b. Social effects of oxytocin in humans: context and person matter. Trends Cogn. Sci. 15, 301—309.

Bartz, J.A., Zaki, J., Ochsner, K.N., Bolger, N., Kolevzon, A., Ludwig, N., Lydon, J.E., 2010. Effects of oxytocin on recollections of maternal care and closeness. Proc. Natl. Acad. Sci. U. S. A. 107, 21371—21375.

Bielsky, I.F., Hu, S.B., Ren, X., Terwilliger, E.F., Young, L.J., 2005. The V1a vasopressin receptor is necessary and sufficient for normal social recognition: a gene replacement study. Neuron 47, 503—513.

Bos, P.A., Panksepp, J., Bluthe, R.M., van Honk, J., 2012. Acute effects of steroid hormones and neuropeptides on human social-emotional behavior: a review of single administration studies. Front. Neuroendocrinol. 33, 17—35.

Bosch, O.J., Meddle, S.L., Beiderbeck, D.I., Douglas, A.J., Neumann, I.D., 2005. Brain oxytocin correlates with maternal aggression: link to anxiety. J. Neurosci. 25, 6807—6815.

Bosch, O.J., Neumann, I.D., 2008. Brain vasopressin is an important regulator of maternal behavior independent of dams' trait anxiety. Proc. Natl. Acad. Sci. U. S. A. 105, 17139—17144.

Caldwell, J.D., Jirikowski, G.F., Greer, E.R., Pedersen, C.A., 1989. Medial preoptic area oxytocin and female sexual receptivity. Behav. Neurosci. 103, 655—662.

Carter, C.S., Grippo, A.J., Pournajafi-Nazarloo, H., Ruscio, M.G., Porges, S.W., 2008. Oxytocin, vasopressin and sociality. Prog. Brain Res. 170, 331—336.

Castagna, C., Absil, P., Foidart, A., Balthazart, J., 1998. Systemic and intracerebroventricular injections of vasotocin inhibit appetitive and consummatory components of male sexual behavior in Japanese quail. Behav. Neurosci. 112, 233—250.

Churchland, P.S., Winkielman, P., 2012. Modulating social behavior with oxytocin: how does it work? What does it mean?. Horm. Behav. 61, 392—399.

De Dreu, C.K., 2012. Oxytocin modulates the link between adult attachment and cooperation through reduced betrayal aversion. Psychoneuroendocrinology 37, 871—880.

De Dreu, C.K., Greer, L.L., Handgraaf, M.J., Shalvi, S., Van Kleef, G.A., Baas, M., Ten Velden, F.S., Van Dijk, E., Feith, S.W., 2010. The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. Science 328, 1408—1411.

De Dreu, C.K., Greer, L.L., Van Kleef, G.A., Shalvi, S., Handgraaf, M.J., 2011. Oxytocin promotes human ethnocentrism. Proc. Natl. Acad. Sci. U. S. A. 108, 1262—1266.

De Vries, G.J., Panzica, G.C., 2006. Sexual differentiation of central vasopressin and vasotocin systems in vertebrates: different mechanisms, similar endpoints. Neuroscience 138, 947—955.

Diakow, C., 1978. Hormonal basis for breeding behavior in female frogs: vasotocin inhibits the release call of *Rana pipiens*. Science 199, 1456—1457.

Donaldson, Z.R., Young, L.J., 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. Science 322, 900—904.

Engelmann, M., Landgraf, R., 1994. Microdialysis administration of vasopressin into the septum improves social recognition in Brattleboro rats. Physiol. Behav. 55, 145—149.

Engelmann, M., Wotjak, C.T., Ebner, K., Landgraf, R., 2000. Behavioural impact of intraseptally released vasopressin and oxytocin in rats. Exp. Physiol. 85, 125S—130S.

Everts, H.G.J., Koolhaas, J.M., 1997. Lateral septal vasopressin in rats: role in social and object recognition? Brain Res. 760, 1—7.

Ferris, C.F., Albers, H.E., Wesolowski, S.M., Goldman, B.D., 1984. Vasopressin injected into the hypothalamus triggers a stereotyped behavior in golden hamsters. Science 224, 521—523.

Ferris, C.F., Delville, Y., 1994. Vasopressin and serotonin interactions in the control of agonistic behavior. Psychoneuroendocrinology 19, 593—601.

Fink, S., Excoffier, L., Heckel, G., 2006. Mammalian monogamy is not controlled by a single gene. Proc. Natl. Acad. Sci. U. S. A. 103, 10956—10960.

Fjellstrom, D., Kihlstrom, J.E., Melin, P., 1968. The effect of synthetic oxytocin upon seminal characteristics and sexual behaviour in male rabbits. J. Reprod. Fertil. 17, 207—209.

Giovenardi, M., Padoin, M.J., Cadore, L.P., Lucion, A.B., 1998. Hypothalamic paraventricular nucleus modulates maternal aggression in rats: effects of ibotenic acid lesion and oxytocin antisense. Physiol. Behav. 63, 351—359.

Goodson, J.L., 1998a. Territorial aggression and dawn song are modulated by septal vasotocin and vasoactive intestinal polypeptide in male field sparrows (*Spizella pusilla*). Horm. Behav. 34, 67—77.

Goodson, J.L., 1998b. Vasotocin and vasoactive intestinal polypeptide modulate aggression in a territorial songbird, the violet-eared waxbill (Estrildidae: *Uraeginthus granatina*). Gen. Comp. Endocrinol. 111, 233—244.

Goodson, J.L., Bass, A.H., 2000. Forebrain peptides modulate sexually polymorphic vocal circuitry. Nature 403, 769—772.

Goodson, J.L., Bass, A.H., 2001. Social behavior functions and related anatomical characteristics of vasotocin/vasopressin systems in vertebrates. Brain Res. Rev. 35, 246—265.

Goodson, J.L., Evans, A.K., Wang, Y., 2006. Neuropeptide binding reflects convergent and divergent evolution in species-typical group sizes. Horm. Behav. 50, 223—236.

Goodson, J.L., Kabelik, D., 2009. Dynamic limbic networks and social diversity in vertebrates: from neural context to neuromodulatory patterning. Front. Neuroendocrinol. 30, 429—441.

Goodson, J.L., Kabelik, D., Schrock, S.E., 2009a. Dynamic neuromodulation of aggression by vasotocin: influence of social context and social phenotype in territorial songbirds. Biotechnol. Lett. 5, 554—556.

Goodson, J.L., Kingsbury, M.A., 2011. Nonapeptides and the evolution of social group sizes in birds. Front. Neuroanat. 5, 13.

Goodson, J.L., Lindberg, L., Johnson, P., 2004. Effects of central vasotocin and mesotocin manipulations on social behavior in male and female zebra finches. Horm. Behav. 45, 136—143.

Goodson, J.L., Schrock, S.E., Klatt, J.D., Kabelik, D., Kingsbury, M.A., 2009b. Mesotocin and nonapeptide receptors promote estrildid flocking behavior. Science 325, 862—866.

Goodson, J.L., Thompson, R.R., 2010. Nonapeptide mechanisms of social cognition, behavior and species-specific social systems. Curr. Opin. Neurobiol. 20, 784—794.

Goodson, J.L., Wang, Y., 2006. Valence-sensitive neurons exhibit divergent functional profiles in gregarious and asocial species. Proc. Natl. Acad. Sci. U. S. A. 103, 17013—17017.

Goodson, J.L., Wilson, L.C., Schrock, S.E., 2012. To flock or fight: neurochemical signatures of divergent life histories in sparrows. Proc. Natl. Acad. Sci. U. S. A. 109 (Suppl. 1), 10685—10692.

Grimm, J.W., Harkness, J.H., Ratliff, C., Barnes, J., North, K., Collins, S., 2011. Effects of systemic or nucleus accumbens-directed dopamine D1 receptor antagonism on sucrose seeking in rats. Psychopharmacology (Berl.) 216, 219—233.

Gutzler, S.J., Karom, M., Erwin, W.D., Albers, H.E., 2010. Arginine-vasopressin and the regulation of aggression in female Syrian hamsters (*Mesocricetus auratus*). Eur. J. Neurosci. 31, 1655—1663.

Harmon, A.C., Huhman, K.L., Moore, T.O., Albers, H.E., 2002a. Oxytocin inhibits aggression in female Syrian hamsters. J. Neuroendocrinol. 14, 963—969.

Harmon, A.C., Moore, T.O., Huhman, K.L., Albers, H.E., 2002b. Social experience and social context alter the behavioral response to centrally administered oxytocin in female Syrian hamsters. Neuroscience 109, 767—772.

Ho, J.M., Murray, J.H., Demas, G.E., Goodson, J.L., 2010. Vasopressin cell groups exhibit strongly divergent responses to copulation and male—male interactions in mice. Horm. Behav. 58, 368—377.

Hoyle, C.H.V., 1998. Neuropeptide families: evolutionary perspectives. Regul. Pept. 73, 1—33.

Huhman, K.L., Albers, H.E., 1993. Estradiol increases the behavioral response to arginine vasopressin (AVP) in the medial preoptic-anterior hypothalamus. Peptides 14, 1049—1054.

Insel, T.R., 2003. Is social attachment an addictive disorder? Physiol. Behav. 79, 351—357.

Insel, T.R., Gelhard, R., Shapiro, L.E., 1991. The comparative distribution of forebrain receptors for neurohypophyseal peptides in monogamous and polygamous mice. Neuroscience 43, 623—630.

Insel, T.R., Hulihan, T.J., 1995. A gender-specific mechanism for pair bonding: oxytocin and partner preference formation in monogamous voles. Behav. Neurosci. 109, 782—789.

Insel, T.R., Shapiro, L.E., 1992. Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. Proc. Natl. Acad. Sci. U. S. A. 89, 5981—5985.

Insel, T.R., Wang, Z.X., Ferris, C.F., 1994. Patterns of brain vasopressin receptor distribution associated with social organization in microtine rodents. J. Neurosci. 14, 5381—5392.

Kabelik, D., Klatt, J.D., Kingsbury, M.A., Goodson, J.L., 2009. Endogenous vasotocin exerts context-dependent behavioral effects in a semi-naturalistic colony environment. Horm. Behav. 56, 101—107.

Kabelik, D., Morrison, J.A., Goodson, J.L., 2010. Cryptic regulation of vasotocin neuronal activity but not anatomy by sex steroids and social stimuli in opportunistic desert finches. Brain Behav. Evol. 75, 71—84.

Keebaugh, A.C., Young, L.J., 2011. Increasing oxytocin receptor expression in the nucleus accumbens of pre-pubertal female prairie voles enhances alloparental responsiveness and partner preference formation as adults. Horm. Behav. 60, 498—504.

Kelly, A.M., Kingsbury, M.A., Hoffbuhr, K., Schrock, S.E., Waxman, B., Kabelik, D., Thompson, R.R., Goodson, J.L., 2011. Vasotocin neurons and septal V1a-like receptors potently modulate songbird flocking and responses to novelty. Horm. Behav. 60, 12—21.

Kendrick, K.M., Da Costa, A.P., Broad, K.D., Ohkura, S., Guevara, R., Levy, F., Keverne, E.B., 1997. Neural control of maternal behaviour and olfactory recognition of offspring. Brain Res. Bull. 44, 383—395.

Kendrick, K.M., Keverne, E.B., Baldwin, B.A., 1987. Intracerebroventricular oxytocin stimulates maternal behaviour in the sheep. Neuroendocrinology 46, 56—61.

Kihlstrom, J.E., Agmo, A., 1974. Some effects of vasopressin on sexual behavior and seminal characteristics in intact and castrated rabbits. J. Endocrinol. 60, 445—453.

Kihlstrom, J.E., Danninge, I., 1972. Neurohypophysial hormones and sexual behavior in males of the domestic fowl (*Gallus domesticus* L.) and the pigeon (*Columba livia*). Gen. Comp. Endocrinol. 18, 115—120.

Klatt, J.D., Goodson, J.L., 2013. Oxytocin-like receptors mediate pair bonding in a socially monogamous songbird. Proc. R. Soc. B. 280, http://dx.doi.org/10.1098/rspb.2012.2396 In press.

Knobloch, H.S., Charlet, A., Hoffmann, L.C., Eliava, M., Khrulev, S., Cetin, A.H., Osten, P., Schwarz, M.K., Seeburg, P.H., Stoop, R., Grinevich, V., 2012. Evoked axonal oxytocin release in the central amygdala attenuates fear response. Neuron 73, 553—566.

Kojima, S., Alberts, J.R., 2011. Oxytocin mediates the acquisition of filial, odor-guided huddling for maternally-associated odor in preweanling rats. Horm. Behav. 60, 549—558.

Koolhaas, J.M., de Boer, S.F., Buwalda, B., van Reenen, K., 2007. Individual variation in coping with stress: a multidimensional approach of ultimate and proximate mechanisms. Brain Behav. Evol. 70, 218—226.

Koolhaas, J.M., de Boer, S.F., Coppens, C.M., Buwalda, B., 2010. Neuroendocrinology of coping styles: towards understanding the biology of individual variation. Front. Neuroendocrinol. 31, 307—321.

Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U., Fehr, E., 2005. Oxytocin increases trust in humans. Nature 435, 673—676.

Kubzansky, L.D., Mendes, W.B., Appleton, A.A., Block, J., Adler, G.K., 2012. A heartfelt response: oxytocin effects on response to social stress in men and women. Biol. Psychol. 90, 1—9.

Landgraf, R., Frank, E., Aldag, J.M., Neumann, I.D., Sharer, C.A., Ren, X., Terwilliger, E.F., Niwa, M., Wigger, A., Young, L.J., 2003. Viral vector-mediated gene transfer of the vole V1a vasopressin receptor in the rat septum: improved social discrimination and active social behaviour. Eur. J. Neurosci. 18, 403—411.

Lee, A.G., Cool, D.R., Grunwald Jr., W.C., Neal, D.E., Buckmaster, C.L., Cheng, M.Y., Hyde, S.A., Lyons, D.M., Parker, K.J., 2011. A novel form of oxytocin in New World monkeys. Biol. Lett. 7, 584—587.

Lema, S.C., 2006. Population divergence in plasticity of the AVT system and its association with aggressive behaviors in a Death Valley pupfish. Horm. Behav. 50, 183—193.

Lema, S.C., Nevitt, G.A., 2004. Variation in vasotocin immunoreactivity in the brain of recently isolated populations of a death valley pupfish, *Cyprinodon nevadensis*. Gen. Comp. Endocrinol. 135, 300—309.

Leng, G., Onaka, T., Caquineau, C., Sabatier, N., Tobin, V.A., Takayanagi, Y., 2008. Oxytocin and appetite. Prog. Brain Res. 170, 137—151.

Leung, C.H., Abebe, D.F., Earp, S.E., Goode, C.T., Grozhik, A.V., Mididoddi, P., Maney, D.L., 2011. Neural distribution of vasotocin receptor mRNA in two species of songbird. Endocrinology 152, 4865—4881.

Leung, C.H., Goode, C.T., Young, L.J., Maney, D.L., 2009. Neural distribution of nonapeptide binding sites in two species of songbird. J. Comp. Neurol. 513, 197—208.

Lim, M.M., Wang, Z., Olazabal, D.E., Ren, X., Terwilliger, E.F., Young, L.J., 2004. Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene. Nature 429, 754—757.

Lim, M.M., Young, L.J., 2004. Vasopressin-dependent neural circuits underlying pair bond formation in the monogamous prairie vole. Neuroscience 125, 35—45.

Liu, J.C., Guastella, A.J., Dadds, M.R., 2012a. Effects of oxytocin on human social approach measured using intimacy equilibriums. Horm. Behav. 62, 585—591.

Liu, J.C., Guastella, A.J., Dadds, M.R., 2012b. Exploring the role of intra-nasal oxytocin on the partner preference effect in humans. Psychoneuroendocrinology.

Liu, Y., Curtis, J.T., Wang, Z., 2001. Vasopressin in the lateral septum regulates pair bond formation in male prairie voles (*Microtus ochrogaster*). Behav. Neurosci. 115, 910—919.

Liu, Y., Wang, Z.X., 2003. Nucleus accumbens oxytocin and dopamine interact to regulate pair bond formation in female prairie voles. Neuroscience 121, 537—544.

Lukas, M., Toth, I., Reber, S.O., Slattery, D.A., Veenema, A.H., Neumann, I.D., 2011. The neuropeptide oxytocin facilitates pro-social behavior and prevents social avoidance in rats and mice. Neuropsychopharmacology 36, 2159—2168.

Luo, A.H., Tahsili-Fahadan, P., Wise, R.A., Lupica, C.R., Aston-Jones, G., 2011. Linking context with reward: a functional circuit from hippocampal CA3 to ventral tegmental area. Science 333, 353—357.

Mahalati, K., Okanoya, K., Witt, D.M., Carter, C.S., 1991. Oxytocin inhibits male sexual behavior in prairie voles. Pharmacol. Biochem. Behav. 39, 219—222.

McGraw, L.A., Young, L.J., 2010. The prairie vole: an emerging model organism for understanding the social brain. Trends Neurosci. 33, 103—109.

McGregor, I.S., Bowen, M.T., 2012. Breaking the loop: oxytocin as a potential treatment for drug addiction. Horm. Behav. 61, 331—339.

Mercer, R.E., Chee, M.J., Colmers, W.F., 2011. The role of NPY in hypothalamic mediated food intake. Front. Neuroendocrinol. 32, 398—415.

Meyer-Lindenberg, A., 2008. Impact of prosocial neuropeptides on human brain function. Prog. Brain Res. 170, 463—470.

Meyer-Lindenberg, A., Domes, G., Kirsch, P., Heinrichs, M., 2011. Oxytocin and vasopressin in the human brain: social neuropeptides for translational medicine. Nat. Rev. Neurosci. 12, 524—538.

Moore, F.L., Miller, L.J., 1983. Arginine vasotocin induces sexual behavior of newts by acting on cells in the brain. Peptides 4, 97—102.
Mulder, R.A., Dunn, P.O., Cockburn, A., Lazenbycohen, K.A., Howell, M.J., 1994. Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. Proc. R. Soc. Lond. B: Biol. Sci. 255, 223—229.
Nephew, B.C., Bridges, R.S., 2008. Central actions of arginine vasopressin and a V1a receptor antagonist on maternal aggression, maternal behavior, and grooming in lactating rats. Pharmacol. Biochem. Behav. 91, 77—83.
Nowak, R., Keller, M., Levy, F., 2011. Mother—young relationships in sheep: a model for a multidisciplinary approach of the study of attachment in mammals. J. Neuroendocrinol. 23, 1042—1053.
Olazabal, D.E., Young, L.J., 2006. Oxytocin receptors in the nucleus accumbens facilitate ''spontaneous'' maternal behavior in adult female prairie voles. Neuroscience 141, 559—568.
Oldfield, R.G., Hofmann, H.A., 2011. Neuropeptide regulation of social behavior in a monogamous cichlid fish. Physiol. Behav. 102, 296—303.
Ophir, A.G., Wolff, J.O., Phelps, S.M., 2008. Variation in neural V1aR predicts sexual fidelity and space use among male prairie voles in semi-natural settings. Proc. Natl. Acad. Sci. U. S. A. 105, 1249—1254.
Parker, K.J., Phillips, K.M., Lee, T.M., 2001. Development of selective partner preferences in captive male and female meadow voles, *Microtus pennsylvanicus*. Anim. Behav. 61, 1217—1226.
Pedersen, A., Tomaszycki, M.L., 2012. Oxytocin antagonist treatments alter the formation of pair relationships in zebra finches of both sexes. Horm. Behav. 62, 113—119.
Pedersen, C.A., Ascher, J.A., Monroe, Y.L., Prange, A.J.J., 1982. Oxytocin induces maternal behavior in virgin female rats. Science 216, 648—650.
Pedersen, C.A., Boccia, M.L., 2006. Vasopressin interactions with oxytocin in the control of female sexual behavior. Neuroscience 139, 843—851.
Pitkow, L.J., Sharer, C.A., Ren, X., Insel, T.R., Terwilliger, E.F., Young, L.J., 2001. Facilitation of affiliation and pair-bond formation by vasopressin receptor gene transfer into the ventral forebrain of a monogamous vole. J. Neurosci. 21, 7392—7396.
Popik, P., Vos, P.E., van Ree, J.M., 1992. Neurohypophysial hormone receptors in the septum are implicated in social recognition in the rat. Behav. Pharmacol. 3, 351—358.
Poulin, M.J., Holman, E.A., Buffone, A., 2012. The neurogenetics of nice: receptor genes for oxytocin and vasopressin interact with threat to predict prosocial behavior. Psychol. Sci. 23, 446—452.
Quirin, M., Kuhl, J., Dusing, R., 2011. Oxytocin buffers cortisol responses to stress in individuals with impaired emotion regulation abilities. Psychoneuroendocrinology 36, 898—904.
Rilling, J.K., Demarco, A.C., Hackett, P.D., Thompson, R., Ditzen, B., Patel, R., Pagnoni, G., 2012. Effects of intranasal oxytocin and vasopressin on cooperative behavior and associated brain activity in men. Psychoneuroendocrinology 37, 447—461.
Robinzon, B., Koike, T.I., Neldon, H.L., Kinzler, S.L., Hendry, I.R., el Halawani, M.E., 1988. Physiological effects of arginine vasotocin and mesotocin in cockerels. Br. Poult. Sci. 29, 639—652.
Ross, H.E., Freeman, S.M., Spiegel, L.L., Ren, X., Terwilliger, E.F., Young, L.J., 2009. Variation in oxytocin receptor density in the nucleus accumbens has differential effects on affiliative behaviors in monogamous and polygamous voles. J. Neurosci. 29, 1312—1318.
Sawyer, W.H., 1977. Evolution of neurohypophyseal hormones and their receptors. Fed. Proc. 36, 1842—1847.
Schneiderman, I., Zagoory-Sharon, O., Leckman, J.F., Feldman, R., 2012. Oxytocin during the initial stages of romantic attachment: relations to couples' interactive reciprocity. Psychoneuroendocrinology 37, 1277—1285.
Silk, J.B., 2007. The adaptive value of sociality in mammalian groups. Philos. Trans. R. Soc. B: Biol. Sci. 362, 539—559.
Smith, A.S., Agmo, A., Birnie, A.K., French, J.A., 2010. Manipulation of the oxytocin system alters social behavior and attraction in pair-bonding primates, *Callithrix penicillata*. Horm. Behav. 57, 255—262.
Smuts, B.B., Gubernick, D.J., 1992. Male—infant relationships in nonhuman primates: paternal investment or mating effort? In: Hewlitt, B.S. (Ed.), Father—Child Relations: Cultural and Biosocial Contexts. Walter de Gruyter, Inc., New York.
Sodersten, P., Henning, M., Melin, P., Ludin, S., 1983. Vasopressin alters female sexual behavior by acting on the brain independently of alterations in blood pressure. Nature 301 .
Stanford, C.B., 1998. The social behavior of chimpanzees and bonobos—empirical evidence and shifting assumptions. Curr. Anthropol. 39, 399—420.
Striepens, N., Scheele, D., Kendrick, K.M., Becker, B., Schafer, L., Schwalba, K., Reul, J., Maier, W., Hurlemann, R., 2012. Oxytocin facilitates protective responses to aversive social stimuli in males. Proc. Natl. Acad. Sci. U. S. A..
Thompson, R.R., George, K., Walton, J.C., Orr, S.P., Benson, J., 2006. Sex-specific influences of vasopressin on human social communication. Proc. Natl. Acad. Sci. U. S. A. 103, 7889—7894.
Thompson, R.R., Walton, J.C., 2004. Peptide effects on social behavior: effects of vasotocin and isotocin on social approach behavior in male goldfish (*Carassius auratus*). Behav. Neurosci. 118, 620—626.
Turner, L.M., Young, A.R., Rompler, H., Schoneberg, T., Phelps, S.M., Hoekstra, H.E., 2010. Monogamy evolves through multiple mechanisms: evidence from V1aR in deer mice. Mol. Biol. Evol. 27, 1269—1278.
Van, I.M.H., Bakermans-Kranenburg, M.J., 2012. A sniff of trust: meta-analysis of the effects of intranasal oxytocin administration on face recognition, trust to in-group, and trust to out-group. Psychoneuroendocrinology 37, 438—443.
Van Wimersma Greidanus, T.B., Kroodsma, J.M., Pot, M.L.H., Stevens, M., Maigret, C., 1990. Neurohypophyseal hormones and excessive grooming behavior. Eur. J. Pharmacol. 187, 1—8.
Wang, Z., Ferris, C.F., De Vries, G.D., 1994. Role of septal vasopressin innervation in paternal behavior in prairie voles (*Microtus ochrogaster*). Proc. Natl. Acad. Sci. U. S. A. 91, 400—404.
Williams, J.R., Insel, T.R., Harbaugh, C.R., Carter, C.S., 1994. Oxytocin administered centrally facilitates formation of a partner preference in female prairie voles (*Microtus ochrogaster*). J. Neuroendocrinol. 6, 247—250.
Winslow, J.T., Hastings, N., Carter, C.S., Harbaugh, C.R., Insel, T.R., 1993. A role for central vasopressin in pair bonding in monogamous prairie voles. Nature 365, 545—548.
Wittfoth-Schardt, D., Grunding, J., Wittfoth, M., Lanfermann, H., Heinrichs, M., Domes, G., Buchheim, A., Gundel, H., Waller, C., 2012. Oxytocin modulates neural reactivity to children's faces as a function of social salience. Neuropsychopharmacology 37, 1799—1807.
Xie, J., Kuenzel, W.J., Sharp, P.J., Jurkevich, A., 2011. Appetitive and consummatory sexual and agonistic behaviour elicits FOS expression in aromatase and vasotocin neurones within the preoptic area and bed nucleus of the stria terminalis of male domestic chickens. J. Neuroendocrinol. 23, 232—243.
Young, K.A., Gobrogge, K.L., Liu, Y., Wang, Z., 2011. The neurobiology of pair bonding: insights from a socially monogamous rodent. Front. Neuroendocrinol. 32, 53—69.
Young, L.J., Lim, M.M., Gingrich, B., Insel, T.R., 2001. Cellular mechanisms of social attachment. Horm. Behav. 40, 133—138.
Young, L.J., Nilsen, R., Waymire, K.G., MacGregor, G.R., Insel, T.R., 1999. Increased affiliative response to vasopressin in mice expressing the V1a receptor from a monogamous vole. Nature 400, 766—768.
Zak, P.J., 2011. The physiology of moral sentiments. J. Econ. Behav. Organ. 77, 53—65.