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# An evolutionary perspective on oxytocin and its behavioral effects

Steven W Gangestad

Oxytocin (OT) has received a tremendous amount of attention from psychologists and neuroscientists over the past decade, most notably through OT administration studies. An understanding of OT's evolved functions in humans, however, requires an understanding of the circumstances under which people are designed to release OT. A phylogenetic perspective suggests that OT's effects in social contexts were evolved from its adaptive regulation of maternal behavior. More generally, OT may function to and gear motivational systems toward maintaining and regulating valued but at-risk relationships of various types, including romantic relationships. A general framework for understanding endocrine hormones suggests that OT may more generally have been shaped by selection to modulate allocation of limited resources.

**Address**
Department of Psychology, University of New Mexico, Albuquerque, NM, USA

Corresponding author: Gangestad, Steven W (sgangest@unm.edu)

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Oxytocin (OT) is a peptide hormone produced by regions of the hypothalamus, stored in the posterior pituitary, and secreted peripherally as well as projected centrally under certain circumstances. In the past decade, an avalanche of research has explored the specific nature of its neurobiological and psychological impacts. In part, recent interest has been fueled by the development of technological and methodological tools. Researchers can now administer a dose of OT through a nasal inhaler and observe its effects in situations of interest. Kits for assaying naturally circulating OT in plasma, urine, and even saliva are now commercially available [1••,2] (1; for one critical analysis of their use, see 2). Undoubtedly, researchers are also driven by the fact that, though research on animals and human mothers (e.g., concerning OT's role in lactation) has being ongoing for decades, until recently little was known about the psychological effects of OT.

Although research on OT has surged, few papers have focused on the functions of OT from a broad evolutionary standpoint (for notable exceptions, see [3•,4]). What are these functions? In what contexts did OT evolve to serve them? What do these functions tell us about the evolution of human sociality and behavior more broadly?

In this paper, I offer an overview of the recent basic science on OT's roles in regulating human behavior. I raise issues about how these roles might be understood from an evolutionary perspective, and offer suggestions for fruitful directions going forward.

## Administration studies

What are the psychological effects of OT? Since the first intranasal administration study published a decade ago (for a review, see [5]), dozens more have sought to answer this question. The literature is impressive in volume yet challenging to interpret theoretically. In one recent study, administration of OT, relative to a placebo, increased activity in brain reward centers in response to viewing infants or sexual stimuli [6]. In romantically involved men, OT does much the same in response to viewing their partners' photo [7]. It leads people to see others' emotional expressions as being more intense [8], and heightens compassion toward women but not men [9]. And an emerging literature finds sex differences. For instance, women administered OT see more warmth in the faces of other women [10] and render moral judgments that are more altruistic [11]. By contrast, following OT exposure, men see less warmth is other men's faces, and offer self-serving moral judgments. Yet another study found that OT led romantically involved men to react more intensely during conflict than did their partners, but also offer more constructive solutions to it [12]. Finally, OT affects non-social behavior and physiological responses too — in one study, OT reduced eating, and increased utilization of fat stores [13].

## Interpretative frameworks

How are these effects to be understood conceptually as systematic changes on how individuals respond the world? A number of theories have been offered. An early view, still championed by some (e.g., [14]), is that OT is a 'love molecule' (e.g., [15]), promoting bonding and prosociality. This view is challenged by findings that, at times, OT administration promotes self-serving or aggressive responses [16••]. Others suggest that OT dampens anxiety ([17,18]; e.g., it suppresses HPA reactivity to stressors (but see [19])). A view now popular is the social salience hypothesis [20], the idea that OT sharpens focus on social events in general, such that its effects

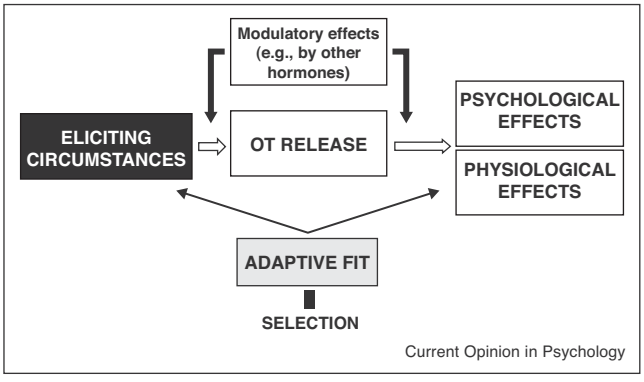
(e.g., prosociality versus aggression) depend on the nature of social information (e.g., whether it invites trust or threaten harm). (For one failure to support this notion, see [21] (21; also [22]).) Finally, neurobiological evidence on non-human animals finds that OT modifies brain reward systems, affecting which activities are actively sought out and the reinforcing value of consequences (e.g., [16••]). Under the influence of OT, then, mother rats may seek to care for offspring [23] and people may find viewing infants, sexual stimuli, and their partners especially rewarding [6,7]. These conceptualizations are not mutually exclusive. For example, effects on what is rewarding may affect the relative salience of information.

## Evolutionary perspectives on function

Even if we understood the effects of OT, we would not necessarily fully understand its functions, as Figure 1 illustrates. The OT system has been shaped by selection so that under specific circumstances, OT is released and projected centrally. The distribution and neuromodulatory properties of OT receptors have furthermore been shaped such that, under those circumstances, OT affects how the organism responds to and acts on the world. To fully understand *why* OT has its effects, then, we must know the circumstances under which OT affects how the organism responds to the world. Adaptation is understood in terms of the fit between response and context.

Indeed, in certain respects a full understanding of OT's psychological effects may require an understanding of these circumstances. In an OT administration study, OT infuses neural circuits under circumstances a researcher chooses, not when selection designed the organism for it to happen. Before the study, no human may have experienced OT infusion under those circumstances. OT's effects in the study may not accurately convey how OT affects behavior in circumstances naturally leading to OT release.

**Figure 1**




Conceptualization of the oxytocin (OT) system. OT has behavioral and physiological effects, modulated by hormonal and other factors. It is produced and released under particular circumstances, modulating by hormonal and other factors. The adaptive fit is to be understood in terms of the benefits of OT's effects, given the circumstances in which OT is released. Adaptive fit is subject to and forged by selection.

What, then, are the circumstances leading to the release of OT? To address this question, we might first consider the evolution of OT systems in animals broadly.

## OT signaling systems in phylogenetic perspective

Not all animals possess functional oxytocin-like peptide signaling systems, but most do, including earthworms, squids, roundworms, insects, and sea urchins [24]. OT-like peptide signaling systems, then, made their evolutionary debut ~700 million years ago. OT evolved to be distinct from vasopressin ~450 million years ago. The evolutionary history of OT is characterized by cooption and extension of function. In many species, OT regulates specialized muscles involved in reproduction. Its role in facilitating birth by stimulating uterine contractions is well-known. In other species, it plays similar roles in egg-laying. As well, OT is released during male ejaculation, and facilitates sperm release [25]. About 250 million years ago, this role of OT (or a related hormone in marsupials, mesotocin) was likely coopted in service of ejecting milk from mammary glands during lactation [26]. Given the recurrent presence of OT in the brains of mammalian mothers, selection may have then shaped new specialized neuromodulatory roles supporting adaptive maternal behavior and infant responses to lactating mothers. In very few species, OT's functions as a neuromodulator supporting infant care may have then been coopted to facilitate consortships — special mating relationships that emerge in otherwise promiscuous mating (e.g., [27]). (E.g., in such instances special effort dedicated to the consortship, fostered by OT, may have bolstered probability of paternity.) In even fewer species, including humans, OT may have been coopted to support pair-bonding, which in humans has been speculated to be characterized by attachment akin, in some ways, to mother–infant attachment (e.g., [28]). Whether OT's role in supporting behavior within special social relationships has been coopted in other contexts (such as human friendships) remains unknown. Mesotocin supports social relations other than mateships in some bird species, but may have acquired those roles since birds diverged from mammals [29••].

The likely contexts in which the OT system has evolved to affect behavior, aside from mother–infant relationships, are romantic relationships and, potentially, other special social relationships (e.g., friendships). Accordingly, OT's effects perhaps should be understood, functionally, within the context of those relationships. A lactating mother should attend to her infant's needs and threats to it. It should not pay her to attend to social cues in general.