Oxytocin and Human Social Behavior

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Abstract

Despite a general consensus that oxytocin (OT) has prosocial effects, there is no clear agreement on how these effects are achieved. Human research on OT is reviewed under three broad research initiatives: attachment and trust, social memory, and fear reduction. As an organizing perspective for scholars' current knowledge, a tentative model of the causes and effects of alterations in OT level is proposed. The model must remain provisional until conceptual and methodological problems are addressed that arise from a failure to distinguish between traits and states, differing research paradigms used in relation to OT as an independent versus dependent variable, and the possibility that OT effects depend on the initial emotional state of the individual. Social and personality psychologists have important roles to play in developing more rigorous and creative research designs.

Keywords

social neuroscience, evolutionary psychology, interpersonal processes

Interest in oxytocin (OT) has spread swiftly from endocrinology journals to the popular media (Young, 2009). Its popularity owes much to the attractive and accessible terms used to describe its psychological effects—*love*, *trust*, and *bonding*—terms that have traditionally been the domain of social, personality, and developmental psychology. The majority of OT research is reported in journals specifically targeted at endocrinologists and biological psychologists, understandably in light of the early pioneering research that was performed on rodents. Recently, however, new techniques have become available that allow experimental research on human participants. It is here that social psychologists, with their extensive history of research in human relationships, have much to offer at a conceptual and methodological level. Currently, studies on humans are relatively few and still inconclusive in their results. Research has been propelled by a wave of enthusiasm that has resulted in a scattergun of studies spanning several psychological domains rather than a systematic program of research.

Although there is general agreement on OT's prosocial effects, there are various suggestions about how these are mediated although these differences are often implicit rather than clearly delineated. In the present article, I examine the evidence behind three proposals about OT's effects with the aim of making explicit the connections among them and with social psychology. These proposals are that (a) OT enhances attachment and trust, (b) OT improves social memory, and (c) OT reduces fear. Although I briefly summarize research on nonhuman animals, the chief focus of this review is the impact of OT on human emotions and behavior. I begin with a short description of the peptide together with some important considerations in interpreting the research literature.

OT: A Primer and Some Caveats

OT is a peptide hormone composed of nine amino acids (for useful reviews, see Gimpl & Fahrenholz, 2001; Goodson, 2008; Lee, Macbeth, Feldman, & Weller, 2009). It is highly conserved across species in terms of structure and function, although there is interspecies variability in the specific behaviors that it controls. OT has both peripheral and central effects. Peripherally, OT regulates uterine contractions during labor and milk ejection during lactation (Keverne & Kendrick, 1992). It is synthesized in magnocellular neurons of the paraventricular (PVN) and supraoptic (SON) nuclei of the hypothalamus, which project to the posterior pituitary where OT is released into blood circulation. Centrally, OT acts as a neuromodulator: Released from all parts of the neuronal membrane, OT diffuses widely in extracellular fluid, affecting many regions of the brain (Landgraf & Neumann, 2004). It is synthesized in the parvocellular neurons of the hypothalamic PVN, which projects to limbic sites (hippocampus, amygdala, striatum, hypothalamus, nucleus accumbens) and to the brain stem. Central OT effects include maternal

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and sexual behavior, pair bonding, and social recognition (Donaldson & Young, 2008).

In interpreting the results of studies that I review here, it is important to note the source of OT. Because peripheral OT can be assayed from blood samples whereas central OT requires more invasive spinal tap measurement of cerebrospinal fluid, most human studies of endogenous OT tell us only about peripheral effects. The extent to which peripheral and central release is coordinated is doubtful (Amico, Challinor, & Cameron, 1990; Engelmann, Ebner, Landgraf, Holsboer, & Wotjak, 1999; Gimpl & Fahrenholz, 2001; Landgraf & Neumann, 2004; Neumann, 2007). In some species a small quantity of peripherally administered OT may cross the blood–brain barrier or influence behavior via afferent feedback to the CNS. Studies of plasma OT also vary in their use of basal versus reactive measures.

Bear in mind also that although both sexes have OT receptors (Goodson & Bass, 2001), OT is of special relevance to females because OT synthesis and OT receptors are upregulated by estrogen (Lim & Young, 2006; Patisaul, Scordalakes, Young, & Rissman, 2003). Indeed, McCarthy, McDonald, Brooks, and Goldman (1996) observe that the OT receptor is "one of the most strongly estrogen-regulated systems in the brain. . . . Estrogen-induced increase in OT receptor binding is integral to its behavior-modifying effects" (p. 1209). OT's sister nonapeptide arginine vasopressin (AVP), which is very similar in structure, appears to play a more important role in males, although OT has been shown to affect some male behaviors including partner preferences, sexual behavior, and social recognition (Cushing & Kramer, 2005). Both sexes have receptors for both neuropeptides (Goodson & Bass, 2001), and to complicate matters further, the structural similarity of AVP and OT means that they may be capable of binding to each other's receptors.

The effects of the same peptide can also vary dramatically in males and females. For example, in men, intranasally administered AVP stimulates agonistic facial expressions and decreased perception of friendliness in response to images of same-sex strangers. In women, administration of the same peptide results in affiliative facial expressions and increased perception of friendliness (Thompson, George, Walton, Orr, & Benson, 2006). Studies that assay plasma OT as a dependent variable are most often performed on women, although some studies also include men. However, nearly all studies where OT is centrally administered as an independent variable use exclusively male participants because of the small possibility of OT entering the bloodstream where it might cause uterine contractions. Thus, there is a potential confound between participant sex, study design (whether OT is an independent or dependent variable), and OT system (central vs. peripheral).

Another note of caution is warranted. Much of our basic knowledge about OT has come from research on rodents, and even here there are important differences between taxa. Extrapolations to humans must be made with caution because there is considerable variation in receptor distribution across mammalian species. In humans, we do not yet know the extent to which "hard-wired" responses, such as maternal behavior, pair bonding, and affiliation, have been superseded by learning and cultural transmission afforded by increased cortical size.

There is general consensus that OT has positive effects on human social behavior, but there are at least three implicit proposals about the mediators of these prosocial effects.

OT: Attachment and Trust

The emotional bond between caregiver and offspring, and between adult partners, lies at the heart of the psychology of relationships. A secure attachment in infancy is important for normal psychological development and provides a base from which the infant explores the world beyond (Bowlby, 1988). The infant's internal working model of attachment has implications for the nature and quality of later adult relationships. The continuities and similarities between these two types of relationship have often been noted by developmental and social psychologists. It has been proposed not only that successful adult pair bonding depends on the early child–parent relationship but also that the two share a common psychological mechanism. Although adult relationships incorporate sophisticated cognitive, social, and cultural components, they may share a basic emotional infrastructure with our earliest experience of attachment (Hazan & Diamond, 2000). Because mother–infant attachment is ubiquitous in mammals, the possibility of a biological basis attracted research interest.

Early work on OT focused on its role in supporting maternal behaviors toward offspring in rodents (see reviews by Broad, Curley, & Keverne, 2006; Insel, 2000; Kendrick, 2000). In pregnancy, triggered by rising estrogen levels, OT receptors are upregulated in the uterus and the brain. Vagino-cervical stimulation during parturition activates OT neurons in the hypothalamus, stimulating OT release in many brain areas including the preoptic area, ventral tagmental area, and olfactory bulb. These pathways are responsible for coordinating a range of maternal behaviors including nest building, pup retrieval, licking, crouching, and maternal aggression. In 1979, Pedersen and Prange first demonstrated that intracerebroventricular (icv) infusion of OT can induce maternal responses in estrogen-primed virgin rats. Reciprocally, the onset of maternal behavior can be inhibited by OT antagonists, lesions of OT cells, and antibodies to OT (Insel, 2000). Recent studies using genetic knockout of OT receptors have confirmed significant deficits in mothering (Takayanagi et al., 2005). Even in rodents, the role of OT however is confined to the initiation not the maintenance of maternal behavior (Kendrick, 2000).

In humans, there is general consensus that prenatal and postpartum OT both enhances the formation of close bonds with the infant and reduces maternal stress reactivity (Nelson &

Panksepp, 1998; Neumann, 2008). During childbirth there is a rise in OT in the cerebrospinal fluid, and postpartum plasma levels are correlated with positive feelings and reduced anxiety (Takagi, Tanizawa, Otsuki, Haruta, & Yamaji, 1985). Immediately after birth and prior to their first feeding, infants massage the mother's breast, resulting in peripheral OT release, which is also elevated during feeding (Matthiesen, Ransio-Arvidson, Nissen, & Uvnas-Moberg, 2001). Subjectively, lactation is associated with lowered stress and less negative mood states (Mezzacappa & Katkin, 2002). Biologically, lactation is associated with lowered cortisol (Amico, Johnston, & Vagnucci, 1994), attenuated ACTH, cortisol and gluocose responses to exercise stress (Altemus, Deuster, Gallivan, Carter, & Gold, 1995), and during suckling there is a negative relationship between plasma OT and ACTH levels (Chiodera et al., 1991). Evidence for more wide-ranging behavioral effects of OT has come from studies that assayed plasma OT levels during the first and third trimester of pregnancy and the first postpartum month. A pattern of increasing OT during pregnancy was associated with higher maternal–fetal bonding (Levine, Zagoory-Sharon, Feldman, & Weller, 2007). OT levels in early pregnancy and postpartum were significantly correlated with maternal bonding measures including attachment-related thoughts, gaze at the infant, affectionate touch, and frequent infant checking (Feldman, Weller, Zagoory-Sharon, & Levine, 2007). Although human maternal behavior does not critically depend on OT as it may do in rodents (in humans, high-quality infant care is given by adoptive mothers, by mothers whose babies have been carried by surrogates and by relatives, and other adult caretakers), OT appears to play a supplementary role in enhancing bonding in the early weeks (Broad et al., 2006; Kendrick, 2000).

Rodent studies then explored the possibility that pair bonding might similarly be associated with OT release, an expectation arising from the proposal that adult attachment may have arisen from or "exapted" the more primitive mechanism of mother–infant bonding. Two closely related species provided a convenient natural experiment (Insel & Shapiro, 1992). The prairie vole shows a strong partner preference and biparental care in contrast to the promiscuous montane vole. In the female prairie vole, OT administration facilitates partner preference, whereas OT antagonists block it, without interfering with mating. OT receptors are found in the nucleus accumbens and prelimbic cortex of the prairie vole—areas rich in dopamine receptors. Administration of OT induces central dopamine release and vice versa, and their coaction appears to be critical for partner preference (Edwards & Self, 2006; Liu & Wang, 2003; Young & Wang, 2004). In the promiscuous montane vole, the OT and dopamine systems are uncoupled.

The roles of OT and dopamine in interpersonal attraction have been rather freely extrapolated to humans. Although love is a human universal (Jankowiak & Fischer, 1992), social psychologists have made finer distinctions between companionate, romantic and passionate love (Hatfield, 1988; Sternberg, 1986). Fisher, Aron, and Brown (2006) proposed a sequential model in which the sex drive (chiefly associated with androgens) motivates general sexual interest, romantic love (associated with dopamine and noradrenaline release) is associated with preference for a specific partner, and partner attachment (associated with OT) enables a long-term bond to be formed to provide biparental care. Others consider the simultaneous activation of dopaminergic reward and OT pathways to be critical to relationship formation (Skuse & Gallagher, 2008). Beyond the mating arena, Depue and Morrone-Strupinsky (2005) argue that OT is implicated in both the motivation and the reward associated with social interactions. They propose that dopaminergic neurons running from the ventral tagmental area to the nucleus accumbens are responsible for the motivation to affiliate. OT and OT receptors are found in these same areas where they interact with the dopamine system. However, experiences of affiliative reward derive from endogeneous opiate release and binding that occurs during many of the same sociosexual experiences that are associated with OT release. OT can increase central opiate release by up to 300% (Csiffary, Ruttner, Toth, & Palkowits, 1992).

Human studies have examined plasma OT levels both as a correlate of long-term attachments and as a short-term response to experimental manipulations of relationship variables. Studies that have examined OT's association with ongoing relationship quality have produced conflicting results. Based on rodent findings, it was hypothesized that OT levels would be enhanced in individuals currently experiencing warm and satisfactory romantic partnerships. However, findings from two studies ran exactly counter to this hypothesis. Turner, Altemus, Enos, Cooper, and McGuiness (1999) found that higher basal levels of OT were associated with greater self-reported interpersonal distress. (Yet, paradoxically, when respondents were asked to recall a sad relationship event OT levels generally decreased.) Subsequently, Taylor et al. (2006), in a study of postmenopausal women, reported consistently negative correlations between OT and marriage quality, physically affectionate partner contact, and partner relations (the extent to which they could open up to their partners and were understood and appreciated by them). OT was also negatively associated with the quality of other relationships and the frequency of social contacts generally. These findings prompted Taylor (2006) to propose that elevated OT levels act as a marker for gaps in relationships and trigger a search for affiliative contact (discussed later).

However, other researchers have reported results supporting the original expectation of a positive association. Tops, van Peer, and Korf (2007) found a positive correlation between OT and attachment (the tendency to express and share emotions and feelings with others). Grewen, Girdler, Amico, and Light (2005) found that individuals who reported

a more supportive relationship with their partner had higher OT levels throughout a series of three blood draws taken before, during, and after warm partner contact. The magnitude of the correlation was quite similar for both sexes (men $r = .38$, women $r = .36$). Although Light, Grewen, and Amico (2005), using the same measure of relationship quality in a subsequent study, found no correlation with basal OT, OT was positively associated with reported frequency of partner hugs and massages. In another ambiguous result, Gordon et al. (2008) found that OT was positively correlated with the quality of unattached young adults' reported bonds with their parents, although it showed no relationship with trait measures of attachment anxiety or attatchment avoidance.

Other studies have examined short-term changes in OT levels as a function of recalling positive and negative experiences of romance. One study reported a tendency for negative recollections to be associated with OT reduction, although there was no effect for positive emotions (Turner et al., 1999). However, a later study by the same team (Turner et al., 2002, p. 269) concluded that OT levels were not reliably altered by either positive or negative emotion induction and were probably "not functionally significant."

In the short term, viewing pictures of a romantic partner activates dopaminergic pathways that are also rich in OT receptors (Bartels & Zeki, 2004; Fisher et al., 2006). More directly, OT level have been reported to rise during genital stimulation, copulation, and orgasm (Carmichael et al., 1987; Uvnäs-Moberg, 1998), though rises in response to massage (typically given by a masseur unacquainted with the participant) are usually nonsignificant (Turner et al., 1999; Wilkstrom, Gunnarsson, & Nordin, 2003). Tactile contact from a partner does not have immediate effects on plasma OT levels (Ditzen et al., 2007; Grewen et al., 2005).

Does OT have effects on social relationships beyond the mother–infant and pair bond? Animal studies suggest that it may be implicated in sociability more generally. Bonnet monkeys, a naturally affiliative species, show higher OT levels in cerebrospinal fluid than the less sociable pigtail macaque (Rosenblum et al., 2002). In rats, gerbils, and squirrel monkeys, intracranial or subcutaneous injection of OT increases social contact time (Razzoli, Cushing, Carter, & Valsecchi, 2003; Winslow & Insel, 1991; Witt, Winslow, & Insel, 1992). Within species, individual differences in affiliation may reflect early nurturing experiences and their effects on the OT system (Cushing & Kramer, 2005). Rhesus monkeys deprived of maternal care display asocial behavior including avoidance of physical contact and gaze, stereotypic and self-directed behaviors, and attachment to inanimate objects. These monkeys also have decreased cerebrospinal OT measured between 18 and 36 months. Levels of cerebrospinal OT (but not plasma OT) are positively correlated with affiliative behavior (Winslow, 2005).

In humans, the experience of being trusted and reciprocating trust is associated with raised OT levels. Zak, Kurzban, and Matzner (2005) employed a Trust Game in which an investor awarded a sum of money (between $1 and $10) to a trustee that was tripled in value by the experimenter. The trustee then had the option of returning some portion of the money to the investor. In a control condition, the amount awarded to the trustee was decided by a random computer draw. Subsequently plasma OT levels in the trustee were significantly higher in the experimental condition. This suggests that the trustees' OT levels were responsive to the intention of trust rather than to the receipt of money per se. The amount returned to the investor (a measure of trustworthiness) was significantly correlated with subsequent OT levels for experimental but not control participants.

Drawing together the research on tactile contact and interpersonal trust, Morhenn, Park, Piper, and Zak (2008) examined their joint effects on changes in plasma OT. Participants received a 15-minute massage or rested before playing the Trust Game (a third group received the massage only). Blood draws for OT assays took place on arrival and at the end of the experiment. For the investors, there was no association between the sum of money they transferred ("trust") and change in OT levels either with or without prior massage. But for those trustees who had received the massage, there was a significant positive association between the sum received (their "trustworthiness") and an increase in their OT level. The amount returned by the trustee to the investor was also correlated with OT change both with and without massage. Because massage alone did not alter OT levels, this study suggests that it is touch associated with being trusted that induces OT elevation. More broadly, one might speculate that it is the positive emotional connotation of touch rather than tactile stimulation per se that raises OT levels.

However, plasma concentrations of nonapetides may not necessarily reflect CNS levels (Landgraf & Neumann, 2004), and recent studies have used intranasal delivery to directly manipulate central OT levels. A quantity of the peptide (usually 24 IU) is inhaled, and it is thought that the molecules take an extracellular route through the olfactory epithelium where they diffuse into subarachnoid space (Born et al., 2002). Cerebrospinal concentrations of the peptide begin to rise within 10 minutes of administration and remain elevated for 80 to 120 minutes. Intranasal delivery means that levels of central OT can be incorporated into an experimental design as an independent variable rather than peripheral levels being used as a dependent variable or correlate. Increasingly psychologists are taking advantage of this powerful, noninvasive technique.

Administration of OT increased the positivity of verbal and nonverbal behaviors in couples during a discussion of conflict, suggesting greater positivity even when engaged in a task likely to provoke animosity (Ditzen et al., 2009). Emotional recognition has been examined under the hypothesis that OT administration may support prosocial behavior by selectively enhancing identification of positive facial

expressions. OT does not appear to increase the identification accuracy, reaction time, gaze duration, or fixation count in response to positive or negative static facial expressions (Di Simplicio, Massey-Chase, Cowen, & Harmer, 2009; Guastella, Carson, Dadds, Mitchell, & Cox, 2009). However, informed by the opposite hypothesis that OT may increase sensitivity to fearful expressions, Fischer-Shofty, Shamay-Tsoory, Harari, and Lefkovitz (2010) recently reported increased and selective accuracy in fear detection from dynamic presentations. Using semantic rather than visual stimuli, Di Simplicio et al. (2009) examined recognition of emotional words. No effect of OT was found for reaction time or accuracy in classifying emotional words as likeable or dislikeable, nor was any effect found for either vigilance or accuracy on a visual probe task of positive or negative emotional words. However, a semantic task oriented to interpersonal relationships produced more encouraging results. Unkelbach, Guastella, and Forgas (2008) presented participants with stimulus words that appeared over 8 seconds from a gradually dissolving black mask. The words were selected from five categories (relationship, sex, safety and threat, happiness and sadness, and other), and participants were asked to rate them as negative or positive in meaning. Although accuracy was not affected by OT, reaction times were significantly shorter for the sex-related and relationship-related word categories.

Eye gaze toward different facial features in photographs was used as an assay of social interest by Guastella, Mitchell, and Dadds (2008). Compared to placebo, OT increased the duration and frequency of men's gaze toward the eyes. The eyes can convey information about a target's emotional state, and this has formed the basis for a measure of empathy called the Reading the Mind in the Eyes test (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). OT increased the correct identification of emotions with the effect being more marked on the most difficult items (Domes, Heinrichs, Michel, Berger, & Herpetz, 2007).

Pursuing the empathy hypothesis, Zak, Stanton, and Ahmadi (2007) compared the effect of OT on two economic games. In the Ultimatum Game, one player is assigned a sum of money to be split with another participant. If the offer is accepted, the money is paid to both participants as agreed, but if the offer is rejected, both parties receive nothing. This game is taken as a measure of perspective taking (because the donor must consider what offer the other party is likely to accept). In the Dictator Game, one player makes a decision as to how much of the assigned sum to award to the second party, which the second party has no option but to accept. OT administration significantly increased the money awarded in the Ultimatum Game but not in the Dictator Game, suggesting that the effect of OT is on empathy-mediated generosity rather than generous behavior per se. This conclusion reinforces that of Kosfeld, Heinrichs, Zak, Fischbacher, and Fehr (2005), in which, following OT or placebo administration, participants played the Trust Game described earlier. OT increased the value of money transferred by the investor, supporting its role in enhancing trusting behavior, although it did not affect subjective ratings of interpersonal trust. However, OT had no effect on the back transfer of money by the trustee, suggesting that OT does not have a generalized effect on reciprocity or generosity in the absence of a requirement to empathize with another's perspective.

In summary, the evidence for social bonding effects is equivocal. The hypothesis that plasma OT levels are higher among those in satisfactory emotional relationships has received some support, but two studies have produced opposite results, giving rise to the suggestion that elevated OT may signal emotional distress and stimulate social contact (Taylor, 2006). Little support has been found for OT changes in response to the recall of bonding emotions. But OT increases trusting behavior and rises in response to it, where this depends on mind reading or empathy.

OT: Social Memory

The ability to recognize conspecifics (kin, mates, offspring, allies, and enemies) forms a crucial basis for our social behavior. Stored information about others' identity and past behavior informs our interactions with them. In humans, faces provide important information about identity, and a specific brain area, the right fusiform gyrus, has been implicated in face recognition (Kanwisher, McDermott, & Chun, 1997). Functional MRI results show that OT administration is associated with activation in the fusiform gyrus (Petrovic, Kalisch, Singer, & Dolan, 2008). This area works in concert with the amygdala and the superior temporal sulcus, which are implicated in the processing of facial expressions. OT receptors are present in the amygdala and hippocampus.

OT is critically involved in social memory in the mouse. OT knockout (OTKO) mice completely fail to recognize a conspecific even after repeated encounters, although there are no deficits in nonsocial learning or olfactory processing (Ferguson, Aldag, Insel, & Young, 2001; Ferguson, Young, & Insel, 2002). Social recognition can be restored by icv injection of OT prior to the initial encounter, indicating that OT is involved in memory acquisition rather than consolidation. In wild-type mice, olfactory cues are relayed to the amygdala where OT enhances encoding of the encounter, as if stamping it with social significance, before this information is relayed to its efferents, the bed nucleus of the stria terminalis and the medial preoptic area. In OTKO mice, the transmission of olfactory information is normal until its arrival at the medial amygdala, where there is an absence of neuronal activation (see Choleris, Clipperton-Allen, Phan, & Kavaliers, 2009; Ferguson et al., 2001). However, OT effects in the rat are much less clear. Central injection of OT can either facilitate or attenuate social recognition depending on the dose (Benelli et al., 1995), and OT antagonists inhibit recognition

in females but not in males (Engelmann, Ebner, Wotjak, & Landgraf, 1999). Such species differences suggest caution about premature extrapolation to humans.

Early human studies examined verbal memory with some finding that OT impaired memory and others reporting no effect (see Heinrichs, Meinlschmidt, Wippich, Ehlert, & Hellhammer, 2004). More recently, researchers have explicitly focused on social memory. They have investigated selective memory for facial identity and for emotional and relationship-relevant stimuli. Following administration of OT or placebo, Rimmele, Hediger, Heinrichs, and Klaver (2009) presented faces and nonsocial stimuli. A surprise recognition test was given 24 hours later. No effect was found for nonsocial stimuli, but, although OT did not affect facial recall ("remember") performance, it increased the accuracy of facial familiarity ("know") ratings independent of the valence of the facial expression. However, Di Simplicio et al. (2009) found no effect of OT (administered before encoding and still active during recognition) on either accuracy or speed using the Cambridge Face Memory Test.

With regard to emotional expressions, it has been hypothesized that, by increasing interpersonal positivity, OT selectively enhances memory for positive emotions. Again, the results are mixed. Following OT or placebo administration, participants viewed neutral, happy, or angry faces (Guastella, Mitchell, & Matthews, 2008). A surprise recognition test conducted the following day revealed that, compared to placebo, OT enhanced the accuracy of "remember" judgments for happy faces only and increased the accuracy of "familiarity" judgments for happy as compared to angry and neutral faces. A second study examined OT effects on memory consolidation with opposite results (Savaskan, Ehrhardt, Schulz, Walter, & Schachinger, 2008). OT was administered after exposure to happy, angry, and neutral faces, and recognition memory was tested after 30 minutes and 24 hours. OT enhanced recognition of neutral and angry but not happy faces.

Other experiments have used semantic rather photographic stimuli. Following OT or placebo administration, participants were shown 60 personality terms (Di Simplicio et al., 2009). OT had no significant effect on the recall or recognition of personality terms 20 minutes later (although there was a nonsignificant trend toward more accurate recognition of positive then negative words by the OT group). Heinrichs et al. (2004) examined the effects of OT on three memory tests following exposure to reproductively relevant (e.g., *sex*, *baby*) and neutral words (e.g., *car*, *sweets*). In two implicit memory tests, participants were instructed to respond to prompts with whatever word came to mind. OT had no effect on implicit perceptual memory (participants were cued with word stems from the encoding phase) but impaired implicit conceptual memory for reproduction-relevant words (participants were cued with category terms relevant to the encoding phase). OT also impaired explicit memory irrespective of semantic category (participants were cued with word stems and explicitly asked to recall the presented words).

Given the hypothesis that OT should enhance social memory, the pattern of results is inconclusive to say the least. For facial identity memory, two studies report opposite effects and the positive effect of OT is confined to familiarity judgments only. For emotional expressions, OT appears to selectively enhance the encoding of happy faces and the consolidation of neutral and angry faces. OT has no impact on the semantic encoding of either positive or negative personality terms, but it impairs explicit recall regardless of word type and implicit recall specifically of reproductively relevant words. Before memory research can be integrated into the full picture of OT effects, clearer hypotheses drawing on the extensive neuropsychological and cognitive literature are needed (Mitte, 2008) that specify the anticipated effects of OT on various forms of memory as a function of their emotional content.

OT: Fear Reduction

The anxiolytic effects of OT are the most unanimously recognized in nonhuman animal research. Administering OT reduces amygdala activation, increases parasympathetic functioning, inhibits corticotropin releasing factor neurons, decreases corticosteroid release, and results in lower levels of fearful behavior (Engelmann, Landgraf, & Wotjak, 2004; Neumann, 2007; Viviani & Stoop, 2008). OT activates neurons in the lateral and capsular portion of the central amygdala, which inhibit, via GABA projections, the fear-inducing effects of AVP in the medial central amygdala (Huber, Veinante, & Stoop, 2005).

In humans, OT administration in conjunction with fMRI imaging has produced interesting and positive findings. In response to fear-provoking visual stimuli, OT reduced amygdala activation and the connectivity between the amygdala and the upper brainstem implicated in autonomic nervous system reactions to threat (Kirsch et al., 2005). Petrovic et al. (2008) conditioned a set of faces to electric shock. After OT treatment, participants showed reduced activity in the anterior medial temporal cortex (anterior to and extending into the amygdala) and in the anterior cingulate cortex. For fear-conditioned faces displaying direct gaze (taken to be the most threatening), activity in the right amygdala was significantly higher in the placebo group. The OT group also showed a significant attenuation in their affective ratings of the fear-conditioned faces. Another study (Domes et al., 2007) found that OT eliminated the heightened right amygdala activation seen in the placebo group to emotional versus neutral faces. However, this effect was seen for happy as well as sad and fearful faces, suggesting that OT effects may not be specific to fear reduction.

However, studies that have examined correlations between psychometric measures of trait anxiety and plasma OT levels

have produced mixed results with reports of negative associations (Scantamburlo et al., 2007; Uvnäs-Moberg, Widström, Nissen, & Björvell, 1990), positive associations (Uvnäs-Moberg, Arn, Theorell, & Jonsson, 1991), and null relationships (Gordon et al., 2008; Taylor et al., 2006; Tops et al., 2007; Uvnäs-Moberg, Arn, Jonsson, Ek, & Nilsonne, 1993).

Experimental studies have manipulated participants' stress to observe situational or "state" effects on OT levels. In a study of older women's response to the Trier Social Stress Test, cortisol levels (an index of stress) were measured at eight points over the course of the task showing the expected elevation followed by decline. However, plasma OT levels were not associated with these changes in cortisol (Taylor et al., 2006). Two further studies confirm these results (Ditzen et al., 2007; Light et al., 2005).

However, two studies suggest the possibility of a trait–state interaction. In response to an uncontrollable auditory stressor, plasma OT rose but only among women high in trait anxiety as measured by the N scale of the Eysenck Personality Questionnaire (Sanders, Freilicher, & Lightman, 1990). In another study, in response to cortisol administration (normally released by the hypothalamic-pituitary-adrenal axis (HPA) in response to stress), OT levels rose but only for women who scored high on a questionnaire assessing a tendency express emotion outwardly (Tops et al., 2007). An individual's basal level of anxiety or emotional expressiveness may augment the "dose" of experimentally manipulated stress revealing increases in OT levels.

Other studies have administered OT prior to stress manipulation to examine possible anxiolytic effects. When asked to discuss an area of conflict in their relationship (designed to induce stress), postdiscussion cortisol levels were significantly lower in those couples who had previously received OT (Ditzen et al., 2009). The separate and joint effects of OT and social support on stress reactivity were examined by Heinrichs, Baumgartner, Kirschbaum, and Ehlert (2003). The experimental design compared four groups resulting from pharmacological condition (OT or placebo administration) and presence or absence of social support (participants brought a friend who accompanied them during the 10-minute preparation period prior to a public speech). Social support was more effective than OT in attenuating cortisol response, but the lowest cortisol reactivity was seen in those participants receiving both social support and OT. A comparison of pre- and poststress anxiety levels showed that OT significantly reduced self-reported anxiety.

A number of researchers have proposed that the prosocial effects of OT (described earlier) derive from its anxiolytic properties. OT, by reducing interpersonal fear or anxiety, allows for the formation of positive bonds. Administration of OT increases ratings of trustworthiness and attractiveness of unfamiliar faces in both men and women (Theodoridou, Rowe, Penton-Voak, & Rogers, 2009). In the trust paradigm described earlier (Kosfeld et al., 2005), the authors concluded that the higher level of trust after OT administration was caused by a decrease in betrayal aversion and social avoidance. Interacting with a stranger, whose reputation and past behavior are unknown to us, is normally associated with a degree of apprehension, which is decreased by OT, thereby permitting trust. But what happens when a stranger's behavior generates a realistic fear of betrayal? Does OT diminish the normal mistrust that would be triggered by their action? A subsequent study (Baumgartner, Heinrichs, Volanthen, Fischbacher, & Fehr, 2008) examined the impact of a breach of trust on trusting behavior by the investor. After being informed that the trustee had repaid them on only 50% of occasions, the placebo group showed a decrease in trusting behavior (reduced money transfer) accompanied by increased activation in bilateral amygdala and brainstem effector sites. These changes in response to feedback were not seen in the OT group. These results are taken to support the view that OT reduces fear and conserves trust even in situations of betrayal.

Toward Integration

With respect to these three broad areas of human research, a range of causal pathways have been suggested that together accommodate almost every possible permutation of relationship. However, a broad consensus has begun to emerge forged on the most robust empirical finding: that OT depresses amygdala activity and HPA stress responses and that this reduction is linked to stronger social approach behavior. As Carter (1998) summarizes it, "Oxytocin . . . may serve to inhibit defensive behaviors associated with stress, anxiety or fear, and allow positive social interactions and the development of bonds" (p. 782).

My elaboration of this proposal is represented in Figure 1, which provides an organizing perspective for our current knowledge of OT stimuli and effects. The initiation of OT release and uptake is triggered by challenges to bodily or psychological integrity. Although we tend to ascribe a positive hedonic valence to sexual relations, childbirth, and lactation, if we take a more biological view these events can also be seen as invasions of the usual bodily boundaries that define the individual as a discrete organism. Such somatic intrusions carry the possibility of trauma (rape, injury, maternal or infant death, pain) as well as satisfaction. Nonetheless, in evolutionary terms such encounters are vital to the continuation of the germ line, and, to reduce the stress occasioned by such encounters, OT is released to depress HPA axis reactivity. This stress reduction is able, under appropriate interpersonal circumstances, to enable positive exchanges by increasing trust, enhancing mind reading, and promoting affiliation. The social buffering effects of social contact suggest that affiliation may also feed back to the oxytocinergic system, modulating stress levels (Heinrichs et al., 2003; Morhenn et al., 2008; Zak et al., 2005).

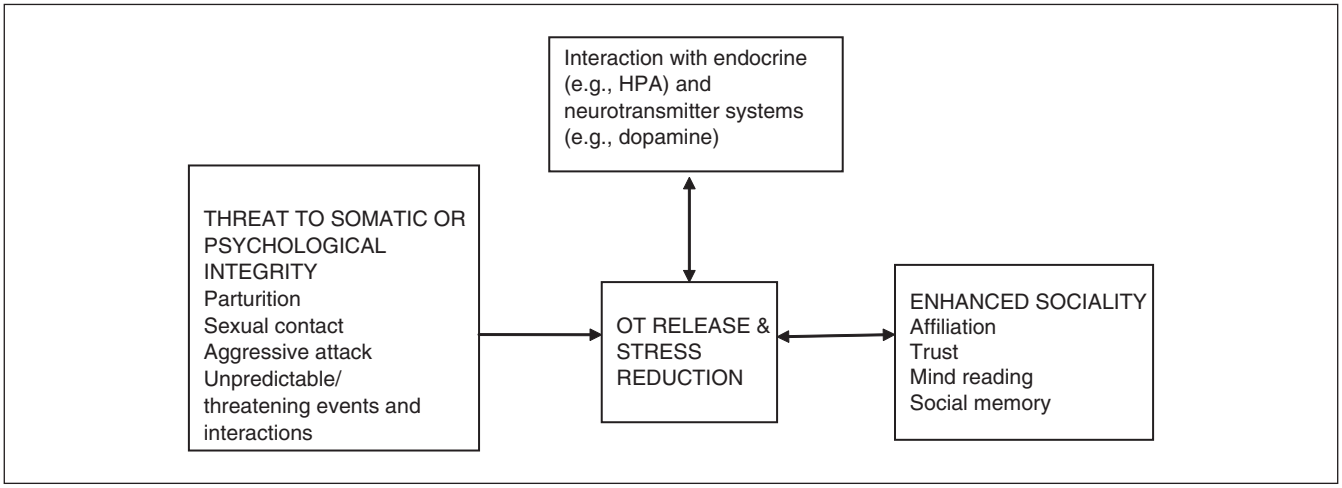

Figure 1. A simplified proposal of oxytocin (OT) action

Traits, States, and Research Paradigms. Although such a proposal is satisfying, it is necessarily an oversimplified schematization of our current knowledge. Complications arise as we consider the problems posed by an empirical failure to distinguish between traits and states, differing research paradigms used in relation to OT as an independent versus dependent variable, and the possibility that OT effects depend on the initial emotional state of the individual.

Before proceeding, we should note that terms such as *stress*, *anxiety*, and *fear* have been used rather loosely in the OT literature. An often unrecognized distinction, though one that is very familiar to personality researchers, is between traits and states. Traits are stable and enduring characteristics of persons; hence, anxiety may be conceived of as a trait or a state. By extension, we can think of relationships in similar terms so that a marriage is an enduring connection parallel to a trait whereas briefer interpersonal exchanges are parallel to states. When we ask about the status of a relationship, we effectively ask the respondent to aggregate and summarize specific events and experiences into a numerical rating, in the same way that self-report personality items implicitly ask the respondent to compute an "average" of his or her responses over many different settings. In contrast, states represent short-term modulations of mood and biological functioning in response to specific events. By analogy, this trait–state distinction holds also for hormones. Basal levels of OT (taken at rest without experimental manipulation) are thought to reflect a stable aspect of neurohormonal functioning that is characteristic of an individual. Reactive levels of OT measure an individual's hormonal response to a specific stimulus. As with psychological traits, these traits and states likely interact to determine hormone levels.

The first part of Figure 1 considers OT level as a dependent variable effectively posing the question: What factors are associated with heightened OT? Some researchers have addressed this question by computing the correlation between a trait and OT level. Individual traits (e.g., anxiety) as well as relationship traits (marriage quality) have been used. In both areas, results have been inconsistent. This suggests that basal OT may not be reliably associated with individual or relationship traits. A lesson learned from the person–situation debate by personality psychologists was the importance of aggregation to increase measurement reliability and thereby expose underlying correlations. Yet in many endocrinology studies, a single plasma sample (or at best several samples taken during a single session) is presumed to reflect a stable basal OT level characteristic of that individual. Regarding trait measurement, the ease of administering a paper-and-pencil inventory has resulted in multiple scales being analyzed in a single study, with the associated danger of inflating Type I errors.

A more stringent experimental approach to the causes of OT release manipulates participants' mood (e.g., by imposing stress, administering cortisol, or providing physical or social contact) and measures alterations in OT. This is a "state" manipulation, but firm conclusions remain compromised by the fact that the dependent variable (OT) is taken from plasma (as it is in correlational studies). The relationship between central and peripheral OT circulation remains uncertain, and it is conceivable that they are differentially responsive to environmental stimuli. Although central OT can be measured in cerebrospinal fluid, this procedure is highly invasive. Blood draws are also uncomfortable, and to the extent that it causes stress or pain, venipuncture itself may affect OT levels either directly or indirectly via its effect on stress hormones. (Researchers are currently developing techniques to recover OT from saliva, making collection less intrusive but assay sensitivity is problematic; White-Traut et al., 2009). Even assuming error-free measurement, we rarely investigate (let alone take into account) OT-level fluctuations as a function of circadian rhythms, menstrual cycle, interactions with other hormones and neurotransmitters, or uncontrolled events beyond the laboratory.

The second part of the figure addresses OT as an independent variable. In these studies OT is typically delivered intranasally and its impact on performance on a given task is evaluated. Although peripheral OT can be manipulated by intravenous delivery, this is rarely done. Because central OT manipulation is relatively straightforward, there has been a recent explosion of such studies. It is likely that we will be much better informed about the effects of central OT, perhaps to the detriment of our understanding of the factors associated with OT release.

Emotional Valence and Intensity: Variable OT Effects. Studies using OT administration are informative about "state" effects of the hormone. In addition to the above distinction between trait and state, I now consider finer distinctions with short-term states and how these may be differentially affected by OT administration.

On a continuum of interpersonal perception, trust and fear reside at opposite extremes. Trust indicates a belief in the reliability and goodwill of another person and can range from provisional favorability to complete confidence. Fear signals threat, hostility, and possible attack and can range from mild apprehension to outright panic. These are not merely semantic distinctions. The behavioral manifestation of OT's anxiolytic action may depend on where an individual is located on this interpersonal continuum between trust and fear. It may downgrade terror to fear or shift mild apprehension to unconditional trust.

Animal research is instructive at the very high end of the fear continuum. OT enhances maternal aggression (Debiec, 2005; Pedersen, 2004). Maternal aggression is associated with low levels of fear (Neumann, 2008; but see Lonstein & Gammie, 2002). Following parturition there is down-regulation of corticotropin releasing factor, which controls activity in the hypothalamic pituitary axis (Lonstein, 2005; Neumann, 2002, 2003). Although it leaves other maternal behaviors unaffected, icv infusion of corticotropin releasing factor (CRF) significantly inhibits maternal aggression (Gammie, Negron, Newman, & Rhodes, 2004). At very high fear levels, with no escape route, both humans and rodents respond with freezing or tonic immobility (Blanchard, Hynd, Minke, Minemoto, & Blanchard, 2001; Moskowitz, 2006). The expression "scared stiff" captures this behavioral effect, which appears to be reduced by OT, thus permitting maternal attack.

The idea of fear down-regulation may shed light on a crucial and unresolved anomaly in the human aggression literature: The well-established sex difference in aggression, found where the target is same sex or unspecified, disappears and even reverses where the target is an intimate partner (Archer, 2000). The usual fear experienced by women contemplating an attack on a stronger, larger male opponent is reduced in the context of partner-directed aggression (Fiebert & Gonzalez, 1997), an effect that may be mediated by the increase in trust associated with physical intimacy and OT release. The trust (reduced fear) necessary for intimate sexual contact may diminish the threshold for female-to-male aggression. We know that in rodents oestrous females are typically wary of a strange male and the release of OT inhibits defensive aggression and facilitates lordosis (Debiec, 2007; Pedersen & Boccia, 2006). At the risk of anthropomorphism, we might conceive of OT as shifting the female from apprehension to the trust necessary to permit mating. In human relationships, male aggression and date rape represent a real danger to women (Surbey & Conohan, 2000), and typically women require some period of social interaction to establish a degree of trust in a potential sexual partner. OT may enhance social affiliation, permit nonsexual physical contact and reduce wariness sufficiently to allow sexual relations.

Most of our social interactions are with mates, acquaintances, or kin where prior knowledge and experience increase the predictability of the exchange. Strangers represent an unknown quantity with correspondingly higher levels of subjective uncertainty about their motives and behavior. In interactions between strangers, terms such as *fear reduction* have been used to describe increased trust after OT administration, yet the effect of OT might be more accurately and modestly described as a reduction in the normal apprehension associated with stranger interaction (Theodoridou et al., 2009). Baumgartner et al.'s (2008) study found that although the placebo group showed a decrease in trust following betrayal, OT was associated with no change in trusting behavior. Betrayal shifted the placebo group from trust toward hostility, whereas the effect of OT was to maintain (but not increase) trusting behavior.

OT facilitates empathy, and the effect of OT on prosocial behavior is most evident when an individual must take into account another's viewpoint. Romantic relationships, associated with OT release, involve continual monitoring of another's viewpoint (Fisher et al., 2006; but see Zeki, 2007), and human mothering involves maternal "mind-mindedness" with regard to the infant (Meins, Fernyhough, Fradley, & Tuckey, 2001). By lowering threat and increasing trust, OT appears to facilitate empathic identification. In summary, the effects of OT may crucially depend on where the individual currently stands on the spectrum of interpersonal emotion, which can range from terror to trust.

Alternative Models. Taylor (2006, Figure 1) has also suggested a social psychological model of OT effects. According to Taylor's model, gaps in social relationships cause OT levels to rise. In interaction with opioid and dopaminergic systems, OT then drives a desire for affiliation and social contact. If such contacts prove positive, stress reduction ensues, but if they are negative, stress increases. This model gives a central role to OT's effect on social attachment, with stress reduction resulting from positive interpersonal contact rather then being a direct effect of OT. A comparison between

her proposal and my own may shed light on key questions for future research. There are three key areas where our proposals diverge.

The first concerns the *triggers of OT release*. Taylor (2006) acknowledges the apparent contradiction between high OT levels being associated with both relationship distress and stress reduction. One resolution of this inconsistency may be that the former link has been established through measurement of peripheral OT and the latter through manipulation of central OT: The coordination of OT release in the two systems remains unresolved. There must also be concern with the degree of confidence that we can place in the negative correlation between plasma OT levels and relationship quality because four studies (reviewed earlier) have reported positive correlations. The nature of this association requires further examination.

Because my proposal views threat as the trigger for OT release, it would suggest that specific relationship events might increase OT levels to the extent that they are perceived as threatening, stressful, or intrusive. The immediate effect of raised OT levels would be stress reduction, in contrast to Taylor's view that they act to promote a search for positive social contacts. Although my model emphasizes OT release in response to acute (state) stimuli, Taylor's focuses on chronic (trait) relationship status. Future research might examine the extent to which specific couple interactions of conflict or harmony (in both high- and low-quality) relationships are associated with OT levels. I would expect a main effect of conflict on OT levels, whereas Taylor's model might predict a stronger effect of relationship quality. We know that administration of OT can mitigate the negativity of conflict talk in couples (Ditzen et al., 2009) but not whether conflict itself spontaneously enhances OT release or uptake. However, again, such research would be constrained to the examination of plasma rather than central levels.

In seeking to establish the types of stimuli that trigger central OT release, the uncertain relationship between peripheral and central OT systems directs us to nonhuman animal research where methodological constraints are fewer. Central OT release in response to different stimuli can be monitored in freely behaving animals using microdialysis (Landgraf & Neumann, 2004). Such studies have revealed OT release in response to an array of stressors both social and nonsocial, including forced swimming (Wigger & Neumann, 2002), shaker stress (Nishioka, Anselmo-Franci, Li, Callahan, & Morris, 1998), pain (Yang et al., 2008), social defeat (Engelmann, Ebner, Landgraf, et al., 1999), maternal defense (Bosch, Kromer, Brunton, & Neumann, 2004), parturition (Kendrick, Keverne, Chapman, & Baldwin, 1988), and suckling (Neumann, Russell, & Landgraf, 1993). This body of work strongly suggests that OT release is not confined to gaps in social relationships but is responsive to many immediate threats to somatic or psychological integrity where stress reduction would be evolutionarily advantageous. The fact that OT affects nociception by raising the threshold for pain (Grewen, Light, Mechlin, & Girdler, 2008) further suggests that it is a response to somatic insult as well as interpersonal distress.

The second area of divergence is the role of *fear reduction*. This is central to my model, whereas for Taylor fear reduction is not a direct effect of OT but a consequence of the social affiliation that it motivates. There can be little doubt that affiliation with others buffers stress (Hennessy, Kaiser, & Sachser, 2009); the question is whether the effect of OT on stress reduction is mediated by and therefore requires the presence of supportive others or whether OT and social contact have additive or interactive effects on stress reduction. Imaging studies have demonstrated reduced amygdala activation, taken to signal fear reduction, in response to threatening faces after OT administration (Kirsch et al., 2005; Petrovic et al., 2008), indicating that OT can reduce stress without social contact. Heinrichs et al. (2003) manipulated both central OT levels and the availability of social support to examine their separate and joint effects on response to a stressor task. Cortisol increase was more strongly attenuated by social support than by OT administration. But the interaction term showed that the combined effect of OT and social support was most effective in controlling cortisol increase, suggesting that they exert additive effects. Measures of self self-rated calmness and anxiety also confirmed the potency of their joint effects. But even in the absence of social support, OT significantly decreased anxiety between pre- and posttest. In plasma studies also, it is unclear whether social buffering of stress depends on peripheral OT. At least one study suggests not: Ditzen et al. (2007) found that physical partner contact prior to a stressor attenuated stress responses (specifically cortisol levels and heart rate) but had no effect on OT levels.

Taylor et al. (2000) further propose that OT-induced affiliative needs motivate interactions with known and trusted others ("befriending"). However, studies that have manipulated central OT in the context of economic games have shown that OT increases trust, empathy, and generosity even toward strangers. After acts of trust are betrayed by a stranger, OT prevents the normal decline in trusting behavior (Baumgartner et al., 2008). This suggests that OT increases the positivity of interactions in general and its effect does not depend on a prior relationship between the parties (Theodoridou et al., 2009). I suggest that this positivity results from a decrease in the wariness with which we typically approach strangers. If this were the case, then we would predict that OT administration to individuals suffering from autism spectrum disorders would ameliorate anxiety symptoms during social interactions. We know that plasma OT levels are depressed in autistic children and that they correlate with social functioning (Modahl et al., 1998). Early results indicate that systemic infusion (Hollander et al., 2007) or intranasal administration (Bartz et al., 2008) of OT can enhance social functioning. Similar developments are under way with social phobia (Guastella, Howard, Dadds,

Mitchell, & Carson, 2009). In contrast to my proposal that OT reduces the anxiety associated with stranger interactions, the Taylor model would propose that it specifically increases the motivation to interact with familiar others. Testing between the two proposals would require specific measurements of motivation versus stress reduction in relation to interactions with strangers and known others.

The third area of divergence between the models is with respect to *female aggression*. Taylor et al. (2000) propose that OT released under threat reduces the probability of aggressive attack and enhances "befriending" (seeking protection by affiliating with familiar females). This is suggested to have evolved because of the centrality of the mother to her infant's survival (Campbell, 1999), which might be jeopardized by direct attack against (or flight from) a hostile conspecific. Yet this leaves maternal aggression, ubiquitous in mammals, unexplained. Although there are abundant anecdotal reports of human maternal aggression, experimental investigation presents ethical problems. However, preliminary work confirms heightened aggression in lactating, as compared to bottle-feeding, women (Hahn-Holbrook, Holt-Lunstead, & Holbrook, 2009).

In accordance with my emphasis on the anxiolytic effects of OT, I would propose that maternal aggression is mediated by the fear reduction associated with OT, as noted earlier. The main point of disagreement between the two models centers on the impact of fear reduction on the probability of aggression. I and others (Campbell, 2006; Neumann, 2008) have argued that extreme fear is antithetical to aggression so that, by reducing it, the likelihood of attack is increased. By contrast, Taylor et al. propose that fear reduction should diminish the likelihood of attack. Here, the disagreement may be resolved by a consideration of fear intensity—the behavioral manifestation of the anxioytic effects of OT on paralyzing fear may be different from those on mild fear. On the other hand, Taylor's emphasis on affiliation might suggest that it is the strength of the affectionate bond between mother and infant, associated with heightened OT levels, that motivates the mother's defensive aggression. Studies might usefully examine whether central OT facilitates aggression toward a range of targets (by reducing fear) or whether the effect is confined to defensive aggression on behalf of a loved one.

Future Directions

The future research agenda is likely to become increasingly complex as we discover more about OT's interactions with its sister nonapeptide AVP as well as with steroid, stress, and classical neurotransmitter systems (Depue & Morrone-Strupinsky, 2005; Jorgensen, Kjaer, Knigge, Moller, & Warberg, 2003). But OT, recently called "the great facilitator of life" (Lee et al., 2009), is too important to be studied only by endocrinologists. It is relevant to psychologists understanding of aggression, affiliation, cooperation, empathy, love, mate choice, and mother–infant attachment. In the clinical area, research has already begun on the application of OT to attention-deficit/hyperactivity disorder and autism spectrum and conduct disorders (e.g., Bartz & Hollander, 2006; Hollander et al., 2003). Social psychology's expertise and ingenuity in operationalizing and measuring complex social constructs has an important role to play in exploring the promise of OT.

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