bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Oxytocin promotes social grooming in bonobos: testing the biobehavioural feedback loop hypothesis

James Brooks[1,2*], Fumihiro Kano[2,3,4*], Hanling Yeow[1,2], Naruki Morimura[1,2], Shinya Yamamoto[1,5]

[1]Wildlife Research Center, Kyoto University

[2]Kumamoto Sanctuary, Kyoto University

[3]Center for the Advanced Study of Collective Behaviour, University of Konstanz

[4]Max-Planck Institute of Animal Behavior

[5]Kyoto University Institute for Advanced Study, Kyoto University

*Co-first authors

Correspondence to: James Brooks

Email: jamesgerardbrooks@gmail.com (JB)

Address: 990, Otao, Misumi, Uki City, Kumamoto Prefecture, 8693201, Japan

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

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*

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

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. 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. [8] 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. 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.

In several primate species, studies have demonstrated exogenous oxytocin can impact a wide range of social behaviours (reviewed in [9]). In macaques, several studies have demonstrated that oxytocin alters social gaze, such as increased attention to eyes [10], reduced attention to negative and fearful facial expressions [11] as well as social threats [12], and more gaze following [13]. 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

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

[14] found evidence that oxytocin flattened the dominance hierarchy and enhanced synchrony of mutual gaze. Marmosets similarly showed an increase in attention to eyes [15] following oxytocin administration and an increase in anxiety and vigilance following administration of an oxytocin antagonist [16]. Another study found that oxytocin promoted huddling in marmosets, while an oxytocin antagonist reduced social proximity and huddling [17]. On the other hand, in capuchin monkeys oxytocin was found to reduce food sharing through increasing interindividual distance [18]; the authors interpreted these results as derived from oxytocin's anxiolytic effect, which increased social distance and thereby decreased opportunities for food sharing [18].

Among non-human great apes, the majority of studies have been conducted through measurement of urinary oxytocin following key social behaviours. These studies have revealed that in chimpanzees oxytocin is released following a number of important social bonding behaviours, including social grooming [7], food sharing [19], and reconciliation [20], and in bonobos following female GG-rubbing [8]. Other studies have additionally demonstrated that urinary oxytocin rises in advance of border patrols as well as group hunting in chimpanzees [21,22], further suggesting its importance to social bonds and coordination.

Three studies have measured behaviour following oxytocin administration in non-human great apes. Proctor et al. [23] 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. [24] similarly found

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

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. [25] 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 or choice of study species.

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. [25] and subsequently observed the change in their gross interactive

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

behavior, including grooming and GG-rubbing, as well as other noninteractive behaviours during their free interaction.

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

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

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

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

Administration procedure:

Oxytocin administration procedures followed Brooks et al. [25]. Briefly, oxytocin was dissolved in saline at a concentration of 40IU/mL. The oxytocin solution or placebo control was nebulized into a box using a portable nebulizer (Omron NE-U100) at a minimum rate of 0.25mL/minute, for a cumulative 4 minutes while apes drank juice (thus a total of 40IU or more was nebulized during the administration period). Timing was stopped while apes' noses were outside the box. Participation was voluntary and apes were never restrained.

Observation procedure:

Observation began 30 minutes after completion of administration criteria of all individuals (30 minutes from the completion of the last individual), in line with previous studies [9], and lasted for one hour. The last individual to complete administration procedures was always within 30 minutes of the first individual to finish, and thus all participants were observed for one hour between 30 minutes and 2 hours following completion of administration procedures on any given day. Observation methods combined scan and event sampling. Specifically, every 2 minutes, interindividual proximity was estimated for each dyad into one of four categories (in contact, within arm's reach-one individual could extend their arm to touch the other, < 3 meters, and > 3 meters) as well as each individual's behaviour (grooming including direction, resting, self-directed behaviour, moving, eating). All occurrences of play, GG-rubbing, abnormal behaviour, and

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

aggression towards groupmates (including displays) were additionally recorded (see Brooks et al. [26] for more details about these observation methods).

Analysis

Behavioural scan data was analyzed with binomial GLMMs (Generalized Linear Mixed Models), 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. 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

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

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.

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Results

Bonobos engaged in active social grooming significantly more in the oxytocin condition than the control condition (β = 0.48, SE = 0.16, χ^2 = 3.94, p = 0.047; Figure 1). Plots of this effect by participant, group, and time can be found in supplementary material (figures S1, S2, and S3).

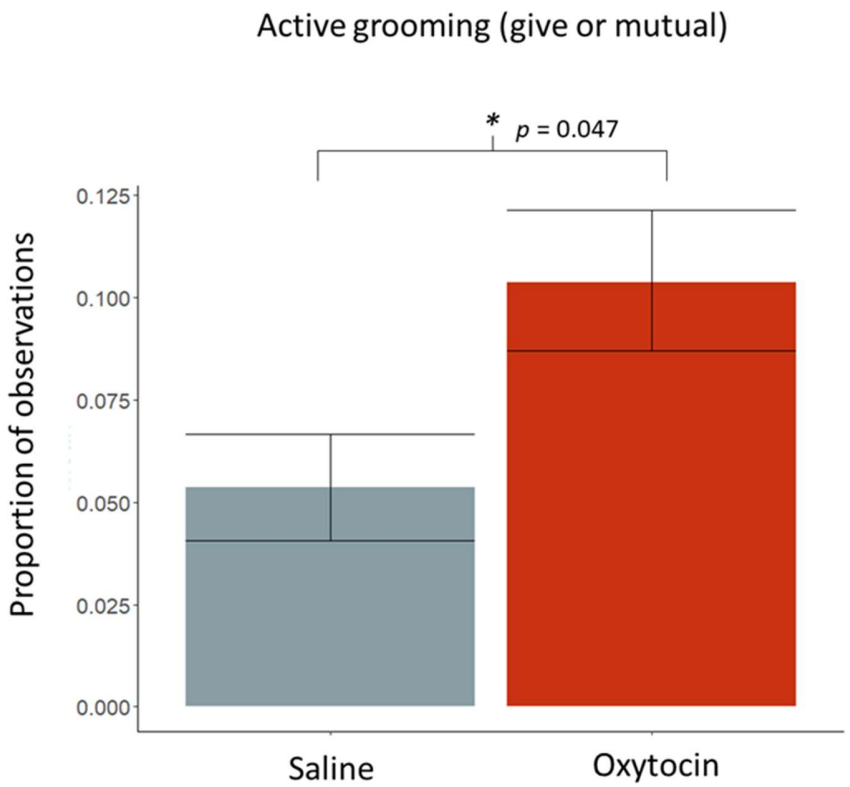

Figure 1. Mean active grooming rates in the oxytocin compared to saline control condition (giving or mutual grooming). Error bars represent 95% confidence intervals.

We did not find significant differences in other behaviors between conditions. However, there was a non-significant trend for closer interindividual proximity in the oxytocin compared to control

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

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.

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Discussion:

Female bonobos groomed groupmates significantly more in the oxytocin condition than in the saline condition. In combination with the previous studies showing oxytocin is released in bonobos and chimpanzees following socio-positive interaction [7,8], our results provide experimental support for the biobehavioural feedback loop hypothesis in bonobos. Other observed behaviours did not largely differ between the oxytocin and saline conditions (self-directed behavior and rest) or were rarely or never observed during our 1-hour observation window (GG-rubbing, play, and aggression). There were non-significant trends for closer inter-individual proximity and reduced rates of regurgitation and reingestion. Brosnan et al. [18] found that oxytocin increased interindividual distance in capuchin monkeys (though individuals were separated by a mesh partition), possibly through oxytocin's known anxiolytic effect, and this increase in interindividual distance then reduced food-sharing. Our results did not demonstrate this pattern in freely interacting bonobos. Potential reduction of regurgitation and reingestion may be explained by oxytocin's effect on anxiety or digestion [27–29].

Although we present the first observation that oxytocin promotes socio-positive interaction in female bonobos, there are several important limitations in this study. First, due to limited possibility of testing, enclosures suitable for detailed observation, and some apes' willingness to join experiments, the sample was limited to just four adult female bonobos. This limits firm conclusions about a biobehavioural feedback loop, as Crockford et al. [7] measured urinary oxytocin after grooming only in chimpanzees, while Moscovice et al. [8] focused on sexual interactions rather than grooming in bonobos. While these previous studies characterized the changes similarly as socio-positive behaviours strengthening bond formation, conclusive proof of a

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

biobehavioural feedback loop in one or both species would require evidence of increased urinary oxytocin following grooming in bonobos, administration of oxytocin promoting GG-rubbing in bonobos, or administration of oxytocin promoting grooming among bond partners in chimpanzees. It remains possible that exogenous oxytocin promotes grooming in bonobos but not chimpanzees, or that oxytocin is released following grooming in chimpanzees but not bonobos. Previous work has also indicated sex-specific effects of oxytocin [30–32], and thus it remains unclear whether our results can be generalized to different sex pairs. However, it should be noted that Crockford et al. [7] did not find significant differences between female-female, female-male, and male-male dyads in urinary oxytocin level following grooming in wild chimpanzees. Second, it has not been demonstrated whether urinary oxytocin shows a similar increase following grooming in wild bonobos, though Moscovice et al. [8] found that urinary oxytocin rose following GG-rubbing which was interpreted as a similar socio-positive behaviour. GG-rubbing was very infrequent in our study, possibly due to low overall social tension, precluding formal analysis. Relatedly, Proctor et al. [23] did not find any behavioural change after administration of oxytocin on captive chimpanzees. While several methodological limitations preclude interpretation of their results (and unlike our study, only one individual, instead of a whole group, was tested and observed at a time), currently it has not been demonstrated whether oxytocin promotes grooming in captive chimpanzees. Finally, the small number of participants did not enable us to test the effect of closeness with and selectivity to a certain groupmate, which may interact with the observed increase in grooming.

In conclusion, although there are several limitations, our finding offered experimental evidence that oxytocin promotes socio-positive interaction in bonobos. We thus suggest that the

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

oxytocin system has been coopted through 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.

Acknowledgements:

We thank the bonobos at Kumamoto Sanctuary for participating in this study. We also thank Etsuko Nogami and the other caretakers at Kumamoto Sanctuary for their support throughout this project, Dr. Satoshi Hirata for his advice and support, and Yutaro Sato for helping in data collection. This study was funded by Japan Society for the Promotion of Science (KAKENHI #21J21123 to J.B., #19H01772 and #20H05000 to F.K., and #19H00629 and #19H05736 to S.Y.)

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

References:

1. Nagasawa M, Okabe S, Mogi K, Kikusui T. 2012 Oxytocin and mutual communication in mother-infant bonding. *Front. Hum. Neurosci.* **6**, 31. (doi:10.3389/fnhum.2012.00031)

2. Rilling JK, Young LJ. 2014 The biology of mammalian parenting and its effect on offspring social development. *Science (80-.).* **345**, 771–776. (doi:10.1126/SCIENCE.1252723)

3. Da Costa APC, Guevara‐Guzman RG, Ohkura S, Goode JA, Kendrick KM. 1996 The Role of Oxytocin Release in the Paraventricular Nucleus in the Control of Maternal Behaviour in the Sheep. *J. Neuroendocrinol.* **8**, 163–177. (doi:10.1046/j.1365-2826.1996.04411.x)

4. Insel TR, Young LJ. 2001 The neurobiology of attachment. *Nat. Rev. Neurosci.* **2**, 129–136. (doi:10.1038/35053579)

5. Nagasawa M, Ogawa M, Mogi K, Kikusui T. 2017 Intranasal Oxytocin Treatment Increases Eye-Gaze Behavior toward the Owner in Ancient Japanese Dog Breeds. *Front. Psychol.* **8**, 1624. (doi:10.3389/fpsyg.2017.01624)

6. Nagasawa M, Mitsui S, En S, Ohtani N, Ohta M, Sakuma Y, Onaka T, Mogi K, Kikusui T. 2015 Oxytocin-gaze positive loop and the coevolution of human-dog bonds. *Science (80-.).* **348**, 333–336. (doi:10.1126/science.1261022)

7. Crockford C, Wittig RM, Langergraber K, Ziegler TE, Zuberbühler K, Deschner T. 2013 Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B Biol. Sci.* **280**, 20122765. (doi:10.1098/rspb.2012.2765)

8. Moscovice LR, Surbeck M, Fruth B, Hohmann G, Jaeggi A V., Deschner T. 2019 The cooperative sex: Sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions. *Horm. Behav.* **116**, 104581. (doi:10.1016/j.yhbeh.2019.104581)

9. Bauman MD, Murai T, Hogrefe CE, Platt ML. 2018 Opportunities and challenges for intranasal oxytocin treatment studies in nonhuman primates. *Am. J. Primatol.* **80**, 1–8. (doi:10.1002/ajp.22913)

10. Dal Monte O, Noble PL, Costa VD, Averbeck BB. 2014 Oxytocin enhances attention to the eye region in rhesus monkeys. *Front Neurosci* **8**, 41. (doi:10.3389/fnins.2014.00041)

11. Parr LA, Modi M, Siebert E, Young LJ, Rd G. 2013 Intranasal oxytocin selectively attenuates rhesus monkeys' attention to negative facial expressions. *Psychoneuroendocrinology* (doi:10.1016/j.psyneuen.2013.02.011)

12. Ebitz RB, Watson KK, Platt ML. 2013 Oxytocin blunts social vigilance in the rhesus macaque. *Proc. Natl. Acad. Sci.* **110**, 11630–11635. (doi:10.1073/pnas.1305230110)

13. Putnam PT, Roman JM, Zimmerman PE, Gothard KM. 2016 Oxytocin enhances gaze-following responses to videos of natural social behavior in adult male rhesus monkeys. *Psychoneuroendocrinology* **72**, 47–53. (doi:10.1016/j.psyneuen.2016.05.016)

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

14. Jiang Y, Platt ML. 2018 Oxytocin and vasopressin flatten dominance hierarchy and enhance behavioral synchrony in part via anterior cingulate cortex. *Sci. Rep.* **8**, 1–14. (doi:10.1038/s41598-018-25607-1)

15. Kotani M, Shimono K, Yoneyama T, Nakako T, Matsumoto K, Ogi Y, Konoike N, Nakamura K, Ikeda K. 2017 An eye tracking system for monitoring face scanning patterns reveals the enhancing effect of oxytocin on eye contact in common marmosets. *Psychoneuroendocrinology* **83**, 42–48. (doi:10.1016/J.PSYNEUEN.2017.05.009)

16. Cavanaugh J, Carp SB, Rock CM, French JA. 2016 Oxytocin modulates behavioral and physiological responses to a stressor in marmoset monkeys. *Psychoneuroendocrinology* **66**, 22–30. (doi:10.1016/J.PSYNEUEN.2015.12.027)

17. Smith AS, Ågmo A, Birnie AK, French JA. 2010 Manipulation of the oxytocin system alters social behavior and attraction in pair-bonding primates, Callithrix penicillata. *Horm. Behav.* **57**, 255–262. (doi:10.1016/j.yhbeh.2009.12.004)

18. Brosnan SF, Talbot CF, Essler JL, Leverett K, Flemming T, Dougall P, Heyler C, Zak PJ. 2015 Oxytocin reduces food sharing in capuchin monkeys by modulating social distance. *Behaviour* **152**, 941–961. (doi:10.1163/1568539X-00003268)

19. Wittig RM, Crockford C, Deschner T, Langergraber KE, Ziegler TE, Zuberbühler K. 2014 Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B Biol. Sci.* **281**, 20133096. (doi:10.1098/rspb.2013.3096)

20. Preis A, Samuni L, Mielke A, Deschner T, Crockford C, Wittig RM. 2018 Urinary oxytocin levels in relation to post-conflict affiliations in wild male chimpanzees (Pan troglodytes verus). *Horm. Behav.* **105**, 28–40. (doi:10.1016/j.yhbeh.2018.07.009)

21. Samuni L, Preis A, Deschner T, Crockford C, Wittig RM. 2018 Reward of labor coordination and hunting success in wild chimpanzees. *Commun. Biol.* **1**, 138. (doi:10.1038/s42003-018-0142-3)

22. Samuni L, Preis A, Mundry R, Deschner T, Crockford C, Wittig RM. 2017 Oxytocin reactivity during intergroup conflict in wild chimpanzees. *Proc. Natl. Acad. Sci.* **114**, 268–273. (doi:10.1073/pnas.1616812114)

23. Proctor D, Calcutt SESE, Burke K, de Waal FBMFBM. 2016 Intranasal Oxytocin Failed to Affect Chimpanzee (Pan troglodytes) Social Behavior. *Anim. Behav. Cogn.* **3**, 150–158. (doi:doi:10.12966/abc.04.08.2016.)

24. Hall K, Smith M, Russell JL, Lambeth SP, Schapiro SJ, Brosnan SF. 2019 Chimpanzees Rarely Settle on Consistent Patterns of Play in the Hawk Dove, Assurance, and Prisoner's Dilemma Games, in a Token Exchange Task. *Anim. Behav. Cogn.* **6**, 48–70. (doi:10.26451/abc.06.01.04.2019)

25. Brooks J, Kano F, Sato Y, Yeow H, Morimura N, Nagasawa M, Kikusui T, Yamamoto S. 2021 Divergent effects of oxytocin on eye contact in bonobos and chimpanzees. *Psychoneuroendocrinology* **125**, 105119. (doi:10.1016/j.psyneuen.2020.105119)

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.30.468796; this version posted December 1, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

26. Brooks J, Onishi E, Clark IR, Bohn M, Yamamoto S. 2021 Uniting against a common enemy: Perceived outgroup threat elicits ingroup cohesion in chimpanzees. *PLoS One* **16**, e0246869. (doi:10.1371/journal.pone.0246869)

27. Dobrovol'skaia ZA, Kosenko AF. 1989 [The role of oxytocin in realizing hypothalamic effects on the motor function of the digestive tract]. *Fiziol. Zh. SSSR Im. I. M. Sechenova* **75**, 734–7.

28. Richard P, Moos F, Freund-Mercier MJ. 1991 Central effects of oxytocin. *Physiol. Rev.* **71**, 331–70. (doi:10.1152/physrev.1991.71.2.331)

29. Uvnäs-Moberg K. 1998 Antistress Pattern Induced by Oxytocin. *Physiology* **13**, 22–25. (doi:10.1152/physiologyonline.1998.13.1.22)

30. Gao S *et al.* 2016 Oxytocin, the peptide that bonds the sexes also divides them. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 7650–4. (doi:10.1073/pnas.1602620113)

31. Caldwell HK. 2018 Oxytocin and sex differences in behavior. *Curr. Opin. Behav. Sci.* **23**, 13–20. (doi:10.1016/J.COBEHA.2018.02.002)

32. Dumais KM, Bredewold R, Mayer TE, Veenema AH. 2013 Sex differences in oxytocin receptor binding in forebrain regions: Correlations with social interest in brain region- and sex- specific ways. *Horm. Behav.* **64**, 693–701. (doi:10.1016/J.YHBEH.2013.08.012)