Hormones and Behavior 105 (2018) 28–40

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Urinary oxytocin levels in relation to post-conflict affiliations in wild male chimpanzees (*Pan troglodytes verus*)

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ARTICLE INFO

Keywords:
Oxytocin
Reconciliation
Bystander affiliation
Relationship repair

ABSTRACT

Many animals living in social groups have evolved behaviors to resolve conflicts between group members, behaviors thought crucial for maintaining stable group life. Several hypotheses, based mainly on observational data, aim to explain how post-conflict (PC) affiliations, such as reconciliation and consolation, resolve conflicts by restoring relationships and/or alleviating anxiety. To examine a potential endocrinological mechanism of PC affiliations, we used an experimental-like procedure to investigate whether the oxytocinergic system is activated during naturally observed reconciliations, receiving bystander PC affiliations and aggressions not followed by PC affiliations in wild male chimpanzees. We compared urinary oxytocin (uOT) levels after reconciliations, receiving bystander PC affiliations or aggressions without affiliations with two control conditions: affiliations without previous aggression and after time periods without social interactions. We furthermore tested the 'valuable relationship' hypothesis of reconciliation, as well as the influence of relationship quality between individuals engaged in each of the three behavioral conditions involving aggression on uOT levels. We found that the probability to reconcile a conflict increased with increasing relationship quality between opponents, thus our results support the 'valuable relationship' hypothesis. However, relationship quality did not influence uOT levels, while behavioral condition had a significant effect on uOT levels. uOT levels after reconciliations, receiving bystander PC affiliations and affiliations not related to conflicts were higher than after aggressions alone and time periods without social interactions. Overall, our results indicate that the oxytocinergic system is activated during affiliative interactions, whether occurring as reconciliation, bystander PC affiliation or affiliation alone. We conclude that the oxytocinergic system, in addition to building and maintaining social relationships, also takes part in repairing them.

1. Introduction

Living in social groups provides benefits such as increased access to mating partners and feeding resources as well as a lower risk of predation and infanticide (Krause and Ruxton, 2002; Sterck et al., 1997; Van Schaik, 1983; Wrangham, 1980). Yet, living in a social group confronts an individual with numerous challenges as well, including increased risk of disease transmission and competition over food, mates or social partners (Krause and Ruxton, 2002; Sussman and Chapman, 2004; Van Schaik, 1983). Competition between group members can therefore escalate into aggressive conflicts, which induces social tension and may disturb group cohesion and cooperative tasks when former opponents increase spatial distance or even leave the group (Aureli, 1997; Aureli et al., 2002; Cheney and Seyfarth, 1997; Cords, 1992; Das et al., 1998; De Waal, 2000a; Wittig and Boesch, 2005). Thus, the dilemma of social living is that individuals compete with the same individuals they need to cooperate with to gain the benefits of being in a group (De Waal, 2000a). While behavioral mechanisms contributing to living in a stable group have been investigated in numerous animal species, few studies have examined proximate mechanisms facilitating behaviors needed to maintain a stable social group.

Aggressive conflicts are costly and socially disruptive events for both aggressor and victim, since they result in relationship uncertainty between former opponents and loss of predictability of future interactions (Aureli, 1997; Aureli et al., 1999; Cords, 1992; Das et al., 1998; De Waal, 2000b, 1989, 1986; Fraser et al., 2009; Palagi and Norscia, 2011; Sapolsky, 2005, 1992; Wittig et al., 2015; Wittig and Boesch, 2005). To overcome the disruptive effects of conflicts many social animals have developed friendly post-conflict (PC) interactions with group members, such as reconciliation (Aureli and De Waal, 2000). Reconciliation is an

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https://doi.org/10.1016/j.yhbeh.2018.07.009
Received 22 March 2018; Received in revised form 17 July 2018; Accepted 18 July 2018

affiliative interaction between former opponents which occurs after an aggressive conflict (De Waal and van Roosmalen, 1979). Behavioral studies have shown that reconciliation has a calming or anxiety reducing effect (Aureli, 1997; Butovskaya et al., 2005; Das et al., 1998; Palagi and Norscia, 2011). Reconciliation functions to reduce uncertainty about future interactions between opponents ('uncertainty-reduction' hypothesis) by reducing the risk of further aggression and therefore repairs the opponents' relationship ('relationship repair' hypothesis) by restoring tolerance levels between former opponents (Aureli, 1997; Butovskaya et al., 2005; Cords, 1992; Das et al., 1998; Koyama, 2001; Palagi and Norscia, 2011; Wittig and Boesch, 2005). Reconciliation is observed more frequently between individuals that share a valuable relationship ('valuable relationship' hypothesis) suggesting that reconciliation is a social strategy used by individuals when they have the most to gain from repairing a relationship (Aureli, 1997; Aureli et al., 2002; Cords, 1992; Koski et al., 2007; Wittig and Boesch, 2005, 2003).

Reconciliation, however, is not the only form of affiliation that can occur after a conflict. Another important PC affiliation is an affiliation offered by a previously uninvolved third party or 'bystander' to one of the former opponents (Call et al., 2002; De Waal and van Roosmalen, 1979; Palagi et al., 2004; Fraser et al., 2009). Consolation is a PC affiliation directed from an uninvolved bystander to the former recipient of an aggression (De Waal and van Roosmalen, 1979), while a PC affiliation directed from an uninvolved bystander to the former aggressor is termed appeasement (De Waal and Aureli, 1996; Romero et al., 2011). In chimpanzees, suggested but mutually non-exclusive functions of consolation include social support (true consolation), third party relationship repair, and self-protection (Fraser et al., 2008, 2009; Fraser and Bugnyar, 2010; Koski and Sterck, 2009; Romero et al., 2010; Wittig and Boesch, 2010). To distinguish among these different functions it is important to consider the relationship quality between the bystander and the former opponents (Fraser et al., 2009). Consolation that functions: (1) to support a distressed valuable partner is offered by a valuable partner, (2) to repair the relationship of former opponents is offered by a valuable partner of the former opponent, and (3) to self-protect a bystander is offered to former opponents by individuals which are frequent targets of redirected aggression (Fraser et al., 2009; Koski and Sterck, 2009). The underlying motivation of the bystander offering consolation to a valuable partner is suggested to be sympathetic concern (De Waal, 2012; Fraser et al., 2008; Palagi et al., 2014). Bystander initiated PC affiliations directed towards aggressors (appeasement) have been suggested to differ in motivation and function from PC affiliations directed to victims of a fight (Das et al., 1998; Fraser et al., 2009; Romero et al., 2011). A study in captive chimpanzees specifically investigating bystander PC affiliations directed to aggressors, concluded that this PC affiliation might serve as a mechanism to reduce the spread of aggression throughout the group, or similarly to consolation might have the function to support a valuable partner (former aggressors) which could be a mechanism to strengthen a bond (Romero et al., 2011).

The adaptive consequences of PC affiliations, like the reduction of future aggression, anxiety and uncertainty, as well as the reestablishment of cooperative and social relationships, have been investigated in numerous animal species, while little effort has been made to understand endocrinological mechanisms underlying affiliative conflict resolution behavior. Social uncertainty, as well as repeated exposure to psychosocial stressors like aggression or loss of status, has been shown to lead to short-term or enduring activation of the Hypothalamic-Pituitary-Adrenal (HPA) axis, especially when coping mechanisms are not available (Bartolomucci et al., 2005; Korte et al., 2005; Wittig et al., 2015). A common measure of HPA axis activity is the investigation of changes in glucocorticoid levels. The uncertainty reduction function of reconciliation has been examined in human children through the comparison of glucocorticoid levels after reconciled and non-reconciled conflicts (Butovskaya et al., 2005). Children had significantly higher salivary glucocorticoid levels after unreconciled than after reconciled conflicts, and reconciliation resulted in the reduction of anxiety induced by the former conflict (Butovskaya et al., 2005). While reconciliatory uncertainty reduction has been measured both on a behavioral and physiological level, the relationship repair function of reconciliation and the social support or bond strengthening function of bystander PC affiliation has mainly been studied on a behavioral level (Aureli, 1997; Butovskaya et al., 2005; Call et al., 2002; Cords, 1992; Das et al., 1998; Fraser et al., 2008; Wittig and Boesch, 2005, 2010). Consequently, much less is known about underlying endocrinological mechanisms of PC affiliations as means of relationship repair and social support.

Endocrine systems rarely act in isolation (Gangestad and Grebe, 2017). It is therefore likely that in addition to the HPA axis other hormonal systems are activated after aggressive conflicts or during PC affiliations, potentially involved in relationship repair, social support and bond strengthening functions of PC affiliations. A possible candidate is the oxytocinergic system, which has been shown to be involved in a variety of social behaviors and processes including affiliative and approach behaviors, bond maintenance and social support, all of which are central elements of PC affiliations (Carter, 1998; Insel and Young, 2001; Crockford et al., 2013; Williams et al., 1994; Gordon et al., 2011; Ross et al., 2009; Snowdon et al., 2010; Lukas et al., 2011; Smith and Wang, 2014). Central and/or peripheral release of oxytocin has been found in response to physical and psychosocial stressors as well as fearful contexts in rodents, non-human primates and humans (Hinde et al., 2016; Neumann and Slattery, 2016). Hence, physical and psychosocial stressors have been shown to activate both the HPA axis and the oxytocinergic system (Brown et al., 2016; de Jong et al., 2015; Hinde et al., 2016; Lang et al., 1983; Torner et al., 2017). In addition, numerous studies demonstrate that the oxytocinergic system interacts with the HPA axis (Neumann and Landgraf, 2012). Naturally and experimentally elevated oxytocin levels after or during stressor exposure in combination with social support have been found to attenuate the perception of a stressor and to reduce anxiety (Grewen et al., 2005; Heinrichs et al., 2003; Seltzer et al., 2010; Ziegler and Crockford, 2017). Receiving social support during or after exposure to a stressor has been shown to facilitate the recovery from an aversive experience, a phenomenon termed 'social buffering' (Cohen and Wills, 1985; Kikusui et al., 2006). The oxytocinergic system has been identified as a key facilitator of social buffering effects (French et al., 2017; Smith and Wang, 2014).

The oxytocinergic system's effects on approach and affiliative behavior during stressful situations are suggested to be mediated through its anxiolytic effects (Carter, 1998; Feldman, 2012; Neumann, 2008). Elevated oxytocin levels have been associated with reduced perception of threatening social stimuli which may induce feelings of safety and thus facilitate approach and affiliative interactions (Feldman, 2012; Kirsch, 2005; Kosfeld et al., 2005; Lukas et al., 2011; Radke et al., 2017). Additionally, the oxytocinergic system is suggested to affect motivational states related to affiliation and social bonding through its connectivity with the dopaminergic reward system (Bartz et al., 2011; Gordon et al., 2011). Thus, increased activity of the oxytocinergic system after or during stressor exposure might enhance the motivation to affiliate with a social partner in order to receive social support (Cavanaugh et al., 2016; Taylor, 2006). Accordingly, the oxytocinergic system's role in reconciliations and bystander PC affiliations could be to enhance the motivation to affiliate and/or to facilitate affiliative behavior through its anxiolytic effects. In both cases elevated oxytocin levels might be expected after aggressive conflicts that are followed by PC affiliations. However, if the oxytocinergic system is activated in response to potential social or energetic stressors, such as aggressive conflicts, elevated oxytocin levels might be associated with aggressions independent of PC affiliations.

The oxytocinergic system might also be involved in the modification of behavioral responses following a conflict. The 'social salience'