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Oxytocin differentially modulates compromise and competitive approach but not withdrawal to antagonists from own vs. rivaling other groups

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ABSTRACT

In humans, oxytocin promotes cognitive and motivational tendencies that benefit the groups on which humans depend for their survival and prosperity. Here we examined decision making in an incentivized two-player poker game with either an in-group or out-group antagonist. Sixty nine healthy males received 24 IU oxytocin or matching placebo, and played four rounds of a simplified poker game. On each round they received either low or high value cards to create differences in competitive strength, and then responded to a bet placed by their (simulated) (in-group or out-group) antagonist. Under placebo, participants withdrew and competed depending on their own (low vs. high) competitive strength, regardless of their antagonist's group membership. Under oxytocin, however, participants settled more and competed less with an in-group as compared to an out-group antagonist; withdrawal was unaffected by group membership. We conclude that oxytocin sensitizes humans to the group membership of their interaction partner, rendering them relatively more benevolent and less competitive towards those seen as belonging to their own group.

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1. Introduction

In their search for the neurobiological bases of social behavior, scientists across the behavioral and brain sciences turned their focus to oxytocin, an evolutionary ancient and structurally highly preserved neuropeptide (e.g., Bartz et al., 2010; Chang et al., 2012; Bos et al., 2012; Ross and Young, 2009; Striepens et al., 2012). Oxytocin is produced in the hypothalamus and released into the blood stream from axon terminals and into the brain from dendrites of hypothalamic neurons (Donaldson and Young, 2008; Ludwig and Leng, 2006). Functioning as both a neurotransmitter and hormone, oxytocin's targets are widespread and include the hippocampus and the amygdala (Kirsch et al., 2005). Oxytocin interacts with dopaminergic, reward processing circuits in the nucleus accumbens shell and in the ventral tegmental area (Skuse and Gallagher, 2008), and exerts anxiolytic effects via direct activation of oxytocin receptors expressed in serotonergic neurons of the raphe nuclei (Veenema et al., 2010; Yoshida et al., 2009).

1.1. Social bond formation and maintenance

Oxytocin is perhaps best known for its critical role in parturition and reproduction on the one hand, and social bond formation and maintenance on the other (e.g., Carter et al., 2008). First, male rodents engineered to lack (fore-brain)

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oxytocin receptors no longer discriminate between familiar and unfamiliar females, whereas normal rodents spent more time investigating unfamiliar female rodents vs. female rodents with whom they had shared a cage for several days (Macbeth et al., 2009; also see Ferguson et al., 2000, 2002). Along similar lines, participants who memorized pictures of faces under oxytocin performed better one day later on measures of familiarity, indicating that oxytocin makes a face in memory more familiar (Rimmele et al., 2009).

In addition to social bond formation, oxytocin also appears to stimulate empathic responding, which is important also to social bond maintenance. For example, in women exposed to infant crying, intranasal oxytocin modulates activity in the inferior frontal gyrus (Riem et al., 2011), fathers given oxytocin rather than placebo stimulate their toddler's exploration more and show less hostility (Naber et al., 2010), and in males exposed to biological motion (a point-light figure representing a walking human), intranasal oxytocin modulates neural circuitries involved in affective perspective taking (Keri and Benedek, 2009; Perry et al., 2010). Other studies showed that participants given oxytocin rather than placebo have increased sensitivity to other's fear (Fischer-Shofty et al., 2010), empathize more with people depicted in emotionally charged situations (Hurlemann et al., 2010; but see Singer et al., 2008), and more accurately infer emotions expressed by others (Domes et al., 2007). Indeed, both humans and non-human mammals show increased benevolence under oxytocin, including tendencies to benefit con-specifics (Chang et al., 2012), to trust others (Baumgartner et al., 2008; Kosfeld et al., 2005), to make fair offers in bargaining (Zak et al., 2007), and to benefit others at a personal cost (e.g., Morhenn et al., 2008).

1.2. *Indiscriminate benevolence vs. group-serving tendencies*

Whereas the heretofore reviewed work suggest that oxytocin promotes indiscriminate benevolence and generosity (e.g., Zak et al., 2007), a more accurate conclusion appears that oxytocin promotes group-serving tendencies (De Dreu, 2012; Goodson, 2013). For example, meerkats live in clans and their survival and prosperity depends on successful in-clan cooperation and coordination and defense to predators and roving competing clans (Drewe et al., 2009). In free-living meerkats, peripheral administration of oxytocin rather than placebo increased an array of cooperative behaviors directed at the own clan, including digging, associating with pups, and *time-on-guard* (Madden and Clutton-Brock, 2011). Other studies documented that oxytocin is key in triggering so-called *maternal defense*, which occurs when a breast-feeding mother is faced with an unfamiliar intruder and lashes out to protect and defend its pups (Bosch et al., 2005; Pedersen et al., 1982).

In humans, similar tendencies have been documented as well. First, the hypothalamic release of oxytocin is promoted by displays of trust and cooperation by others, especially familiar others like parents and intimate partners (e.g., Ditzen et al., 2007; Feldman et al., 2010; Gordon et al., 2010; Holt-Lunstad et al., 2008; Morhenn et al., 2008; Uvnas-Moberg, 1998; Zak et al., 2005). Second, when given oxytocin rather than placebo, humans display more positive attitudes and empathize only with members of their own group and not with those classified as rivaling out-group members (De Dreu et al., 2011, 2012b; Sheng et al., 2013). Third, individuals given oxytocin rather than placebo conform to opinions of in-group members more than to (identical) opinions voiced by out-group members (Stallen et al., 2012). Fourth, individuals given oxytocin self-sacrifice more, and contribute to their own group more than to the broader collective that includes both their own group and other groups (Israel et al., 2012). Finally, when their own group competes with an out-group, individuals given oxytocin prefer strong allies (De Dreu et al., 2012a; also see Kret and De Dreu, 2013) and display parochial altruism – a tendency to cooperate with the in-group and to compete against the out-group (De Dreu et al., 2010, 2012b; also see Choi and Bowles, 2007; Israel et al., 2012).

Taken together, it thus stands to reason that oxytocin does not promote indiscriminate pro-social tendencies. Instead, it appears that oxytocin promotes cognitive, motivational, and behavioral tendencies that are beneficial to the groups within which humans operate and upon which they depend for survival and prosperity (De Dreu, 2012; van Ijzendoorn and Bakermans-Kranenburg, 2012). Such tendencies include in-group love and, if necessary for in-group protection, out-group hate as well.

1.3. *Current study: decision making in competitive interactions*

The conclusion that oxytocin promotes group-serving tendencies rests on studies examining relatively cooperative situations where humans faced the choice to contribute to their group or not, to trust others or not, or to make (un)fair offers. However, in addition to these more benign situations, group life is marked also by conflict when, for example, individuals compete for status and scarce resources. Typically, such conflicts trigger a tendency towards (i) withdrawal and subordination, (ii) matching and compromise, or (iii) aggressive approach (De Dreu, 2010; Deutsch, 1973). Although individuals have an incentive to compete through aggressive approach, their overarching group fares better when conflict is mitigated through withdrawal and compromise (De Dreu, 2010). Accordingly, our conjecture that oxytocin promotes group-serving tendencies implies that in competitive interactions, oxytocin increases (i) costly withdrawal and/or settlement, and (ii) reduces aggressive approach, especially when (iii) antagonists are part of one's in-group rather than coming from rivaling out-groups.

We examined this possibility in an incentivized two-player poker game adapted from Ten Velden et al. (2012). Fig. 1 provides a schematic overview of the experimental procedures (see section 4 for further detail).

Participants received oxytocin or matching placebo, and were paired to a (simulated) antagonist from their own in-group, or from a rivaling out-group. In this simplified poker-game, participants are given chips with monetary value, and handed a card from a 52-card deck. Following an initial forced bet which starts the game, participants observe their antagonist's bet, to which they may respond by withdrawing from the game at a personal cost (i.e., "fold," where the bet is lost and the pot is handed to the opponent), by (ii) *compromising* (i.e., "call;" they match their antagonist's bet and the player