

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

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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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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'

hypothesis states that oxytocin increases the sensitivity to social cues, resulting in enhanced sensitivity to emotional stimuli, independent of their valence (Bartz et al., 2011; Domes et al., 2007; McQuaid et al., 2014; Shamay-Tsoory et al., 2009). By identifying overarching patterns across studies, it was proposed that the oxytocinergic system promotes anxiety and aggressive behaviors in response to unpredictable threats and competitive situations, but stimulates affiliative behaviors in response to positive supportive and familiar contexts (De Dreu and Kret, 2016; Shamay-Tsoory and Abu-Akel, 2016). Thus, whether prosocial or anti-social effects are facilitated by the oxytocinergic system strongly depends on the social situation and inter-individual differences (Bartz et al., 2011; Crockford et al., 2014; Olf et al., 2013). In line with the ‘social salience’ hypothesis, the oxytocinergic system might, therefore, be activated after aggressive conflicts, even after those that are not followed by affiliation.

Finally, the oxytocinergic system could also be involved in the relationship repair function of reconciliation through mechanisms associated with bond maintenance, since the oxytocinergic system plays a crucial role in the formation and maintenance of social bonds (Carter, 1998; Feldman, 2012; French et al., 2017; Insel and Young, 2001; Ross and Young, 2009). Social bonds are formed and maintained through repeated affiliative contacts and positive social behaviors (Carter, 1998; Uvnäs-Moberg, 1998). The quality of social relationships is positively associated with oxytocin levels and rates of affiliative and sexual behaviors in monogamous primates and grooming in chimpanzees (Crockford et al., 2013; Finkenwirth et al., 2015; Snowden et al., 2010). Similar patterns have been found in humans (Feldman et al., 2010; Grewen et al., 2005; Holt-Lunstad et al., 2015; Light et al., 2005). Additionally, elevated activity of the oxytocinergic system has been found following mate separation in monogamous prairie voles and titi monkeys (Bosch et al., 2016; Hinde et al., 2016), as well as after pair-mate reunion (Hinde et al., 2016). Separation from a social partner may function to stimulate partner-seeking behavior which could be an additional mechanism of bond maintenance facilitated by the oxytocinergic system (Bosch et al., 2016; French et al., 2017). Likewise, humans experiencing uncertain or disturbed relationships have elevated oxytocin levels (Grebe et al., 2017). The latter authors proposed an ‘identify and invest’ hypothesis under which the oxytocinergic system is activated in relation to challenges or actual threats to a valued relationship to facilitate coping mechanisms to rescue or maintain the threatened relationship (Gangestad and Grebe, 2017; Grebe et al., 2017). Relationship repair through reconciliation could be an example of such a coping mechanism facilitated by the oxytocinergic system. Thus, in accordance with the oxytocinergic systems involvement in bond maintenance, elevated oxytocin levels might be associated with both aggressive conflicts that disturb social relationships and reconciliations between valuable partners.

In this study we combined detailed behavioral observations of wild male chimpanzees (*Pan troglodytes verus*) with direct, non-invasive urinary oxytocin (uOT) measurements. Since PC affiliations occur more often in males having up to 14 times higher aggression rates than females (Muller, 2002; Wittig and Boesch, 2003), we decided to only select males as focal individuals to maximize urine sample collection after single behavioral events. In a first step, we examined conciliatory and affiliative tendencies of focal individuals involved in aggressive conflicts to demonstrate the occurrence of reconciliation and bystander PC affiliation in our study groups. We therefore quantified the frequency of aggressions followed by reconciliations or bystander PC affiliations that were initiated sooner than dyadic (reconciliation) and non-dyadic (bystander PC affiliation) affiliation baselines, respectively (Veenema et al., 1994; Wittig and Boesch, 2003, 2005). Second, we tested the ‘valuable relationship’ hypothesis of reconciliation and investigated if aggressive conflicts are reconciled more often when opponents share a valuable relationship. Third, due to the oxytocinergic systems involvement in social buffering and bond maintenance and its anxiolytic, motivational and social salience enhancing effects we

hypothesized that the oxytocinergic system is part of the relationship repair function of reconciliation and the social support/bond strengthening function of bystander PC affiliation.

We therefore compared uOT levels of individual chimpanzees after naturally observed aggressions not followed by affiliations (aggressions alone), aggressions followed by affiliation between former opponents (reconciliation), and aggressions followed by an affiliation initiated by an uninvolved bystander to one of the former opponents (bystander PC affiliation) with two control conditions: affiliations without previous aggression (affiliations alone) and after time periods without social interactions (non-social control). We formulated our predictions in accordance with the oxytocinergic systems’ involvement in different behavioral processes outlined above, and distinguished between possible associations of the oxytocinergic system with aggressive and/or affiliative behavior. Due to the oxytocinergic system’s potential activation in response to physiological and psychosocial stressors and social salience enhancing effects we predicted higher uOT levels after aggressions alone than after the non-social control condition. In accordance with the oxytocinergic system’s involvement in social buffering, affiliative and approach behavior, as well as bond-maintenance we predicted higher uOT levels after aggressive conflicts followed by reconciliations and bystander PC affiliations than after the non-social control condition and affiliations alone. Furthermore, based on previous findings in chimpanzees and in relation to the oxytocinergic system’s involvement in bond maintenance, we predicted a positive association between uOT levels and the relationship quality of PC affiliation partners. In addition, previous findings in chimpanzees revealed that reconciliations of short and long duration had the same, positive effect on the reestablishment of tolerance between former opponents (Wittig and Boesch, 2005) and variation in grooming duration of grooming bouts with a minimum length of 10 min had no effect on uOT levels (Crockford et al., 2013; Samuni et al., 2017). Thus, we predicted that changes in uOT levels in relation to PC affiliations should be independent of the duration of the affiliative interaction, if they indeed function in relationship repair, signaling social support or bond strengthening.

2. Methods

2.1. Data collection

Data were collected from two habituated chimpanzee groups at the Taï National Park, Côte d’Ivoire (5°52’N, 7°20’E), between September 2014 and May 2015 (Wittig, 2018). AP & LS conducted all-day focal animal sampling (Altmann, 1974) on all males > 11 years old (N = 10 males, age 12–37; 5 males in each group) for a total of 1361 observation hours in East group and 1284 h in South group. During focal follows, we collected urine samples and recorded all social interactions and changes in activity using CyberTracker software (v3.389; <http://www.cybertracker.org/>). Social interactions included any affiliative or aggressive interaction between two or more individuals. Aggressive interactions included contact aggressions (e.g., bites, hits), non-contact aggressions (e.g., chases, charges and displays) and threats, e.g. arm waves (Wittig and Boesch, 2003). Affiliative interactions were defined as any friendly social interaction between one or several individuals which included body contact such as grooming, kissing, embracing, touching, playing, inspecting genitals and mounting.

2.2. Post-conflict (PC) affiliations

PC affiliations are affiliative interactions between an opponent and any other group member following an aggressive conflict. Here, we considered only the very first interaction of the focal individual after an aggressive conflict, and referred to it as PC affiliation only if the interaction was affiliative (Wittig and Boesch, 2003, 2005). We did not consider a specific time window for the occurrence of an affiliation after

an aggression; however, the aggression and the PC affiliation had to happen on the same day. A PC affiliation between former opponents was considered as reconciliation (De Waal and van Roosmalen, 1979), while a PC affiliation between a former opponent and any other group member uninvolved in the aggression was regarded as bystander PC affiliation. Bystander PC affiliations were considered as such when the affiliation was initiated by the bystander and directed to one of the former opponents, aggressor or victim (De Waal and Aureli, 1996; Wittig and Boesch, 2010). Both aggressors and victims were part of reconciliations and bystander PC affiliations, depending on the role a focal individual had during a conflict.

2.3. Occurrence of reconciliation and bystander PC affiliation

In our study, we considered all first affiliations after a conflict, that happened on the same day, as PC affiliations for a focal individual (Wittig and Boesch, 2003, 2005, 2010). Thus, we did not apply a specific time window during which a PC affiliation had to occur to be considered as such. To demonstrate the occurrence of reconciliation in our study groups we used the corrected conciliatory tendency (CCT) method (Veenema et al., 1994) in a similar way as described in Wittig and Boesch, 2005. For every focal individual we calculated an average latency between consecutive affiliation events for all of the focal's reconciliation partners (dyadic affiliation baseline), using consecutive affiliations without a conflict in between that occurred on the same day. Affiliative interactions between the same partners reoccurring within 1 min were summarized into bouts. Thus, to calculate the latency between consecutive affiliations for independent affiliation events, only latencies between affiliations greater than 1 min were considered. We then compared the dyadic affiliation baseline to the actual latency between the end of the aggression and the start of the affiliation for every reconciliation of that dyad. A dyad that started reconciliation sooner after a conflict compared to their dyadic affiliation baseline was labelled as attracted pair and a dyad that started a reconciliation later than their dyadic affiliation baseline was labelled as dispersed pair (Wittig and Boesch, 2005). Dyads for which no affiliation baseline could be assessed because consecutive affiliations did not occur in these pairs during the data collection period, but for which reconciliations were recorded, were as well labelled as attracted pairs, since affiliation rates between these pairs were generally low.

To demonstrate the occurrence of bystander PC affiliations, we used a similar method as described for reconciliations. However, we did not use a dyadic affiliation baseline to assign attracted and dispersed pairs of bystander PC affiliation. Instead we calculated a non-dyadic average affiliation latency for each focal individual using all of the focal's consecutive affiliation bouts (latency greater than 1 min) that happened on the same day without aggressions in between, irrespective of the affiliation partner's identity (non-dyadic affiliation baseline). Attracted and dispersed pairs of bystander PC affiliations were calculated by comparing a focal individual's non-dyadic affiliation baseline to every latency between the end of an aggression and the start of an affiliation initiated by an uninvolved bystander. Finally, CCTs were calculated for every focal individual for reconciliations and corrected affiliative tendencies (CAT) for bystander PC affiliations separately, using the formula: (attracted pairs-dispersed pairs)/total number of aggressions (Veenema et al., 1994). Thus, the CCT or CAT indicates the amount of conflicts that were followed by reconciliations or bystander PC affiliations, respectively, that occurred sooner than the dyadic or non-dyadic affiliation baselines. The number of aggressions (N = 443) used to calculate CCTs was a subset of all aggressions observed (N = 860; Table A1), after excluding aggressions with an unknown partner or no partner, e.g. non-directed displays (N = 363) and unknown PC affiliations (N = 54). Since we were not interested in individual variation in CCTs or CATs we present the CCTs and CATs as average in percent across all focal individuals.

2.4. Urine sample collection and analysis

We systematically recorded all urinations and when possible collected every urination of the focal subjects during each focal follow (mean \pm SD = 1.1 \pm 0.7 per hour) using methods as described in Samuni et al., 2017 (Appendix, Section 1.2). We used a total of 219 samples (22 \pm 7 samples/individual) collected after reconciliations (N = 18), receiving bystander PC affiliations (N = 12), aggressions alone (N = 31), affiliations alone (N = 97) and non-social control periods (90 min durations of feeding, resting or travelling without social interactions except for vocalizations; N = 61).

The clearance of oxytocin into urine is estimated to be around 15 to 60 min after secretion (Amico et al., 1987; Crockford et al., 2013). uOT measures showed consistent changes in uOT levels following target behaviors or social interactions that occurred within this time window (Crockford et al., 2013; Seltzer et al., 2010). For this study, we used a more conservative time window which was extended to > 10 min after the start of a target behavior to < 75 min after the end of a target behavior (Appendix, Section 1.2). We excluded samples when the focal animal was out of sight or lost > 15 min during the period between 0 and 90 min before urination. Samples were furthermore excluded when several behaviors happened at the same time, 10–75 min before urination, e.g. a PC affiliation was followed by an affiliation between other partners or when food sharing occurred in combination with any of the behavioral conditions considered in this study. In addition, we excluded samples when prolonged behaviors, such as patrols, inter-group encounters, hunts and meat sharing, which are known to have protracted effects on uOT levels in chimpanzees, had happened < 90 min before urination (Samuni et al., 2017; Wittig et al., 2014). For all samples, copulations were not considered as affiliation and therefore samples where one or several copulations occurred between 0 and 90 min before urination were included into the analyses (see Appendix for a detailed description of sample in- and exclusion criteria, Section 1.2).

Sample collection, extraction and analysis followed an established protocol (Crockford et al., 2013) with minor changes described in Samuni et al., 2017 (Appendix, Section 1.3). The assay sensitivity was 15 pg/mL and the standard curve ranged from 15.62 to 1000 pg/mL. Inter-assay variation of low- (50 pg/mL) and high- (250 pg/mL) quality controls were 21.7 and 8.4% (N = 23), respectively. Intra-assay variation of low- (50 pg/mL) and high- (250 pg/mL) quality controls were 14.0 and 9.1%, respectively. To control for variation in urine concentration, we measured creatinine levels in all urine samples and expressed uOT values as pg/mg creatinine (Bahr et al., 2000).

2.5. Relationship quality (DDSI)

Relationship quality was assessed using directed grooming interactions between all group members which were independent of their mothers, since infant and juvenile chimpanzees social interactions are largely influenced by the social relationships and status of their mothers (Lonsdorf et al., 2014; Murray et al., 2014). Thus, relationship quality was calculated between all group members above the age of nine (start of adolescence), except for orphans who were assumed to gain independence after their mother's death. Orphans, below the age of nine (N = 4), were five (N = 3) and seven (N = 1) years old during the study period and all of them were weaned when their mothers died or disappeared. To evaluate relationship quality based on duration, frequency and directionality of grooming interactions and their changes over time, we used a total of 13,038 grooming interactions (East group: 6042 interactions of 506 dyads and 23 individuals, South group: 6996 interactions of 368 dyads and 20 individuals) collected between January 2012 and May 2015. We implemented a method similar to the Elo-rating principle, the Dynamic Dyadic Sociality Index (DDSI), where daily dyadic values change through positive interactions (Kulik, 2015; Mielke et al., 2017). Following the Elo rating's principle, grooming

interactions increase the score of a given dyad, while the scores of both interactors with all other group members decrease. This provides a continuous daily measure, in which each interaction leads to an update of the dyadic score. The impact of an interaction is dependent on predictability, such that interactions between individuals with a high value have a weaker impact (Kulik, 2015). DDSI scores were standardized between zero and one. Each grooming interaction increases the DDSI score of a dyad, while the value added to the interacting dyad is divided by all other dyads and then subtracted from their scores, so that the average index of all dyads within a group remains at a constant value of 0.5 (Kulik, 2015; Mielke et al., 2017). Thus, a focal individual's DDSI scores were based on data obtained during focal follows and on data from other focal individuals.

To assess the impact of relationship quality of interacting chimpanzees on the probability to reconcile and on uOT levels we used DDSI grooming scores from the day before the urine collection, which reflect grooming interactions of the entire observation time until this day and are independent of behavioral interactions occurring on the sampling day (Mielke et al., 2017). We calculated DDSI grooming scores for each focal individual using duration and frequency of grooming behavior. To account for directionality of grooming interactions between a focal individual and his grooming partners, we computed two scores per day for each focal dyad combination, including all of the grooming up to this date. One score was based on grooming directed from the focal to a specific individual and one directed from the same individual to the focal. For each dyad, we averaged both scores to get a single DDSI grooming score per day. The values of the averaged DDSI grooming scores reflect to some extent mutuality of grooming within a given dyad, since highest scores can only be obtained when both individuals groom each other repeatedly over months. When only one individual actively grooms, but receives little grooming from the same partner, the DDSI grooming scores will be average or lower. Thus, DDSI grooming scores incorporate grooming interactions between two individuals over the past months and reflect the most current state of dyadic grooming patterns due to the daily update. Furthermore, DDSI grooming scores indicate stable relationships when dyadic interaction rates are kept constant. A summary of DDSI grooming scores for all behavioral interactions is shown in Table A2 (Appendix). A graphical example of DDSI grooming scores for one of the focal individuals with all independent group members is given in Fig. A1 (Appendix).

2.6. Statistical analysis

To test whether relationship quality influenced the probability to reconcile an aggression ('valuable relationship' hypothesis), we fitted a Generalized Linear Mixed Model (GLMM; Baayen, 2008) with binomial error structure and logit link function (McCullagh and Nelder, 1989). To investigate whether uOT levels were influenced by PC affiliations, by relationship quality between interaction partners or by the duration of affiliative interactions, we fitted three Linear Mixed Models (LMM; Baayen, 2008) with gaussian error structure and identity link function. All analyses were conducted in R version 3.3.1 (R Core Team, 2016), using the functions `glmer` or `lmer` of the R package `lme4` (Bates et al., 2015). To achieve a more symmetrical distribution of the response, uOT levels were log-transformed. We z-transformed all covariates to a mean of zero and a standard deviation of one (Schielzeth, 2010). In all four models we included random slopes when the variation of a fixed effect within a random effect was sufficiently large, in order to keep type I error rate at the nominal 5% (Barr et al., 2013; Schielzeth and Forstmeier, 2009).

Model stability was examined by excluding levels of the random effects one at a time from the respective model and comparing the resulting model estimates for these data with those of the full data set. Model stability results of all models did not indicate any influential levels of random effects to exist. Variance Inflation Factors (VIF, Field, 2009) were derived using the function `vif` of the R-package `car` applied

to a standard linear model without including random effects nor interactions in case any were present in the full model. Derived VIFs (all below 1.2) did not indicate collinearity to be an issue in any of the four models. To check whether residuals of the three LMMs fulfilled the assumptions of being normally distributed and homogeneous, we visually inspected qqplots and the residuals plotted against fitted values for all three models, which did not indicate deviations from these assumptions. The fit of each full model was compared with that of a respective null model which did not include the test predictors but which was otherwise identical to the respective full model (Forstmeier and Schielzeth, 2011). The significance of the full-null model comparison was derived from a likelihood ratio test (R function `anova` with argument `test = "Chisq"`; Dobson and Barnett, 2008; Forstmeier and Schielzeth, 2011). P-values for individual fixed effects were derived from likelihood ratio tests comparing the full with a respective reduced model (R function `drop1`; Barr et al., 2013). Effect sizes (R^2) were calculated with the R package `MuMIn` using the function `r.squaredGLMM` (Bartoń, 2017). Effect sizes for the generalized mixed effects models were derived for the entirety of fixed effects (R_m^2) and for the entirety of fixed and random effects, R_c^2 (Nakagawa and Schielzeth, 2013).

Post-hoc pairwise comparisons of uOT levels among target behaviors were calculated using the function `glht` of the R package `multcomp` (Bretz et al., 2016) and without an adjustment of P-values. This is equivalent to Fisher's protected *t*-test or *Least Significant Difference* (LSD) test, in which the type I error rate is appropriately controlled by the model when one conducts post-hoc tests only after the null hypothesis was rejected, due to an overall significant effect of a test predictor (Cohen et al., 2013). Such an approach leads to a better balance of type I and type II error rates (Cohen et al., 2013). See SI for further details about sample sizes and model structures (Appendix, Section 2).

2.7. Model 1: Testing the 'valuable relationship' hypothesis

To test whether relationship quality influenced the probability to reconcile an aggression, we conducted a GLMM with dyadic aggressive interactions followed by reconciliation (yes or no) as the response variable and relationship quality (DDSI grooming scores) as the test predictor (fixed effect). We controlled for sex of the partner and group identity as fixed effects in the model. As random effects we included date nested in group, to control for several aggressions happening on the same day, and identities of the focal animal, partner and dyad, to control for differences between individuals and specific characteristics of interaction partners. We had to exclude 79 aggressive interactions which were not dyadic or for which the relationship quality could not be assessed (recently immigrated females). The final sample size for this model was 364 dyadic aggressive interactions between 108 different dyads of which 68 were followed by reconciliation. We did not account for directionality of reconciliations, e.g. initiated by the aggressor or victim, since whether or not reconciliation occurs is not dependent on who initiated the reconciliation.

2.8. Model 2: Testing the association between behavioral conditions and uOT levels

To test whether uOT levels were influenced by behavioral conditions (non-social control, aggression alone, affiliation alone, reconciliation or bystander PC affiliation) we run a LMM with behavioral condition as a test predictor and log-transformed uOT level as the response variable. The reference level of the test predictor was the non-social control condition. As control predictors we included group identity (South or East group) and the occurrence of cooperative group-level behaviors (such as patrols, intergroup encounters and hunts) on the day a urine sample was collected (yes or no), to control for behaviors which could have a protracted influence on uOT levels. The latter control predictor was included to account for samples which were

Table 1

Distribution of behavioral events (# Events) among focal individuals and respective urinary oxytocin ng/mg creatinine (uOT) that were part of model 2. For this table, uOT levels were averaged when more than one behavioral event was collected per behavioral condition for a focal individual.

Focal ID	Group ID	Non-social control		Affiliation alone		Aggression alone		Reconciliation		Bystander PC	
		uOT	#Events	uOT	#Events	uOT	#Events	uOT	#Events	uOT	#Events
Athos	East	193.8	7	179.9	8	130.2	6	–	0	174.0	1
Fredy	East	–	0	172.4	9	77.4	2	–	0	–	0
Poseidon	East	175.9	4	179.3	9	99.5	3	–	0	174.2	2
Richelieu	East	110.3	6	243.7	10	128.6	3	357.0	2	–	0
Willy	East	144.2	14	191.9	16	114.4	4	158.6	1	278.2	2
Ibrahim	South	81.3	2	130.6	5	122.2	5	172.2	6	86.6	1
Jacobo	South	182.6	3	196.2	11	49.6	2	143.2	3	241.0	4
Kuba	South	115.1	10	133.7	8	72.0	2	169.0	2	161.0	2
Shogun	South	111.6	10	147.3	11	50.3	2	90.2	3	–	0
Woodstock	South	128.0	5	220.0	10	105.4	2	91.5	1	–	0

collected on days with cooperative group-level behaviors which were not excluded from the analysis because the sample was collected > 90 min before a cooperative group-level behavior started or > 90 min after it ended. As random effects we included the identities of the focal animal, date of data collection nested in group, and the identity of the sampled event. Due to the comparison with non-social control periods we could not include or control for dyadic variables in this model, such as the identity of a partner or dyad. All bystander PC affiliations included in the uOT analyses were directed from an uninvolved bystander to a former aggressor (appeasement). During the entire data collection period we observed 78 bystander PC affiliations of which 26% were directed to victims and 74% to aggressors (one aggression was unknown). However, we obtained only a few urine samples after bystander PC affiliations directed to former victims (N = 4) which had to be excluded from the analyses due to the occurrence of other behaviors within the time window (see Appendix Section 1.2 for sample exclusion criteria). The overall sample size for this model was 219 urine samples. The dataset was unbalanced, not all individuals were equally represented in all behavioral contexts (Table 1). Linear mixed effects models are well suited to handle unbalanced datasets and repeated measurements, thus permitting an analysis despite the uneven representation of individuals across factors (Baayen et al., 2008). However, since a low sample size in combination with an unbalanced dataset can cause problems, an inspection of the model stability is essential to decide whether model results can be trusted. As already indicated above for all models, model stability results did not indicate any problems (Table A3, Appendix).

2.9. Model 3: Testing the effect of relationship quality on uOT levels in relation to behavioral conditions involving aggression

In accordance with our predictions, relationship quality could have differing effects on uOT levels among the three behavioral conditions involving aggression (aggressions alone, reconciliation and bystander PC affiliation). We predicted a positive association between relationship quality and uOT levels after reconciliations and bystander PC affiliations, but we did not have a specific prediction for aggressions alone. Therefore, we first fitted a model that included an interaction between relationship quality and behavioral condition. Since we were also interested in the effects of both test predictors as main effects, we removed all test predictors and their interaction from the full model to obtain the null model (Forstmeier and Schielzeth, 2011). Aggression alone was the reference level of the test predictor behavioral condition. Control predictors and random effects were similar to the second model but, we also included the identity of the interaction partner and dyad as additional random effects to account for specific characteristics of interaction partners. In order to fit the model on a dyadic level, we used a subset of the original dataset for model 2, containing only dyadic interactions of aggressions alone (N = 18), reconciliations (N = 18), and

bystander PC affiliations (N = 11). We had to exclude one bystander PC affiliation for which we could not reliably assess the relationship quality (recently immigrated female). Due to low sample size and availability of samples for only aggressors receiving bystander PC affiliation, we could not investigate differences in uOT levels between aggressors and victims. 12 aggressors and 6 victims were part of the aggression alone condition, 9 aggressors and 9 victims were part of the reconciliations, and 11 aggressors and no victims were part of the bystander PC affiliations. The overall sample size for this model was a total of 47 urine samples. Model stability results for this model were as well acceptable (Table A4, Appendix) despite the dataset being unbalanced (Table A5).

2.10. Model 4: Testing the impact of the duration of affiliative behavior on uOT levels for all behavioral conditions involving affiliation

To test for the potential effect of affiliation duration on uOT levels, we fitted a model on a reduced data set comprising only dyadic events of behavioral conditions involving affiliation: affiliation alone (N = 59), reconciliation (N = 18), and bystander PC affiliation (N = 11). The test predictor for this model was duration of the affiliation while controlling for relationship quality, behavioral condition, group identity and group-level cooperation occurring on a given day. Random effects were the same as described above for the third model. The sample size for this model was 88 urine samples, affiliation alone (N = 59), reconciliation (N = 18) and bystander PC affiliation (N = 11). We had to exclude three affiliations alone and one bystander PC affiliation for which relationship quality between affiliation partners could not be reliably accessed.

3. Results

3.1. Demonstrating the occurrence of reconciliation and bystander PC affiliation

Out of 443 conflicts, 69 were followed by reconciliation. Thus, 16% of conflicts were reconciled. Reconciliations were initiated with a median latency of 1.2 min after aggressions (range = 0.02–224.45 min) and 78% of reconciliations (N = 54) were initiated within 10 min. The average CCT of reconciliations of all focal individuals (N = 10) was $11.73\% \pm 6.63$ (mean \pm SD; see Appendix for individual CCT values, Table A6). Out of 443 conflicts, 78 were followed by bystander PC affiliation (18%; consolation: 26%, appeasement: 74%). Bystander PC affiliations had an average CAT of $3.71\% \pm 4.07$ (mean \pm SD; Appendix, Table A6) and were initiated with a median latency of 13.87 min after aggressions (range = 0.05–213.00 min), and 41% (N = 32) were initiated within 10 min after the conflict.

Table 2
GLMM results of model 1, testing the influence of relationship quality on the probability to reconcile an aggressive conflict.

Predictor variable	Estimate	SE	CI lower	CI upper	χ^2 (1)	P
Intercept	-1.38	0.44	-2.39	-0.55	-	-
Relationship quality	0.96	0.34	0.37	1.79	7.97	0.005
Sex partner (f = 0, m = 1)	-0.67	0.51	-1.81	0.30	1.63	0.201
Group (east = 0, south = 1)	-0.01	0.41	-0.78	0.80	0.01	0.978

Relationship quality was z-transformed. Original values mean \pm SD = 0.63 \pm 0.17.

Sex partner is the sex of the aggression partner. Bold: $P \leq 0.05$. CI: 2.5% (lower) and 97.5% (upper) confidence interval.

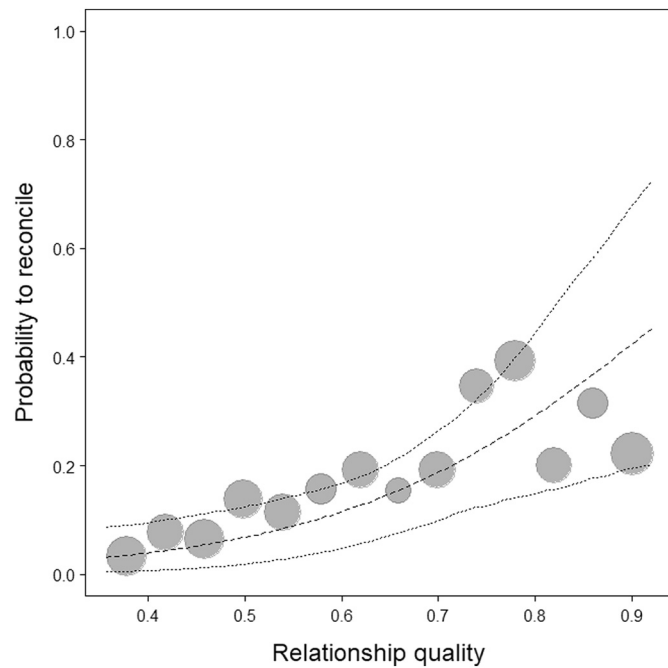


Fig. 1. The probability of a focal individual to reconcile an aggression as function of relationship quality (DDSI grooming scores) between the aggression partners (model 1). Relationship quality scores of 108 unique dyads were pooled in 15 equally wide segments. Larger point areas depict a larger number of observations (N = 364). The dashed line shows the fitted model and the dotted lines its 95% confidence intervals (based on sex of the aggression partner and group identity manually dummy coded and then centered).

3.2. Testing the ‘valuable relationship’ hypothesis (model 1)

We found that relationship quality significantly affected the likelihood to reconcile (likelihood ratio test: $\chi^2 = 7.92$, $df = 1$, $P = 0.005$), with a higher probability to reconcile for dyads with a better relationship quality (Table 2, Fig. 1). Neither the sex of the partner nor group identity had a significant effect on the likelihood to reconcile. Overall variance explained by the fixed effects was 14% ($R_m^2 = 0.14$) and 23% ($R_c^2 = 0.23$) by random and fixed effects together.

3.3. The association between behavioral conditions and uOT levels (model 2)

Behavioral condition had a significant effect on uOT levels (full-null model comparison: $\chi^2 = 20.39$, $df = 4$, $P < 0.001$). More specifically, post-hoc analyses revealed that uOT levels after reconciliations were higher than after aggressions alone and tended to be higher than after non-social control periods (Table 3, Fig. 2). Likewise, uOT levels after

Table 3
Results of the LMM and post-hoc analysis of model 2, analyzing urinary oxytocin (uOT) levels in relation to different behavioral conditions with two reference levels shown for clarity.

Predictor variable	Condition	Estimate	SE	CI lower	CI upper	df
Behavioral condition	Control (Intercept)	4.89	0.11	4.68	5.12	4
	Aggression alone	-0.19	0.13	-0.45	0.07	-
	Affiliation alone	0.26	0.10	0.08	0.45	-
	<i>Reconciliation</i>	<i>0.28</i>	<i>0.16</i>	<i>-0.05</i>	<i>0.59</i>	-
	Bystander PC	0.49	0.20	0.11	0.88	-
Behavioral condition*	Aggression alone (Intercept)	4.70	0.13	4.43	4.94	4
	Affiliation alone	0.45	0.12	0.22	0.68	-
	Reconciliation	0.47	0.18	0.10	0.82	-
	Bystander PC	0.68	0.21	0.28	1.08	-
	Group south	-0.28	0.10	-0.46	-0.09	1
Group cooperation yes	-0.10	0.10	-0.29	0.09	1	

Bystander PC: One of the former opponents receiving a bystander initiated post-conflict (PC) affiliation. CI: 2.5% (lower) and 97.5% (upper) confidence interval. Bold: $P \leq 0.05$; Italic: $P < 0.1$. * redundant comparison with non-social control condition not shown again.

bystander PC affiliations were higher than after non-social control periods and aggressions alone. However, uOT levels of reconciliations and bystander PC affiliations were not significantly different from uOT levels of affiliations alone (reconciliations: z-value = 0.07, $P = 0.944$; bystander PC affiliations: z-value = 1.20, $P = 0.230$). Moreover, uOT levels after affiliations alone were significantly higher than uOT levels after non-social control periods and aggressions alone, while uOT levels after aggressions alone did not differ from uOT levels after non-social control periods. In addition, uOT levels of individuals from the South group were lower than levels from East group ($\chi^2 = 6.86$, $df = 1$, $P = 0.009$). The occurrence of cooperative group-level behaviors on the day of sample collection had no significant effect on uOT levels ($\chi^2 = 1.11$, $df = 1$, $P = 0.293$). Overall variance explained by the fixed effects was 12% ($R_m^2 = 0.12$) and 33% ($R_c^2 = 0.33$) by the entirety of random and fixed effects.

3.4. The effect of relationship quality on uOT levels in relation to behavioral conditions involving aggression (model 3)

We found that the model including both test predictors, relationship quality (DDSI grooming), and behavioral conditions involving aggression, explained more of the variation in uOT levels than the model lacking these test predictors (full-null model comparison: $\chi^2 = 13.97$, $df = 5$, $P = 0.016$). The interaction between behavioral condition and relationship quality was not significant ($\chi^2 = 3.02$, $df = 2$, $P = 0.221$). Since we were also interested in the effects of behavioral condition and relationship quality as test predictors, we excluded their interaction from the analysis. The reduced model revealed an effect of behavioral condition, but no significant effect of relationship quality on uOT levels (Table 4). Post-hoc analyses showed that compared with aggressions alone, uOT levels were significantly higher after bystander PC affiliations and tended to be higher after reconciliations (Table 4, Fig. 3). However, uOT levels did not differ between reconciliations and bystander PC affiliations (z-value = -1.19, $df = 1$, $P = 0.234$). Overall variance explained by the fixed effects was 25% ($R_m^2 = 0.25$) and 25% ($R_c^2 = 0.25$) by the sum of random and fixed effects. Effect sizes indicate that the identity of partners and dyads (random effects) did not explain any variation of uOT levels in this model.

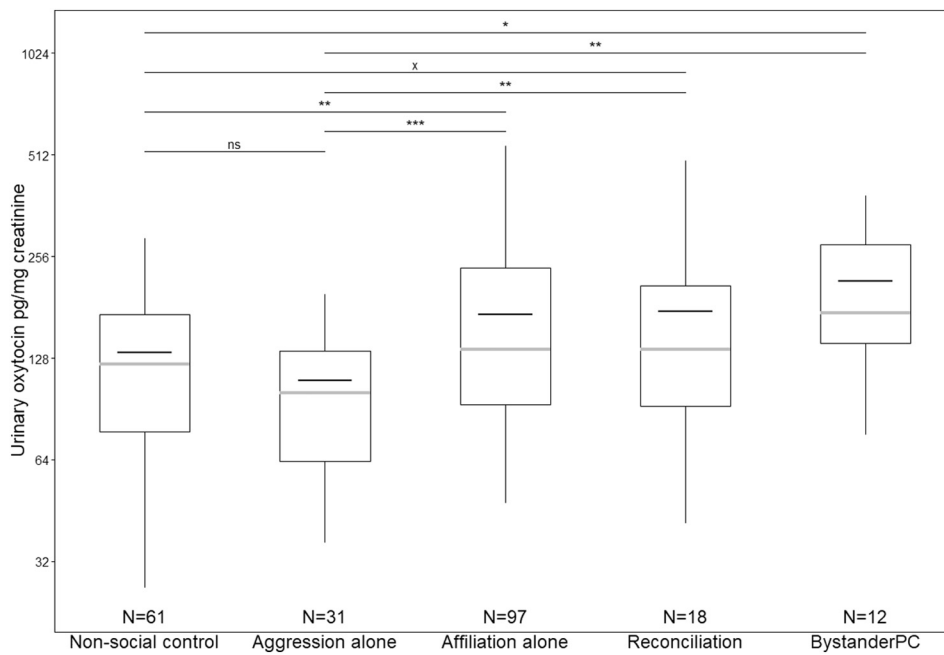


Fig. 2. Urinary oxytocin (uOT) levels after non-social control periods, aggressions alone, as well as affiliations alone, reconciliations, and receiving bystander initiated post-conflict affiliations (BystanderPC; model 2). Grey bars indicate the median and thin black bars the fitted model. Boxes indicate quartiles (25% and 75%) and vertical lines represent quantiles (2.5% and 97.5%). $P \leq 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***), $P < 0.1$ (x), $P > 0.1$ (ns).

3.5. The influence of the duration of affiliative behavior on uOT levels for all behavioral conditions involving affiliation (model 4)

Reconciliations (median duration = 6.30 min, range = 0.15–21.62 min) and bystander PC affiliations (median duration = 6.63 min, range = 0.07–49.13 min) varied in duration due to the variability of affiliation types and their combination in PC affiliations (grooming, kiss, embrace, etc.; Appendix, Table A7). Affiliation durations of reconciliations and bystander PC affiliations were shorter than the durations of affiliations of the behavioral condition affiliation alone (median duration = 15.67 min, range = 0.07–85 min). However, the full-null model comparison revealed that the duration of affiliations had no effect on uOT levels ($\chi^2 = 0.46$, $df = 1$, $P = 0.497$).

4. Discussion

Two key goals of this study were to determine whether the oxytocinergic system is involved in relationship repair processes of reconciliations and is activated in receivers of bystander initiated PC affiliations. In accordance with our predictions, based on the oxytocinergic system's involvement in social buffering, affiliative and approach behavior, as well as bond-maintenance, we found that uOT levels were higher following reconciliations and receiving bystander PC affiliations than uOT levels after the non-social control condition. This finding indicates that the oxytocinergic system is activated after PC

affiliations and might therefore be part of the relationship repair and social support function of reconciliation and bystander PC affiliation, respectively. However, in contrast to our predictions following the social salience hypothesis and the suggested activation of the oxytocinergic system in response to physiological and psychosocial stressors, uOT levels were not higher after aggressions alone compared to uOT levels after the non-social control condition. Thus, aggressions alone seem not to activate the oxytocinergic system in male chimpanzees. Furthermore, uOT levels after affiliations alone did not differ from uOT levels after reconciliations and bystander PC affiliations. The latter findings suggest that it is the affiliative interaction rather than the context that involves oxytocin activity. Furthermore, while aggressive conflicts between valuable social partners increased the probability that a conflict was reconciled, uOT levels after PC affiliations were not influenced by the relationship quality of interaction partners which was in contrast to our predictions based on the oxytocinergic systems involvement in bond-maintenance.

4.1. Occurrence of reconciliation and bystander PC affiliation

Even though all PC affiliations probably function as conflict management (Veenema et al., 1994), we used the corrected conciliatory tendency (CCT) method to quantify the frequency of aggressions followed by reconciliations and a modified version of the CCT to quantify corrected affiliative tendencies (CAT) of bystander PC affiliations, that

Table 4

Results of the LMM and post-hoc analysis of model 3, analyzing the influence of relationship quality and behavioral condition involving aggression on urinary oxytocin (uOT) levels.

Predictor variable	Condition	Estimate	SE	CI lower	CI upper	df	χ^2	z-value	P
Relationship quality		0.07	0.09	-0.11	0.26	1	0.63	-	0.427
Behavioral condition		-	-	-	-	2	8.05	-	0.018
	Aggression alone (Intercept)	4.78	0.22	4.34	5.18	-	-	-	-
	Reconciliation	<i>0.40</i>	0.22	-0.04	0.82	-	-	1.85	0.065
	Bystander PC	0.66	0.23	0.21	1.14	-	-	2.93	0.003
Group	south	-0.36	0.20	-0.74	0.03	1	3.03	-	0.082
Group cooperation	yes	-0.09	0.19	-0.49	0.27	1	0.23	-	0.632

(1) Relationship quality was z-transformed. Original values mean \pm SD = 0.48 \pm 0.16. Bystander PC: One of the former opponents receiving a bystander initiated post-conflict (PC) affiliation. CI: 2.5% (lower) and 97.5% (upper) confidence interval. Bold: $P \leq 0.05$; Italic: $P < 0.1$. Post-hoc pairwise comparisons were conducted with the Tukey test.

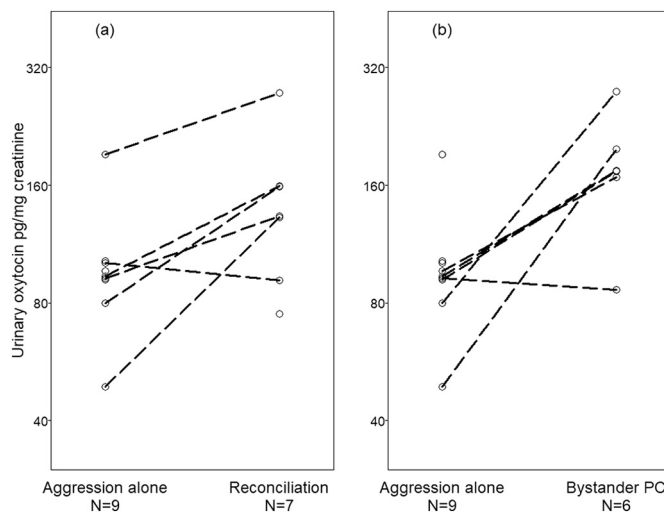


Fig. 3. (a) Average urinary oxytocin (uOT) levels of aggressions alone ($N = 18$) and reconciliations ($N = 18$) and (b) average uOT levels of aggressions alone and bystander PC (receiving bystander initiated post-conflict affiliations; $N = 11$), plotted for each focal individual. Lines connect corresponding average uOT levels of the same focal individual after the different behavioral conditions involving aggression (see Table 1). Circles which are not connected to a line represent focal individuals for which only one of the presented behavioral condition was available (see Table A5 in the Appendix for the distribution of events across behavioral conditions among focal individuals).

were initiated earlier than dyadic (reconciliation) and non-dyadic (bystander PC affiliation) affiliation baselines (Wittig and Boesch, 2005, 2003). The CCT (11.7%) averaged across all focal individuals for aggressions followed by reconciliations in our study is comparable to CCTs averaged across individuals in other studies of wild chimpanzees (*Pan troglodytes schweinfurthii*: Arnold and Whiten, 2001: CCT = 12.3%, Kutsukake and Castles, 2004: CCT = 14.4%; *Pan troglodytes verus*: Wittig and Boesch, 2005: CCT = 15.9%). This indicates that conciliatory tendencies do not differ much between and within chimpanzee subspecies and that our dataset is comparable to other studies. The frequency of aggressions followed by bystander PC affiliations that were initiated earlier than a focal individuals' affiliation baseline (CAT = 3.7%) was much lower than for reconciliations. A previous study conducted with another group of Tai chimpanzees found that all bystander PC affiliations were initiated earlier than the affiliation baseline (Wittig and Boesch, 2003), while in our study 60% of bystander PC affiliations were initiated earlier than the individual's affiliation baseline. However, the overall occurrence of bystander PC affiliation was similar between the previous (19%) and our study (18%).

4.2. The 'valuable relationship' hypothesis

One of our main study goals was to investigate whether the oxytocinergic system is involved in the relationship repair function of reconciliations. According to the 'valuable relationship' hypothesis the benefits of repairing a relationship are higher than the potential costs of renewed aggression upon approaching a former opponent, when the opponents share a valuable relationship (Aureli, 1997; Aureli et al., 2002; Cords, 1992; Koski et al., 2007; Wittig and Boesch, 2005, 2003). Accordingly, we found that the probability to reconcile a conflict increased with increasing relationship quality between former opponents. Thus, as has been found in several previous studies, repairing a valuable relationship is a relevant function of reconciliation and was used by the male chimpanzees in our study.

4.3. Association between uOT levels, behavioral conditions and effects of relationship quality

4.3.1. Aggressions not followed by affiliation (aggressions alone)

We found that uOT levels after aggressions did not differ from uOT levels after non-social control conditions, which indicates that peripheral oxytocin is not secreted after aggressive conflicts in chimpanzees, or at least not in quantities measurable using this method. Aggressions are recognized as energetic and psychosocial stressors for aggressors and victims, respectively, that have been shown to activate the HPA axis (Bronson and Eleftheriou, 1964; Wittig et al., 2015). In addition to the activation of the HPA axis, elevated activity of the oxytocinergic system after exposure to social and non-social stressors have been demonstrated in rodents (Bosch et al., 2016; Engelmann et al., 2001; Lang et al., 1983; Torner et al., 2017; Wotjak et al., 1998). It is possible that we did not find elevated oxytocin levels after aggressive conflicts because aggressions that are not followed by PC affiliations might not be strong social or physiological stressors, since conflicts which do not require PC management are usually short and less intense (Wittig and Boesch, 2003). However, 12 of the 31 aggressions that were part of model 2 were energetically demanding displays, which involved exaggerated locomotion, branch shaking, and branch dragging (Muller and Wrangham, 2004). Since we did not measure HPA axis activity in this study, we cannot be certain that the aggressive interactions were energetically or psychologically stressful events. Thus, we advise future studies to examine both hormonal systems HPA axis and oxytocinergic system at the same time. Glucocorticoid hormones are one possibility to measure the HPA axis activity. Here, we could not evaluate both hormones simultaneously in relation to a single behavioral event due to too many behavioral events occurring within the glucocorticoid clearance time window which is estimated to take place between 2 and 4.5 h after an event (Wittig et al., 2015).

It is also possible that we did not find higher uOT levels after aggressions alone than after non-social control periods since not all stressors might trigger oxytocin secretion. Most of the studies that examined the effect of stressor exposure on peripheral release of oxytocin, have investigated non-social stressors, such as forced swimming or restraint. While non-social stressors have been shown to increase central and peripheral oxytocin levels across studies (Engelmann et al., 2004; Jezova et al., 1995; Lang et al., 1983; Torner et al., 2017; Wotjak et al., 1998), results from the few studies investigating social stressors showed inconsistencies, like increased central but not peripheral oxytocin reactivity (Engelmann et al., 2001; Hinde et al., 2016), or no involvement of the oxytocinergic system at all (Trainor et al., 2010). The latter study examined central and peripheral activity of the oxytocinergic system in relation to aggressive conflicts towards intruders and found no involvement of the oxytocinergic system in male mice, but central and peripheral oxytocin activity in females (Trainor et al., 2010). Two other studies which did not reveal peripheral but central activity of the oxytocinergic system both investigated separation distress (Engelmann et al., 2001; Hinde et al., 2016), which suggests that different release patterns could reflect different contexts of social stress, species-specific differences and/or sex differences in endocrine responses (Crockford et al., 2017; Ziegler and Crockford, 2017). In addition, while there is evidence for the involvement of the oxytocinergic system in defense and territorial aggression (De Dreu and Kret, 2016; de Jong and Neumann, 2017), it might not be involved in antagonistic aggression, like aggression over dominance or mating partners, which are modulated primarily by vasopressin and testosterone in males (Trainor et al., 2010; van Anders et al., 2011).

Central measurements of the oxytocinergic system are very limited in humans, non-human primates and other large mammals, since they can only be performed via restraint or by sacrificing study subjects (Crockford et al., 2014). Coordinated central and peripheral release patterns of oxytocin have been found in relation to several behavioral contexts and physiological stimuli (Neumann and Landgraf, 2012).

However, some behaviors or stimuli seem to activate central or peripheral oxytocin excretion independently (Engelmann et al., 2001; Hinde et al., 2016; Neumann and Landgraf, 2012). Since our study only examined differences in peripheral levels of oxytocin, we cannot know if central activation of the oxytocinergic system occurred correspondingly or independently. However, similar limitations are true for all studies investigating endocrinological correlates of naturally occurring behaviors non-invasively. Thus, while central oxytocin activity in relation to stressor exposure is unknown in humans and old-world non-human primates, most studies using peripheral oxytocin measures did not find an elevated activity after stressor exposure (Old world non-human primates: Kalin et al., 1985; Humans: Light et al., 2005; Seltzer et al., 2010; Taylor et al., 2006). In line with the latter studies, we did not find support for increased peripheral oxytocin activity in relation to a potential social stressor in the form of antagonistic aggressive interactions. Overall, our results indicate that uOT levels vary between behavioral conditions and that uOT levels are significantly higher after affiliative behavioral contexts than after aggressions alone.

4.3.2. Aggressions followed by affiliation between former opponents (reconciliation)

uOT levels after reconciliations were not as pronounced as has been observed in relation to food sharing, hunting, patrols, or intergroup encounters in chimpanzees (Samuni et al., 2017; Wittig et al., 2014), but effects (Fig. 2) were comparable to what has been found for bond-partner grooming (Crockford et al., 2013). Most importantly, uOT levels related to reconciliations seemed to be independent of the identity of the partner or dyadic relationship quality. The lack of influence of relationship quality on oxytocin levels has also been found for food sharing in chimpanzees (Wittig et al., 2014). The latter authors proposed that food sharing may act as a facilitator of bond formation and maintenance between unrelated individuals via the oxytocinergic system (Wittig et al., 2014). Similarly, our results might indicate that the oxytocinergic system is activated during reconciliations and that, through a mechanism related to building and maintaining valuable relationships, the oxytocinergic system may also take part in repairing them.

We only measured uOT levels after reconciliations and not after the aggressive conflicts that preceded the reconciliations, thus we cannot exclude that uOT levels were already elevated after these aggressions – even though oxytocin levels were not elevated after aggressions alone. There are several, not mutually exclusive ways for how the oxytocinergic system could be involved in repairing disturbed relationships or resetting tolerance levels between former opponents. Oxytocin could be released before a reconciliation, triggered by a destructive social event, to stimulate the motivation to affiliate or to invest in a threatened valuable relationship (Gordon et al., 2011; Grebe et al., 2017; Taylor, 2006), to reduce anxiety to facilitate prosocial behavior (Feldman, 2012; Radke et al., 2017), or to increase salience to social stimuli to facilitate appropriate behavioral responses (Shamay-Tsoory and Abu-Akel, 2016). On the other hand, oxytocin might only be excreted during the affiliative contact of a reconciliation and may in this way stimulate calming and tolerance re-establishing effects (Morrison, 2016). Since uOT levels were not elevated after aggressions alone, it seems more likely that the act of reconciliation, involving positive affiliative tactile experience, activates the oxytocinergic system. Moreover, uOT levels were not influenced by the duration of an affiliation, nor by the latency between the aggression and the start of the PC affiliation (Appendix Section 2, Model A5), which additionally indicates that the PC affiliation itself is related to an activation of the oxytocinergic system.

uOT levels after reconciliations did not differ from uOT levels after affiliations alone. It is possible that we did not find differences in uOT levels after reconciliations and affiliations alone since some of the affiliations alone might have been reconciliations for the chimpanzees. For example, the behavioral condition affiliations alone could include delayed reconciliations of conflicts from the previous day, or some affiliations between former opponents might have been reconciliations

for the chimpanzees, despite the fact that a bystander PC affiliation preceded the affiliation between former opponents. However, we were not able to control for these possibilities. Furthermore, since uOT levels of both reconciliations and bystander PC affiliations did not differ from uOT levels after affiliations alone, it is more likely that the affiliative interaction is associated with the oxytocinergic activity, independent of the behavioral context. Indeed, affiliative interactions in the form of repeated physical contact, such as the exchange of touch or grooming, have been shown to activate the oxytocinergic system in numerous animal species including humans (Morrison, 2016; Uvnäs-Moberg, 1998). Oxytocin might therefore be released in response to somatosensory stimuli like social contact and grooming (Uvnäs-Moberg, 1998). Support for this suggestion comes from studies in rodents and humans. For example massage-like stroking of the abdomen in rats led to increased oxytocin levels (Agren et al., 1995). Similarly, massages in humans were associated with higher plasma oxytocin levels compared to oxytocin levels before the massage (Morhenn et al., 2012; Turner et al., 1999).

However, while there is some evidence for affiliative interactions generally activating the oxytocinergic system, other studies indicate that oxytocin levels are more strongly associated with the frequency of positive affiliative contacts and relationship quality between the affiliation partners. Studies in humans found that more frequent hugs between partners were associated with higher baseline oxytocin levels (Light et al., 2005) and peripheral oxytocin levels after parent-infant interactions were positively related to high levels of affectionate touch in mothers and high levels of stimulatory contact in fathers (Feldman et al., 2010). Furthermore, warm partner contact was only related to increased oxytocin levels in couples with stronger partner relationship quality (Grewen et al., 2005) and high relationship quality of married couples was associated with higher salivary and plasma oxytocin levels (Holt-Lunstad et al., 2015). Similar patterns have been found in non-human primates (Finkenwirth et al., 2015; Maestripieri et al., 2009; Snowdon et al., 2010), including chimpanzees (Crockford et al., 2013).

In our study relationship quality did not affect uOT levels after reconciliations. It is possible that relationship quality did not have an effect on uOT levels after reconciliations because reconciliation might function to repair all relationships, independent of their quality (Wittig and Boesch, 2005). Additionally, relationship quality scores of dyads who reconciled had higher average scores (mean = 0.75) than dyads engaged in aggressions not followed by PC affiliation (mean = 0.61; Appendix Table A2). It is therefore possible that we did not find an effect of relationship quality on uOT levels in our dataset because the relationship quality of reconciling chimpanzees was already quite high and did not show much variation. However, since our dataset was limited in sample size our results have to be taken with caution and further investigations are needed for a more conclusive understanding of the role of relationship quality in relation to different types and contexts of affiliative interactions on the oxytocinergic system's activity.

Moreover, irrespective of relationship quality, the secretion of peripheral oxytocin is not always dependent on tactile stimulation or affiliation. For example elevated uOT levels have been found after cooperative group-level behaviors in wild male and female chimpanzees, which did not necessarily involve affiliative contact, like hunting, intergroup encounters and patrolling (Samuni et al., 2017), and vocal contact with mothers was associated with increased uOT levels in human children (Seltzer et al., 2010). Additionally, in our previous study uOT levels after at least 10 min of polyadic grooming did not differ from uOT levels after a non-social control condition in male and female chimpanzees (Samuni et al., 2017). Furthermore, despite pronounced variation in duration and complexity of PC affiliations, the duration of an affiliation had no effect on uOT levels in our study, or in previous studies in chimpanzees (Crockford et al., 2013; Samuni et al., 2017). Thus, tactile stimulation and affiliation are certainly important mechanisms triggering oxytocin secretion in some but not all social

contexts.

4.3.3. Bystander PC affiliation directed to a former aggressor (bystander PC affiliation)

Comparable to the effects of reconciliation, uOT levels after receiving bystander PC affiliations were higher than uOT levels after aggression alone and the non-social control condition, and were not influenced by relationship quality, partner's identity, affiliation duration, nor by the latency between the aggression and the start of the PC affiliation (Appendix, model A5). All bystander PC affiliations for which samples could be included in this study were directed towards aggressors (appeasement). Suggested functions of appeasement are the reduction of the spread of aggression in the group and the provision of encouragement or support to a valuable partner (Fraser et al., 2009; Romero et al., 2011). A study in captive chimpanzees found that bystanders directed PC affiliations more often towards male aggressors when bystanders were males and socially close to the aggressor (Romero et al., 2011). The authors concluded that this PC affiliation might serve as a mechanism to reduce aggressive tendencies of an aggressor, or might have the function to support a valuable partner (former aggressors) which could be a mechanism to strengthen bonds (Romero et al., 2011). Comparable to the latter study, within the data used for the oxytocin analyses, we found that males were more likely to initiate bystander PC affiliation (8 of 11 samples) and that the average relationship quality between the bystander and the aggressor was high (mean = 0.74; Appendix, Table A2). Thus, elevated uOT levels in aggressors receiving bystander PC affiliation might indicate that this PC affiliation functions as a mechanism to strengthen bonds between the bystander and the former aggressor, as suggested by Romero and colleagues (Romero et al., 2011). Furthermore, receiving social support from a bystander in the form of affiliation resulted in higher uOT levels than aggressions alone which supports the oxytocinergic systems involvement in social buffering (Smith and Wang, 2014). However, similar to bystander PC affiliations directed to victims, appeasement might have multiple functions that need to be investigated further.

In addition to the investigation of the oxytocinergic systems' activity in receivers of bystander PC affiliation, it would have been informative to examine uOT levels of the bystanders initiating a PC affiliation, which would further the understanding of the oxytocinergic systems involvement in motivational processes facilitating social support. For example, a recent study in monogamous prairie voles found an increased activity of the oxytocinergic system in the bystander offering consolation behavior (Burkett et al., 2016). This study showed that a vole who observed its mate in distress, opposed to observing a stranger vole in distress, mirrored the physiological fear response of its mate and showed an increased activity of the oxytocinergic system, and subsequently increased affiliative behavior towards its distressed mate (Burkett et al., 2016). Due to our low sample size we could not investigate uOT levels of bystanders initiating PC affiliations. Nevertheless, our results support the suggested social support function of appeasement and the involvement of the oxytocinergic system in social buffering processes.

5. Conclusions

In line with previous studies, we found support for the 'valuable relationship' hypothesis, which indicates that repairing a valuable relationship is a relevant function of reconciliation applied by the male chimpanzees in our study. Affiliative social interactions were associated with higher peripheral oxytocin levels, whether occurring as reconciliation, bystander PC affiliation or affiliation alone, than uOT levels after aggression alone and non-social control periods. Affiliative interactions are known to have calming and anxiety reducing effects in the context of conflicts as well as in neutral situations and are important behavioral mechanisms of bond maintenance (Aureli et al., 1999; Carter, 1998; Morrison, 2016; Uvnäs-Moberg, 1998; Wittig et al.,

2016). Furthermore, affiliative interactions after conflicts and affiliative interactions not related to conflicts do not necessarily differ in complexity or involve different behavioral components. Thus, it is not unexpected that similar behaviors induce comparable levels of uOT in differing social contexts. While behavioral functions might differ between affiliative interactions and as well within PC affiliations, our results suggest that physiological mechanisms facilitating these functions might be similar. Furthermore, uOT levels after reconciliations and receiving bystander PC affiliations were not influenced by the relationship quality between interacting individuals. Therefore, it seems more likely that the affiliative behavior, involving positive physical contact, and not the identity of the affiliation partners, activated the oxytocinergic system. For reconciliations, this might indicate a mediating role of the oxytocinergic system in post-conflict relationship repair. While the activation of the oxytocinergic system in former aggressors that received affiliation from an uninvolved bystander might be part of a mechanism that strengthens the relationship between the former aggressor and the bystander. Both reconciliation and bystander PC affiliation occurred more often between individuals that had a higher relationship quality than the group average. Hence, it is possible that we did not find an effect of relationship quality on uOT levels because the relationship between affiliation partners was generally high and showed little variation. Overall, our findings indicate that like with affiliative interactions, the oxytocinergic system contributes to relationship repair through mechanisms related to bond formation and maintenance. Thus, the oxytocinergic system likely helps to offset negative effects associated with disrupted relationships, which enables social animals to live together and cooperate with one another in spite of aggressive competition.

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Ethics statement

Permissions to conduct the research was granted by the Ministries of Research and Environment of Ivory Coast and Office Ivoirien des Parcs et Reserves. Methods were approved by the Ethikrat der Max-Planck-Gesellschaft.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2018.07.009>.

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