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INVITED REVIEW

Deconstructing sociality, social evolution and relevant nonapeptide functions

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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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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.