Oxytocin promotes social grooming in bonobos

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Abstract:

Oxytocin has attracted research attention due to its role in promoting social bonding. One notable recent hypothesis is the biobehavioral feedback loop, which posits that the oxytocin system has evolved to support the formation and maintenance of social bonds through a positive feedback loop, where oxytocin promotes social behaviours which then cause oxytocin release themselves. In the two *Pan* species, humans' closest relatives, oxytocin is known to be released following key behaviours related to social bonding, such as social grooming in chimpanzees and female-female sexual behaviour in bonobos. However, no experimental evidence has demonstrated that oxytocin promotes such socio-positive behaviours. To test this, we administered nebulized oxytocin or saline placebo to a group of female bonobos and subsequently observed the change in their gross behavior during free interaction. We found that bonobos groomed other group members significantly more frequently in the oxytocin compared to placebo condition. Other behavioural measures did not largely differ between conditions, except for a nonsignificant trend for reduction in abnormal regurgitation/reingestion behaviour. Overall, we found that oxytocin promoted socio-positive interaction in bonobos, providing support for the biobehavioural feedback loop hypothesis of oxytocin in bonobo social evolution.

Keywords: Oxytocin, bonobos, social bonding, biobehavioural feedback loop, social grooming, *pan paniscus*

Introduction:

Oxytocin is a hormone neuropeptide conserved through mammalian evolution and plays diverse roles in regulating social behaviors across species. Evidence has accumulated for a biobehavioural feedback loop in mammalian social behaviours such as maternal care [1–3], pair bonding [4], and even the dog-human bond [5,6], where oxytocin both promotes and is released by key behaviours related to social bonding. In the great ape species most closely related to humans the presence of such a positive feedback loop has also been suggested [7], though the importance of it in human and other great ape species' evolution remains unclear. Currently, experimental evidence is lacking as to whether oxytocin promotes socio-positive interaction in these species, a key piece of evidence that would support the presence of such a positive feedback loop in the *Pan* species.

Among non-human great apes, the majority of studies have been conducted through measurement of urinary oxytocin following key social behaviours. Crockford et al. [7] showed that urinary oxytocin levels in wild chimpanzees increase following social grooming, a key socio-positive behavior widely present in nonhuman primates, and proposed that a positive feedback loop may have evolved to support social bonding in this species. Relatedly, Moscovice et al. [18] found that urinary oxytocin levels in wild female bonobos increased following same-sex sexual behaviour, genito-genital (GG) rubbing. Bonobos also increased proximity and coalitionary support among females after GG-rubbing; though it remains unclear if oxytocin played a direct role in these behavioural changes. Other studies have additionally demonstrated that urinary oxytocin rises after food sharing [19], reconciliation [20], border patrols [21,22], and group hunting [21,23], further suggesting its importance to social bonds and coordination.

In several primate species, studies have demonstrated exogenous oxytocin can impact a wide range of social behaviours (reviewed in [8]). In macaques, several studies have demonstrated that oxytocin alters social gaze, such as increased attention to eyes [9], reduced attention to negative and fearful facial expressions [10] as well as social threats [11], and more gaze following [12]. In one of the first to test the effect of oxytocin in spontaneous social behaviour among multiple macaques, although still confined to primate chairs in a laboratory setting, Jiang and Platt [13] found evidence that oxytocin flattened the dominance hierarchy and enhanced synchrony of mutual gaze. Marmosets similarly showed an increase in attention to eyes [14] following oxytocin administration and an increase in anxiety and vigilance following administration of an oxytocin antagonist [15]. Another study found that oxytocin promoted huddling in marmosets, while an oxytocin antagonist reduced social proximity and huddling [16]. On the other hand, in capuchin monkeys oxytocin was found to reduce food sharing through increasing interindividual distance [17]; the authors interpreted these results as derived from oxytocin's anxiolytic effect, which increased social distance and thereby decreased opportunities for food sharing [17].

Tthe results of three studies measuring behaviour following oxytocin administration in non-human great apes were mixed. Proctor et al. [24] administered oxytocin to eight chimpanzees individually for one trial each in both saline and oxytocin conditions then observed them in their regular social groups. Although they did not find significant effects for any behaviours measured, the authors note that it may be due to methodological issues, such as failures to find effective dose of oxytocin for chimpanzees and effective time window to test the oxytocin effect, or due to influence from groupmates who did not receive oxytocin before social interaction. Hall et al. [25]

similarly found no effect of oxytocin when chimpanzee dyads were administered oxytocin or saline placebo and subsequently tested in a token exchange task. Each participant chose one of two tokens to exchange and received rewards based on the choice of both participants in distributions based on games such as the prisoner's dilemma and hawk-dove. However, although this study administered oxytocin to a dyad, the authors reported the same methodological concerns for the oxytocin administration procedure as well as a confound between experimental condition and order. No clear patterns emerged in either the placebo or oxytocin conditions, limiting interpretation of oxytocin's possible effect. On the contrary to these studies reporting null results, Brooks et al. [26] found that oxytocin enhanced species-typical social gaze, increasing eye contact in bonobos but not chimpanzees, indicating that oxytocin can modulate gaze behaviour. While the species difference in the latter study cannot be attributed to differences in oxytocin administration procedure, it remains unclear whether the lack of effect in the prior studies is due to methodology of oxytocin administration or that exogenous oxytocin fails to significantly affect chimpanzee social behaviour.

Critically, although it is central to the biobehavioural feedback loop hypothesis that both socio-positive interactions cause oxytocin release and that oxytocin can lead to socio-positive interactions, there is no direct evidence showing that oxytocin promotes any socio-positive interaction in *Pan*. Given recent progresses in this line of research, it is worthwhile to test whether oxytocin promotes key social behaviours related to social bonding in *Pan*, particularly in bonobos using the updated methods of oxytocin administration. Therefore, this study administered nebulized oxytocin or saline placebo to a whole group of female bonobos following the methods employed in Brooks et al. [26] and subsequently observed the change in their gross interactive

behavior, including grooming and GG-rubbing, as well as other noninteractive behaviours during their free interaction. Based on previous studies, we developed two hypotheses regarding how oxytocin would impact bonobos' social behaviour. As mentioned, the biobehavioural feedback loop hypothesis suggests that an oxytocin positive feedback loop has evolved to support *pan* social bonding, and in particular we predicted that oxytocin would promote social grooming, which is known to be released through social grooming in wild chimpanzees [7]. This would suggest that oxytocin acts in a self-reinforcing loop through grooming as proposed by Crockford et al. [7], forming a part of the endocrine basis of *pan* bond formation and maintenance. Alternately, the social satiation hypothesis predicted that the oxytocin released through grooming instead evolved to serve as a socially mediated anxiolytic. This hypothesis predicted that oxytocin, through its anxiolytic effect, would reduce the need for grooming due to lower social tension, similar to the reduced food sharing observed in Brosnan et al. [17] .

Methods:

Ethics statement:

All ape participants received regular feedings, daily enrichment, and had ad libitum access to water. No change was made to their daily care routine for the purpose of this study. Apes were never restrained at any point. Ethical approval number was WRC-2020-KS014A.

We carefully considered the safety of the OT administration as in previous studies. Again, we based this decision on the fact that 1) OT is often administered to human children and adults, 2) OT is active for only a short period of time following administration with no known side effects in humans (MacDonald et al., 2011), 3) OT is naturally produced in bonobos and chimpanzees following relevant behaviors (Crockford et al., 2013; Moscovice et al., 2019), and 4) no previous studies administering OT intranasally to chimpanzees or bonobos reported any agonistic interaction (Brooks et al., 2021; Hall et al., 2019; Proctor et al., 2016).

Participants:

Four adult female bonobos at Kumamoto Sanctuary participated in this research. Details about participant ages and rearing histories can be found in supplementary material (Table S1). Animals were not food or water deprived at any time and were given both physical and social environmental enrichment in their daily life. The bonobos live in a dynamic grouping structure where three of the four females are together on any given day, and the fourth is with two male bonobos. These two males were not involved in this study because one male refused to participate in any oxytocin experiments, and our aim was to test whole groups at a time. Three of the females join the male bonobos with varying frequency, while the fourth (Lenore) is always with other

136 female bonobos. Individuals thus had a varying number of trials, with Lenore having the most due
137 to never joining the male group (24 trials), followed by Lolita (20 trials), followed by Louise and
138 Ikela (14 trials each) who are most often with the males.

139 Administration procedure:

140 Oxytocin administration procedures followed Brooks et al. [26]. Briefly, oxytocin was dissolved in
141 saline at a concentration of 40IU/mL. The oxytocin solution or placebo control was nebulized into
142 a box using a portable nebulizer (Omron NE-U100) at a minimum rate of 0.25mL/minute, for a
143 cumulative 4 minutes while apes drank juice (thus a total of 40IU or more was nebulized during
144 the administration period). Timing was stopped while apes' noses were outside the box.
145 Participation was voluntary and apes were never restrained.

146 Observation procedure:

147 Observation began 30 minutes after completion of administration criteria of all individuals (30
148 minutes from the completion of the last individual), in line with previous studies [8], and lasted for
149 one hour. The last individual to complete administration procedures was always within 30 minutes
150 of the first individual to finish, and thus all participants were observed for one hour, starting and
151 finishing between 30 minutes and 2 hours following completion of administration procedures on
152 any given day. Observation methods combined scan and event sampling. Specifically, every 2
153 minutes, interindividual proximity was estimated for each dyad into one of four categories (in
154 contact, within arm's reach-one individual could extend their arm to touch the other, < 3 meters,
155 and > 3 meters) as well as each individual's behaviour (grooming including direction, resting, self-
156 directed behaviour, moving, eating). All occurrences of play, GG-rubbing, abnormal behaviour, and

aggression towards groupmates (including displays) were additionally recorded (see Brooks et al. [27] for more details about these observation methods).

Analysis

All analyses were conducted in R [28]. Behavioural scan data was analyzed with binomial GLMMs (Generalized Linear Mixed Models) with package lme4 [29], where each individual at each point in time was characterized as either engaged in (1) or not engaged in (0) a given behaviour. The model included a test fixed effect of condition in addition to control fixed effects of day (counting upwards from first experimental day) and time, with random effects of dyad and grouping structure (a unique value was given for each possible combination of individuals) and random slopes of each fixed effect for each random effect. Numeric effects were scaled to a mean of 0 and standard deviation of 1. Random slope structure was kept maximal, except that the interaction between random slopes and intercepts was removed due to issues with convergence. For grooming data, we analyzed rates of active grooming (giving or mutual grooming), and receiving grooming was valued as 0 for not actively grooming another individual.

Proximity data was analyzed using a CLMM (cumulative link mixed model) on ordinal data using the package “ordinal” [30]. Fixed and random effect structures were the same as those in the behavioural scan data analysis, except for the individual participant variable was replaced by dyad (a unique value for each dyad), and the addition of two random effects to represent the two individuals within a dyad (randomly distributed as individual variable 1 and 2). Random slope structure was kept maximal and the interaction between random slopes and intercepts was retained in this model.

All occurrence data was analyzed with a binomial GLMM, where each individual for each day was characterized as having engaged in (1) or not engaged in (0) a given behaviour. The fixed and random effect structure was the same as in the scan behaviour models, except for the time variable removed due to data being summarized across a given observation day. Model syntax for all model types can be found in supplemental material.

184 Results

185 Bonobos engaged in active social grooming significantly more in the oxytocin condition than the

186 control condition (= 0.48, SE = 0.16, χ^2 = 3.94, p = 0.047; Figure 1). Plots of this effect by

187 participant, group, and time can be found in supplementary material (figures S1, S2, and S3).

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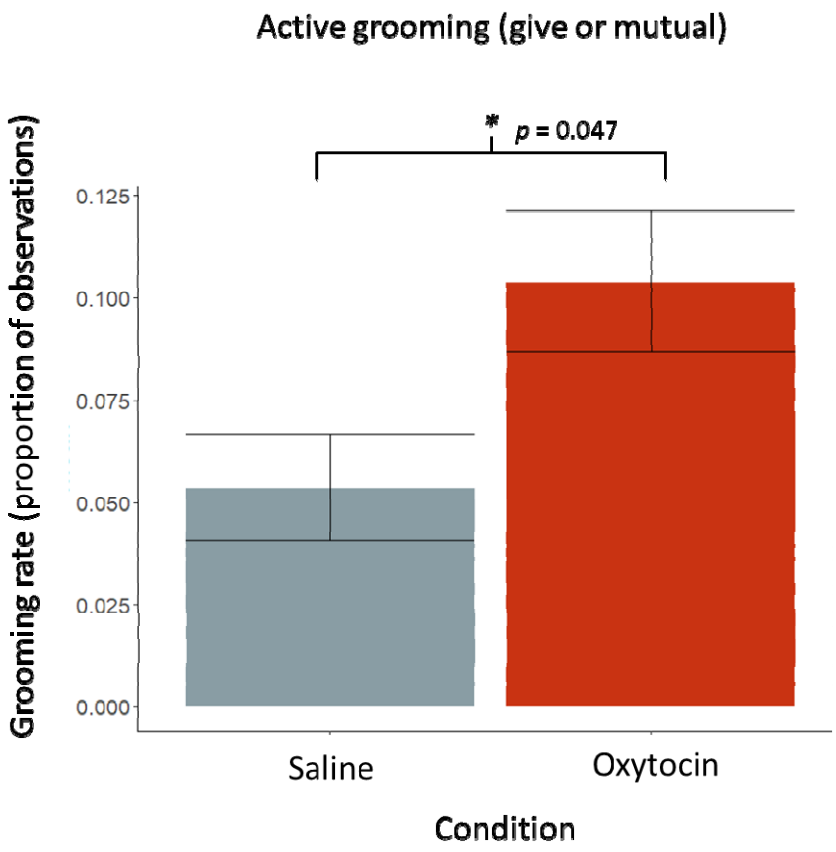

189

190 Figure 1. Mean active grooming rates in the oxytocin compared to saline control condition (giving

191 or mutual grooming). Error bars represent 95% confidence intervals.

192

We did not find significant differences in other behaviors between conditions. However, there was a trend for closer interindividual proximity in the oxytocin compared to control condition (β = -0.22, SE = 0.12, χ^2 = 2.85, p = 0.091) and for a reduction in the abnormal behaviour regurgitation and reingestion in the oxytocin compared to control condition (β = -0.73, SE = 0.36, χ^2 = 3.08, p = 0.079). There were no significant changes in self-directed behaviour (β = -0.33, SE = 0.18, χ^2 = 2.04, p =0.15) or rest (β =-0.13, SE = 0.18, χ^2 = 0.47, p =0.49). Bonobos engaged in GG-rubbing only once (oxytocin condition) and displayed no aggression toward groupmates or any bouts of play during the observation period. See supplementary material Table S2 for full details of all models.

202 Discussion:

203 Female bonobos groomed groupmates significantly more in the oxytocin condition than in the
204 saline condition. In combination with the previous studies showing oxytocin is released in bonobos
205 and chimpanzees following socio-positive interaction [7,18], our results provide experimental
206 support for the biobehavioural feedback loop hypothesis in bonobos. Other observed behaviours
207 did not largely differ between the oxytocin and saline conditions (self-directed behavior and rest)
208 or were rarely or never observed during our 1-hour observation window (GG-rubbing, play, and
209 aggression). There were trends for closer inter-individual proximity and reduced rates of
210 regurgitation and reingestion. Brosnan et al. [17] found that oxytocin increased interindividual
211 distance in capuchin monkeys (though individuals were separated by a mesh partition), possibly
212 through oxytocin's known anxiolytic effect, and this increase in interindividual distance then
213 reduced food-sharing. Our results did not demonstrate this pattern in freely interacting bonobos
214 and thus did not support the social satiation hypothesis. Potential reduction of regurgitation and
215 reingestion may be explained by oxytocin's effect on anxiety or digestion [31–33].

216 Although we present the first observation that oxytocin promotes socio-positive
217 interaction in female bonobos, there are several important limitations in this study. First, due to
218 limited possibility of testing, enclosures suitable for detailed observation, and some apes'
219 willingness to join experiments, the sample was limited to just four adult female bonobos. This
220 limits firm conclusions about a biobehavioural feedback loop, as Crockford et al. [7] measured
221 urinary oxytocin after grooming only in chimpanzees, while Moscovice et al. [18] focused on sexual
222 interactions rather than grooming in bonobos. While these previous studies characterized the
223 changes similarly as socio-positive behaviours strengthening bond formation, conclusive proof of a

224 biobehavioural feedback loop in one or both species would require evidence of increased urinary
225 oxytocin following grooming in bonobos, administration of oxytocin promoting GG-rubbing in
226 bonobos, or administration of oxytocin promoting grooming among bond partners in chimpanzees.
227 It remains possible that exogenous oxytocin promotes grooming in bonobos but not chimpanzees,
228 or that oxytocin is released following grooming in chimpanzees but not bonobos. Previous work
229 has also indicated sex-specific effects of oxytocin [34–36], and thus it remains unclear whether our
230 results can be generalized to different sex pairs. However, it should be noted that Crockford et al.
231 [7] did not find significant differences between female-female, female-male, and male-male dyads
232 in urinary oxytocin level following grooming in wild chimpanzees. Second, it has not been
233 demonstrated whether urinary oxytocin shows a similar increase following grooming in wild
234 bonobos, though Moscovice et al. [18] found that urinary oxytocin rose following GG-rubbing
235 which was interpreted as a similar socio-positive behaviour. GG-rubbing was very infrequent in our
236 study, possibly due to low overall social tension, precluding formal analysis. Relatedly, Proctor et al.
237 [24] did not find any behavioural change after administration of oxytocin on captive chimpanzees.
238 While several methodological limitations preclude interpretation of their results (and unlike our
239 study, only one individual, instead of a whole group, was tested and observed at a time), currently
240 it has not been demonstrated whether oxytocin promotes grooming in captive chimpanzees.
241 Finally, the small number of participants did not enable us to test the effect of closeness with and
242 selectivity to a certain groupmate, which may interact with the observed increase in grooming.

243 In conclusion our finding offered experimental evidence that oxytocin promotes socio-
244 positive interaction in bonobos. The oxytocin system thus may have been coopted through
245 evolution to the formation and maintenance of social bonds though a positive feedback loop.

Moreover, we suggest that oxytocin administration can be an effective tool in great ape research involving free interactions among groupmates. Future work should further test potential differences in oxytocin's effect between species, should examine inter-individual variation with respect to social closeness and centrality, and should study how social contexts such as feeding tension interact with this effect. We demonstrate that exogenous oxytocin can affect great ape behaviour in naturalistic, spontaneous social interactions and provide experimental support for the biobehavioural feedback loop hypothesis of oxytocin in the evolution of bonobo social bonding.

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