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3 **Oxytocin promotes species-relevant outgroup attention in**

4 **bonobos and chimpanzees**

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21 Abstract (250 words):

22 Previous research has found that oxytocin (OT) is associated with intergroup behavior in humans  
23 as well as wild chimpanzees, and that exogenous OT affects *Pan* social attention. The two *Pan*  
24 species, bonobos and chimpanzees, differ drastically from one another in their intensity of  
25 intergroup competition, with lethal intergroup aggression often led by males in chimpanzees and  
26 more tolerant associations often centered around females in bonobos. However, it remains  
27 unclear how exogenous OT changes the two species' responses to ingroup and outgroup  
28 individuals. In this study, after intranasal administration of nebulized OT or placebo control,  
29 chimpanzees and bonobos viewed image pairs of ingroup and outgroup conspecifics while their  
30 eye movements were tracked with an eye-tracker. Although the overall effect of OT was small, we  
31 found that OT shifted bonobos' and chimpanzees' attention to outgroup images of the sex  
32 primarily involved in intergroup encounters in each species. Specifically, OT selectively shifted  
33 attention toward outgroup photos of female conspecifics in bonobos, and those of outgroup male  
34 conspecifics in chimpanzees. This suggests that OT generally promotes outgroup attention in both  
35 bonobos and chimpanzees but this effect is restricted to the sex most relevant in intergroup  
36 relations. These results suggest that, although OT may have a generally conserved role in hominid  
37 intergroup behavior, it may act in species-relevant ways under the influence of their socio-  
38 ecological backgrounds.

39 Keywords: bonobos, chimpanzees, oxytocin, groupmindedness, social attention, social salience

40

41 Introduction:

42 Oxytocin (OT) has attracted considerable research interest for its role in mammalian social  
43 evolution. A hormone neuropeptide shared across mammals, it has important roles in behaviours  
44 such as maternal care (Da Costa et al., 1996; Nagasawa et al., 2012; Pedersen et al., 1982) and  
45 social bonding (Insel and Young, 2001, 2000; Nagasawa et al., 2015), and has more recently been  
46 implicated in the psychology of intergroup relations, including outgroup aggression (De Dreu,  
47 2012; De Dreu et al., 2010; Zhang et al., 2018). A body of research in the past decade has begun to  
48 unravel this role of OT in promoting group-based behaviours. Though most of such literature has  
49 come from humans, some research has implicated OT in aggression towards intruders in rodents  
50 (such as mice, Hattori et al., 2015, and rats, Calcagnoli et al., 2014; Gulevich et al., 2019; Hattori et  
51 al., 2015), and one field study found increases in urinary OT in advance of and during border  
52 patrols in wild chimpanzees (Samuni et al., 2017). In humans, research has shown administration  
53 of intranasal OT promotes parochial altruism (De Dreu, 2012; De Dreu et al., 2010; Israel et al.,  
54 2012), ingroup favouritism (De Dreu and Kret, 2016), ethnocentrism (De Dreu et al., 2011; Ma et  
55 al., 2014), and outgroup attack (Zhang et al., 2018).

56 These studies, among others, have led to general hypotheses about the effect of OT beyond the  
57 classic prosocial views of oxytocin. For example, the social salience hypothesis (Shamay-Tsoory et  
58 al., 2009; Shamay-Tsoory and Abu-Akel, 2016) predicts that OT enhances existing social biases  
59 (thus ingroup favoritism and outgroup defence in the context of intergroup behaviour), the social  
60 approach hypothesis (Kemp and Guastella, 2011) predicts OT is specifically involved in promoting  
61 social approach, and the general approach-avoidance hypothesis (Harari-Dahan and Bernstein,  
62 2014) predicts its role extends beyond social stimuli. While ongoing research is further developing

and testing the predictions of such hypotheses, each highlights OT as an important part of the endocrine basis of intergroup conflict.

Humans' two closest living relatives, bonobos and chimpanzees, significantly differ in their intergroup relations. In chimpanzees, intergroup aggression is common, physical encounters are typically violent and can be lethal (Watts et al., 2006; Wilson et al., 2014). Males form border patrols near the edge of their territory, often attacking lone outgroup males if encountered (Wilson and Wrangham, 2003). In some communities, females join border patrols as well (Samuni et al., 2019) though across sites males are far more likely to be both attackers and victims of attack (Wilson et al., 2014). Bonobos, on the other hand, typically engage in affiliative behaviour during intergroup encounters, predominantly with females centrally engaging behaviours such as grooming, food sharing, and non-copulatory sexual interaction (i.e. genito-genital rubbing) and males spending more time on the periphery (Furuichi, 2011). While bonobo intergroup encounters are not entirely peaceful and often include aggression between males (Cheng et al., 2021; Tokuyama et al., 2019), lethal aggression has never been observed and tolerant associations can last for several days at a time (Hare and Yamamoto, 2017; Lucchesi et al., 2021; Pisor and Surbeck, 2019).

Although the physiology and function of OT in great apes remain understudied compared to laboratory model species, recent field research has demonstrated OT is richly involved in *Pan* social behaviour. More specifically, in chimpanzees urinary OT increases following behaviours such as grooming (Crockford et al., 2013), food sharing (Wittig et al., 2014), group hunting (Samuni et al., 2018), and reconciliation (Preis et al., 2018), in addition to intergroup encounters as

mentioned above (Samuni et al., 2017). Less work has focused on bonobos, but urinary OT was found to rise following affiliative non-conceptive sexual behaviour (Moscovice et al., 2019).

In experiments administering nebulized OT to great apes, two studies found no significant effect of exogenous OT on chimpanzee social behaviour (Hall et al., 2019; Proctor et al., 2016) while one found an effect on social attention in bonobos and chimpanzees (Brooks et al., 2021a) and another found a positive effect of OT on social grooming when administered to whole subgroups of bonobos (Brooks et al., 2021b). Of the null results, one focused on observing natural social behaviour after giving OT or placebo to one individual at a time (Proctor et al., 2016), and the other measured responses in a token exchange task after OT or placebo was given to one or both individuals (Hall et al., 2019). As the authors of these studies noted, such null results may be due to methodological constraints, for example in interactions with non-OT administered individuals in the observational study (Proctor et al., 2016) and no consistent patterns emerging with or without OT in the token exchange task (Hall et al., 2019).

Using eye-tracking technology, Brooks et al. (2021) found that OT had an effect on *Pan* social attention (Brooks et al., 2021a). More specifically, exogenous OT was found to differentially affect bonobos' and chimpanzees' attention to eyes, increasing eye contact in bonobos but not chimpanzees, thereby enlarging known species differences (Brooks et al., 2021a). While this previous study suggests that OT may play an important role in modulating social attention in bonobos and chimpanzees, no study has investigated the effect of exogenous OT on group-related behaviour in non-human great apes.

Recent work using eye-tracking (not an OT study) has also revealed group-related gaze patterns in bonobos and chimpanzees (Lewis et al., 2021). In a preferential looking paradigm, where both

ingroup and outgroup faces were presented simultaneously, chimpanzees tended to look more to ingroup males while bonobos tended to look more to ingroup females. This study interpreted the results as a bias towards ingroup of the sex typically occupying the highest dominance ranks. Of particular relevance here is that in bonobos it is females who primarily initiate and engage in intergroup encounters (Furuichi, 2011), and in chimpanzees is typically males (Wilson and Wrangham, 2003). If OT is involved in both species' intergroup behaviour, we could predict that OT would impact attentional bias in such ingroup-outgroup gaze patterns.

Based on these previous studies, we examined how administration of OT affects bonobos' and chimpanzees' attention when presented with image pairs of ingroup and outgroup individuals (i.e. the eye-tracking test design is similar to that of Lewis et al., 2021). We developed two primary hypotheses about the effect of administered oxytocin on group-related gaze patterns. First, we developed the general intergroup relations hypothesis based on previous literature linking the oxytocin system to intergroup behaviour in many of the species which have been more extensively studied (primarily humans and rodents). This hypothesis predicted that OT has a conserved evolutionary role in intergroup behaviour in general across species. Therefore, OT may affect attention to ingroup and outgroup members in both bonobos and chimpanzees, despite the differences in the specific form of intergroup encounters between the two species.

Our second primary hypothesis was the intergroup aggression hypothesis. This hypothesis instead predicted that the oxytocin system more specifically forms part of the evolutionary basis of intergroup competition. Studies in humans have consistently linked OT to promoting, rather than alleviating, intergroup competition and outgroup aggression (De Dreu, 2012). As mentioned above, there are known differences between bonobos and chimpanzees in their aggressive

responses to outgroup encounters (Furuichi, 2011; Wilson and Wrangham, 2003). Furthermore, the previous eye-tracking study found that OT enhanced species differences in a behaviour in bonobos and chimpanzees (Brooks et al., 2021a). The intergroup aggression hypothesis therefore suggests that the oxytocin system may be more closely connected to the evolution of chimpanzees' aggressive, but not bonobos' more tolerant, species-typical intergroup behaviour. This hypothesis thus predicted that OT would influence group-related attention in chimpanzees but not bonobos.

Within each of these hypotheses, we formed sub-hypotheses about the specific ways OT would change looking behaviour. Regarding the direction of effect, the ingroup bias sub-hypothesis predicted that OT would increase attention towards the ingroup, as greater looking time to ingroup is associated with greater ingroup bias in humans (Kelly et al., 2005; Moradi et al., 2020, 2018). Alternatively, the outgroup vigilance sub-hypothesis predicted that OT would increase attention towards the outgroup, as previous studies in humans have found increased outgroup salience (lower response latency and higher accuracy in an attentional task) (Egito et al., 2020), greater defensive aggression in intergroup competition settings (De Dreu et al. 2021), and more sensitivity to unpredictable threats (Grillon et al., 2013) following OT administration compared to placebo. Regarding stimulus characteristics, because in both species one sex is more predominantly involved in initiating and engaging in intergroup encounters (male chimpanzees and female bonobos; Furuichi, 2011; Wilson and Wrangham, 2003) and Lewis et al. (2021) found a higher baseline looking time only towards this sex in a similar study design, we predicted the effect of OT may be mediated by sex in the images. More specifically, we hypothesized that OT

149 would affect attention to female bonobos and male chimpanzees more strongly than that to the  
150 other sexes.



151 Methods:

152 Participants:

153 Five bonobos (4 females, 1 male) and 16 chimpanzees (12 females, 4 males) participated in this  
 154 experiment at Kumamoto Sanctuary (KS) and Primate Research Institute (PRI). We tested one  
 155 group of chimpanzees and one group of bonobos living at KS, each comprising of 6 conspecific  
 156 individuals, and two groups of chimpanzees living at PRI, comprising 4 and 7 conspecific  
 157 individuals. One male bonobo at KS and one female chimpanzee at PRI (in the group of 4) did not  
 158 participate in this experiment respectively due to his refusal of nebulizer and her inclination to sit  
 159 in front of eye-tracking apparatuses. See Table 1 for the details about the participants.

160

161 Table 1. Participant list with institution, species, sex, age, and rearing history.

Name	Institute	Species	Sex	Age	Rearing history
Ikela	KS	Bonobo	F	29	Nursery-peer
Lenore	KS	Bonobo	F	38	Mother
Lolita	KS	Bonobo	F	31	Nursery-peer
Louise	KS	Bonobo	F	48	Nursery-peer
Vijay	KS	Bonobo	M	17	Nursery-peer
Hatsuka	KS	Chimpanzee	F	12	Nursery-peer
Iroha	KS	Chimpanzee	F	12	Mother
Misaki	KS	Chimpanzee	F	21	Mother
Mizuki	KS	Chimpanzee	F	24	Nursery-peer

Zamba	KS	Chimpanzee	M	25	Mother
Ai	PRI-A group	Chimpanzee	F	44	Wild born
Akira	PRI-A group	Chimpanzee	M	44	Wild born
Ayumu	PRI-A group	Chimpanzee	M	20	Mother
Chloe	PRI-A group	Chimpanzee	F	40	Nursery-peer
Mari	PRI-A group	Chimpanzee	F	44	Wild born
Pan	PRI-A group	Chimpanzee	F	37	Nursery-peer
Pendesa	PRI-A group	Chimpanzee	F	43	Nursery-peer
Cleo	PRI-B group	Chimpanzee	F	20	Mother
Gon	PRI-B group	Chimpanzee	M	54	Wild born
Pal	PRI-B group	Chimpanzee	F	20	Mother

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162 \*Mother indicates individuals were reared in captivity by their biological mothers, Nursery-peer  
 163 indicates the individuals were reared by human caretakers and conspecific peers, and Wild-born  
 164 indicates individuals were born in the wild and taken into captivity.

165 \*KS stands for Kumamoto Sanctuary, and PRI stands for Primate Research Institute.

166

167 Ethical note:

168 All ape participants were tested in testing booths or sleeping rooms constructed for each species,  
 169 and their daily participation in this study was voluntary. They received regular feedings, daily  
 170 enrichment, and had *ad libitum* access to water. No change was made to their daily care routine  
 171 for the purpose of this study. All apes participating in this study live in a social group comprising 4-

7 individuals with daily access to both indoor and outdoor spaces. Apes were never restrained at any point. Ethical approval numbers were WRC-2019-KS013A for chimpanzees at Kumamoto Sanctuary, WRC-2019-KS014A for bonobos at Kumamoto Sanctuary, and 2020-113 at Primate Research Institute.

As in Brooks et al. (2021), the safety of the OT administration was carefully considered and accepted given 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., 2021a; Hall et al., 2019; Proctor et al., 2016).

OT administration apparatus and procedure:

OT or saline placebo control were administered noninvasively following the methods employed by Brooks et al. (2021). A mist of OT or saline placebo control was produced by a portable nebulizer (NE-U100, Omron, Kyoto, Japan) into a custom-designed box while apes were drinking a dripping of juice thorough a nozzle attached to the box (13 w × 16.5 h × 8 d cm), via a custom-made juice dispenser. While the apes drank juice, they passively breathed the nebulized mist. We chose to use a nebulizer rather than nasal spray following studies with macaques finding elevated levels of OT in cerebrospinal fluid after receiving OT from a nebulizer (Modi et al., 2014) and with great apes finding changes in social attention using this method (Brooks et al., 2021a). Criteria for successful administration was 4 cumulative minutes (in a 10-minute window), with their nose

inside the box, counted with a stopwatch. Counting was paused while their noses were outside the box. The nebulizer created a mist at a rate of 0.25 mL/minute, and the OT was dissolved at a concentration of 40 IU/mL, meaning 40 IU was nebulized during the time the apes had their nose in the box. As in the previous study (Brooks et al., 2021a), a dose of 40 IU was chosen because it is well within the range of human and monkey studies (commonly 24-40 IU; Bauman et al., 2018; MacDonald et al., 2011). Because some amount of mist is expected to evaporate from the box, we selected a value on the higher end of those typically used with macaques and humans. We visually confirmed that individuals breathed the mist through their nose during administration. The eye tracking test on each day was both started and completed 30-60 minutes after the end of administration procedure, an interval also well within that of previous studies (Bauman et al., 2018; Brooks et al., 2021a).

#### Eye tracking apparatus:

Ape eye movements were recorded non-invasively with an infrared eye tracker (300 Hz; TX300, Tobii Technology AB, Danderyds, Sweden). To keep their heads relatively still, apes drank a dripping of juice (as in the administration procedure) while they freely viewed the stimuli (provision of juice was independent of their viewing behaviors). The stimuli were presented on a screen with a resolution of  $1,280 \times 720$  pixels at a viewing distance of 70 cm on a 23-inch LCD monitor ( $43 \times 24^\circ$ ) with Tobii Studio software (ver. 3.2.1). Automated calibration was performed by presenting small images or objects on two reference calibration points. After this calibration, we checked the calibration accuracy in Tobii Studio. Moreover, we presented a still image having small icons (squares in about 2 degrees on its side) on the monitor and checked in

real-time that gaze of an ape landed on at least one of these icons. When we saw a poor calibration result indicated by Tobii Studio or detected that gaze of an ape substantially deviated from the presented icons, we repeated calibration until it satisfied these two-step checking procedures. These procedures typically lead to accuracy within one degree of error (Kano et al., 2011), sufficient to distinguish between gaze at the ingroup and outgroup faces in this study.

#### Stimuli and procedure:

Stimuli consisted of image pairings of sex matched ingroup and outgroup faces side by side. All images showed neutral facial expressions. All images were cropped so that the size of ingroup and outgroup faces were equally sized in all pairings. In all images, backgrounds were blurred to the extent that those background objects became unidentifiable in order to avoid attracting attention to those areas (we also avoided deleting the background to keep facial edges as natural as possible). Examples of stimuli for both species can be found in supplementary material (Figure S1 and S2). We prepared two different stimulus videos containing different sets of images for each social group (KS and the two groups of PRI). Each of the two stimulus videos contained 3 unique images of each ingroup member and 3 unique images of each of a matched number of outgroup individuals (e.g. in a group of 6, 3 images of each ingroup member, total 18 images, 3 images of 6 outgroup members, total 18 images were used in a stimulus video). Each ingroup member for a given group was included in the stimuli for that group to ensure the range of dominance relations and social closeness were included. All outgroup members were unknown to participants (complete strangers rather than former groupmates or neighbours). Within each of the two stimulus videos, apes saw each image twice, paired with a different image each time (e.g. for a group of 6, 18 ingroup images, each paired with 2 outgroup images, yielding 36 pairings, were

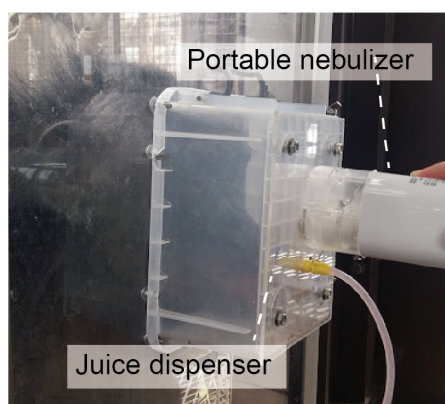
presented in a stimulus video). The number of pairings was thus dependent on group size, with larger groups viewing a larger number of pairings, but the same number of images were included for each ingroup member in each group per stimulus video (for the PRI-A group with 7 members, total 42 parings; for the PRI-B group with 4 members, total 24 parings; for the KS chimpanzee group with 6 members, total 36 parings; for the KS bonobo group with 6 members, total 36 parings were presented in a stimulus video). In some pairings, the ingroup and outgroup individuals were looking in different directions (one making direct gaze with the camera and the other with averted gaze). Given that gaze direction of facial images tends to affect looking patterns in apes (Myowa-Yamakoshi et al., 2003), we considered this variance in our analyses (see below and supplementary material).

Each pairing was presented for 3 seconds, and a fixation cross was shown for 0.5 seconds before the presentation of each paring (e.g. for a group of 6, this gives 36 pairings at 3 seconds each, yielding 126 seconds total per stimulus video, of which 108 seconds were image pairings used in analysis). The order of presentation of pairings was pseudo-randomized such that, within each stimulus video, apes 1) saw an image of all individuals once before seeing a second image of any individual, 2) saw each image once before any image was repeated, and 3) never saw two pairings in a row containing the same ingroup or outgroup individuals. Additionally, 4) the ingroup/outgroup images appeared an equal number of times on the right and left side, and 5) ingroup/outgroup images were never on the same side more than twice consecutively.

Each ape saw one stimulus video in each experimental session and the same stimulus video consecutively across the two experimental sessions (with a minimum of 4 days in between those two experimental sessions), once in the OT condition and once in the saline condition, and the

258 other stimulus video on the next two experimental sessions (i.e. total 4 sessions; e.g. Video 1 -OT,  
 259 Video 1 -Saline, Video 2 -Saline, Video 2 -OT). Half of individuals in each group saw the first video  
 260 with OT first and the second video with saline first, and the other half saw the first video with  
 261 saline first and the second video with OT first.

(a)



(b)

A pair of ingroup and outgroup conspecific images

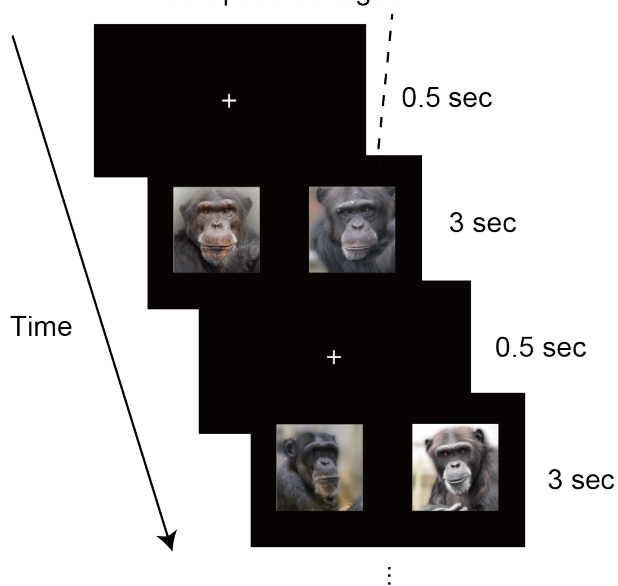


Figure 1. Experimental design. a) bonobo participating in oxytocin administration procedure. b) stimulus design with chimpanzee stimulus examples.

Analysis:

Eye movement was filtered using Tobii Fixation Filter with default parameters. Areas of interest (AOIs) were defined in the Tobii Studio software for each ingroup and outgroup image. We defined AOIs as slightly larger than the exact boundaries of the images (roughly 5% larger) following Kano and Tomonaga (2010) to accommodate certain degree of errors in recorded gaze positions. As self images (images of the participant) could not be categorized either as ingroup or outgroup images, they were excluded from all analyses (3 self images in each stimulus video, each included in two pairings; i.e. 6 pairing per stimulus video).

To quantify each participant's looking bias for each pairing of images, we calculated a looking difference score in a pairing by subtracting looking time to the ingroup image from that to the outgroup image. We chose a looking difference score as opposed to a "differential looking score" (ingroup looking time minus outgroup looking time divided by the sum of ingroup looking time and outgroup looking time) because apes occasionally made only one fixation at one image of a pairing and thus the latter score could overestimate the looking bias on such occasions. When apes did not look to either image in a pairing, we did not include this data in our analysis (10.0 % of all data, 11.5 % of chimpanzee data and 5.8 % of bonobo data).



To examine the effect of condition and species/individual differences on the looking bias, we ran a Linear Mixed Model with species (bonobo, chimpanzee), condition (OT, saline placebo), participant sex, and sex in the images as fixed factors in addition to their interactions (excluding any interactions involving both participant sex and species due to insufficient levels for comparison with only one male bonobo participant). We also included into the model experimental session (1, 2, 3, 4) and presentation order of image pairings within a session as control fixed factors. Finally, we included into the model participant, ingroup member in the pairing, and outgroup member in the pairing as random intercepts in addition to the random slopes of all fixed effects. The random-effects structure was kept maximal to maintain conservativity according to the recommendation of Barr et al. (2013), except that we removed the correlation between the intercepts and slopes to improve convergence and fit model assumptions. The model syntax in R was: Looking difference ~ participant species\*condition\*sex in image + condition\*sex in image\*participant sex + day + image order + (1 + condition\*sex in image + image order + day || subject) + (1 + condition\*participant sex + image order + day || ingroup in image) + (1 + condition\*participant sex + image order + day || outgroup in image). Because this model could not look at the interaction effect between participant species and participant sex due to our data including just one male bonobo, we additionally ran a model focused on the chimpanzee data to explore any possible effects of participant sex in chimpanzees. We used the same model structure, excluding species and its interactions.

In our preliminary analysis, we also included in our model an additional fixed factor “gaze direction matched” which was coded 1 if both individuals in an image pairing had the same gaze direction and 0 if only one was looking at the camera and the other had averted gaze, because we

suspected that this is a potential confounding factor based on the previous study showing that direct gaze attracts more attention than averted gaze (Myowa-Yamakoshi et al., 2003). This analysis revealed that the factor “gaze direction matched” significantly interacted with species, condition, and sex in image, and the follow-up analysis revealed no significant effects in the data set with gaze-unmatched image pairings, suggesting that this was indeed a confounding factor. We therefore decided to include only the data set with gaze-matched image pairings in our main analyses (62.2 % of all data; 61.1 % of chimpanzee data, 64.8% of bonobo data). Although it was admittedly a potential design error to have included the gaze-unmatched image pairings when preparing the stimuli, this was largely unavoidable due to the difficulty in finding fully comparable, recent, high quality images of all groupmates of all subjects. The details of these analyses are described in the supplementary material.

Lewis et al. (2021) additionally ran an analysis reclassifying the sex of each species as “dominant sex” in image, coding 1 for female bonobos and male chimpanzees and 0 for male bonobos and female chimpanzees based on previous findings that male chimpanzees generally outrank female chimpanzees and female bonobos often outrank male bonobos (particularly when the females are gregarious; Surbeck and Hohmann, 2013; Tokuyama and Furuichi, 2016). Lewis et al. found this variable most explanatory in predicting ingroup-outgroup looking patterns in bonobos and chimpanzees. Although Lewis et al.’s reclassification may be too simplistic to describe the role of sex in each species, this analytic strategy was useful to interpret the detected interaction effects in their additional model. We thus decided a priori to follow the same strategy as Lewis et al., but preferred to call this reclassified factor “sex primarily involved in intergroup encounters” rather

than “dominant sex,” because the more relevant information to this study in chimpanzees it is males who primarily engage in intergroup encounters while in bonobo it is females (Furuichi, 2011; Wilson and Wrangham, 2003). We ran a model in which the sex (in images) factor was substituted with this reclassified sex (in images) factor. For this analysis again we used only the gaze-matched data set. Thus, the model syntax was: Looking difference ~ participant species\*condition\*sex in image + condition\*sex in image\*participant sex + day + image order + (1 + condition\*sex in image + image order + day | subject) + (1 + condition\*participant sex + image order + day | ingroup in image) + (1 + condition\*participant sex + image order + day | outgroup in image).

A decrease in looking difference score (ingroup minus outgroup) in response to OT could be driven either by increased looking time to outgroup images or decreased looking time to ingroup images (or both). While paired presentation of ingroup and outgroup images can make it difficult to distinguish between these two possibilities, in our study apes tended not to view images for the whole presentation duration (3 seconds) and it was therefore meaningful to examine whether the observed effects of oxytocin were driven by an increase or decrease in outgroup or ingroup looking time. We ran models separately for ingroup and outgroup images to test the effect of oxytocin on attention to each stimulus set, namely including either the time looking to the ingroup images or that looking to the outgroup images as a response in each model. In these models, we chose to average looking times to all images per experimental session because apes tended not to view all images in each presentation and thus the distribution of looking time was severely zero-inflated, violating assumptions of normally distributed residuals. We also considered a model with Poisson distribution on the raw data, however while the data had a peak at zero it did not follow a

Poisson distribution but closer to normal in the non-zero data, and thus Poisson structures were not appropriate at led to problematic model diagnostics. The structure of fixed and random effects was the same as our main analyses (with looking difference score as a response) except that we did not include ingroup member identity, outgroup member identity, and image order due to the summarizing across trials.

We checked the assumptions of normally distributed and homogeneous residuals by visual inspection of diagnostic plots (q-q plots and scatterplots of the residuals plotted against fitted values) in all models. We also checked Variance Inflation Factors (VIF) in a R package “car” and found that collinearity was not an issue in any model (all VIF < 3). To check the model stabilities, we excluded each level of the random effects (subject and/or stimulus) one by one and calculated Cook’s distances as measures of influence in a R package “influence.Me”. When this manipulation suggested any influential cases (Cook’s distance > 1), we confirmed that excluding that influential case did not change the main results.

For all models, statistical significance of effects was calculated using a likelihood ratio test (using the “drop1” function in R). We first tested the highest-order interaction term in each model, and when it was not significant, we then removed it and ran the model again (Engqvist, 2005); this procedure was followed until we reach a final model including only significant interaction effects (if any) and all the main effects. When we found significant interaction effects in the final model, we investigated those effects further by running follow-up models to test simple effects on subsets of the data at each level of the predictors (to gain more precise information about the detected interaction effects). For the intercept, we calculated statistical significance with a Wald

368 test through the ANOVA function with type III sum of squares in the “car” package. We used a  
369 significance threshold of 0.05 when reporting p-values.

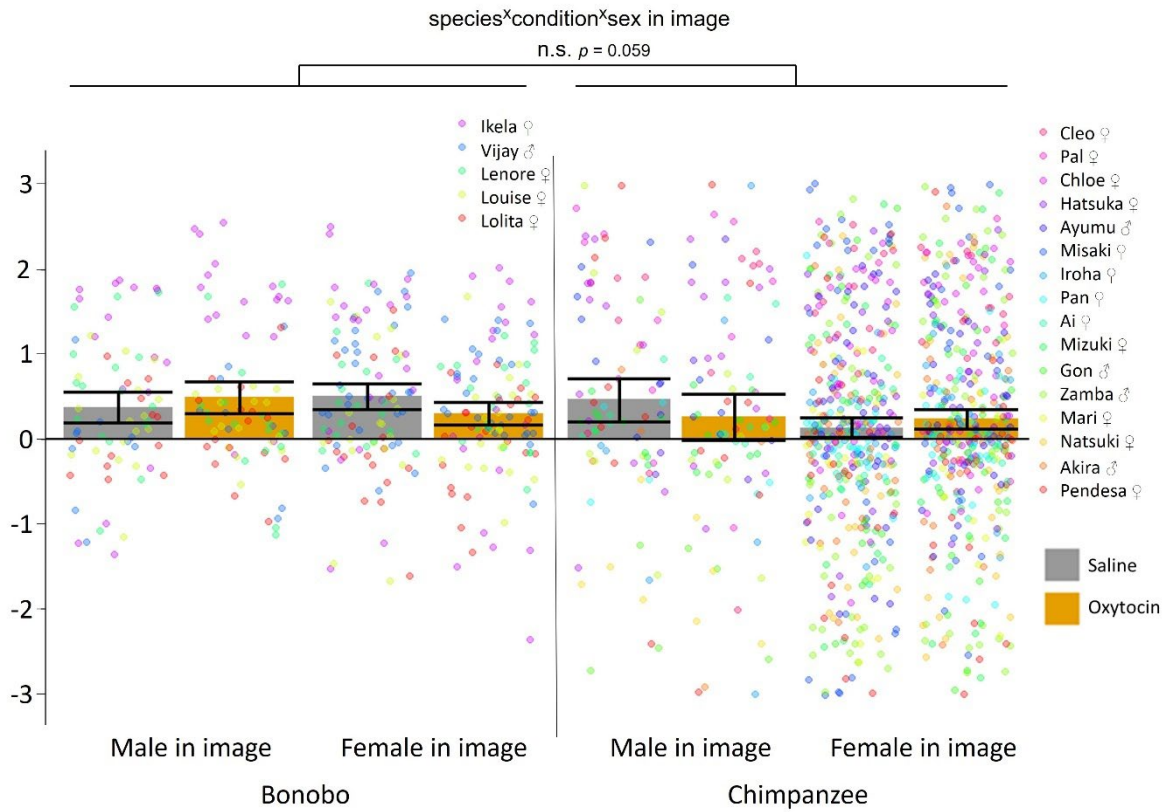
370 Results:

371 In our first model, we did not find any significant effects. However, visual inspection of results  
372 suggested a high-level interaction effect between condition, species, and sex in images, which was  
373 not significant in our first model (n.s.,  $p = 0.059$ ,  $\beta = -0.055$ ,  $SE = 0.028$ ,  $\chi^2 = 3.92$ ; Figure 2). Our  
374 second model following Lewis et al., 2021 simplified the interaction between the latter two factors  
375 by reclassifying the sex in images as noted above. In our chimpanzee model to examine the effect  
376 of participant sex, we found no significant effects or interactions with participant sex ( $ps > 0.21$ ,  
377 full model details in supplementary material).

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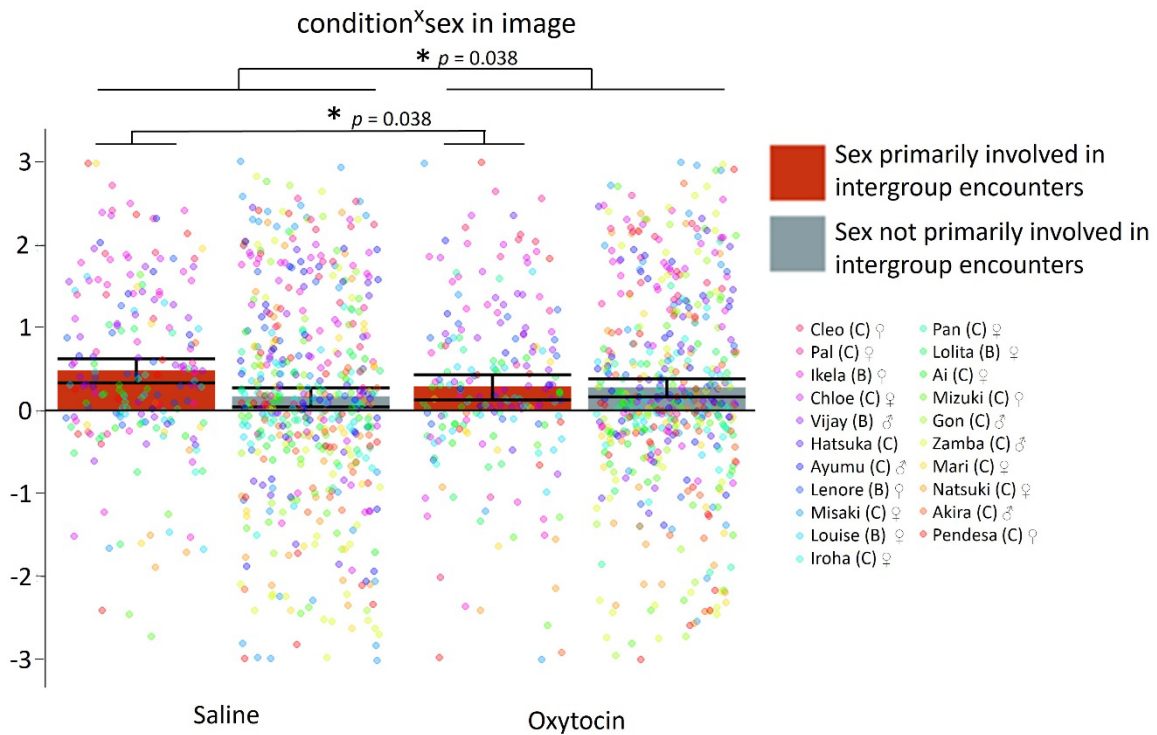


381

382 Figure 2. Mean difference in looking time (seconds) as a function of species, condition, and sex in  
 383 image with 95% confidence intervals. Y-axis represents ingroup minus outgroup gaze, higher  
 384 values thus represent greater ingroup attentional bias.

385

386



387

388 Figure 3. Mean difference in looking time (seconds) as a function of condition and sex in image  
 389 with 95% confidence intervals. Sex primarily involved in intergroup encounters refers to male  
 390 chimpanzees and female bonobos.

391

392 In our second model where the factor “sex in image” was substituted with the reclassified factor  
 393 “sex primarily involved in intergroup encounters,” (female bonobos and male chimpanzees were  
 394 coded as 1 and male bonobos and female chimpanzees were coded as 0, as in Lewis et al., 2021)  
 395 we found a significant interaction between condition and the new sex category ( $p = 0.038$ ,  $\beta = -$   
 396  $0.066$ ,  $SE = 0.030$ ,  $\chi^2 = 4.79$ ; Figure 3). This suggests an effect of condition on the main effect



found in Lewis et al. (i.e. the effect of “dominant sex”). We further investigated this pattern by running follow up models for each sex category separately. In this analysis, there was a significant main effect of condition in the model for the sex primarily involved in intergroup encounters ( $p = 0.038$ ,  $\beta = -0.095$ ,  $SE = 0.046$ ,  $\chi^2 = 4.32$ ), where the looking difference score (ingroup minus outgroup) decreased in OT compared to saline condition, while the effect of condition was not significant in the model for the sex not primarily involved in intergroup encounters ( $p = 0.14$ ,  $\beta = 0.052$ ,  $SE = 0.10$ ,  $\chi^2 = 2.18$ ).

Table 2. Model results with unchanged sex in image factor (sex in image represents male/female).

Term	Estimate	SE	$\chi^2$	$p$
Intercept	0.26	0.1	-	-
<i>Species × Condition × Sex in image</i>	<i>-0.055</i>	<i>0.028</i>	<i>3.92</i>	<i>0.059</i>
Species × Condition	0.023	0.033	0.48	0.50
Species × Sex in image	-0.0072	0.060	0.015	0.91
Species	-0.077	0.10	0.59	0.45
Sex in image	0.0044	0.065	0.0046	0.95
Condition × Sex in image	-0.013	0.034	0.14	0.71
Condition	0.0091	0.033	0.074	0.79
Participant sex × Condition × Sex in image	-0.026	0.036	0.54	0.46
Participant sex × Condition	0.0044	0.029	0.024	0.88
Participant sex × Sex in image	-0.0019	0.070	0.0007	0.98
Participant sex	-0.071	0.10	0.51	0.48
Day	-0.061	0.047	1.70	0.21
Image order	-0.044	0.047	0.91	0.35

Table 3. Model results with reclassified sex in image factor (sex in image represents sex primarily involved in intergroup encounters, referring to male chimpanzees and female bonobos). Full details of follow-up model can be found in supplementary material.

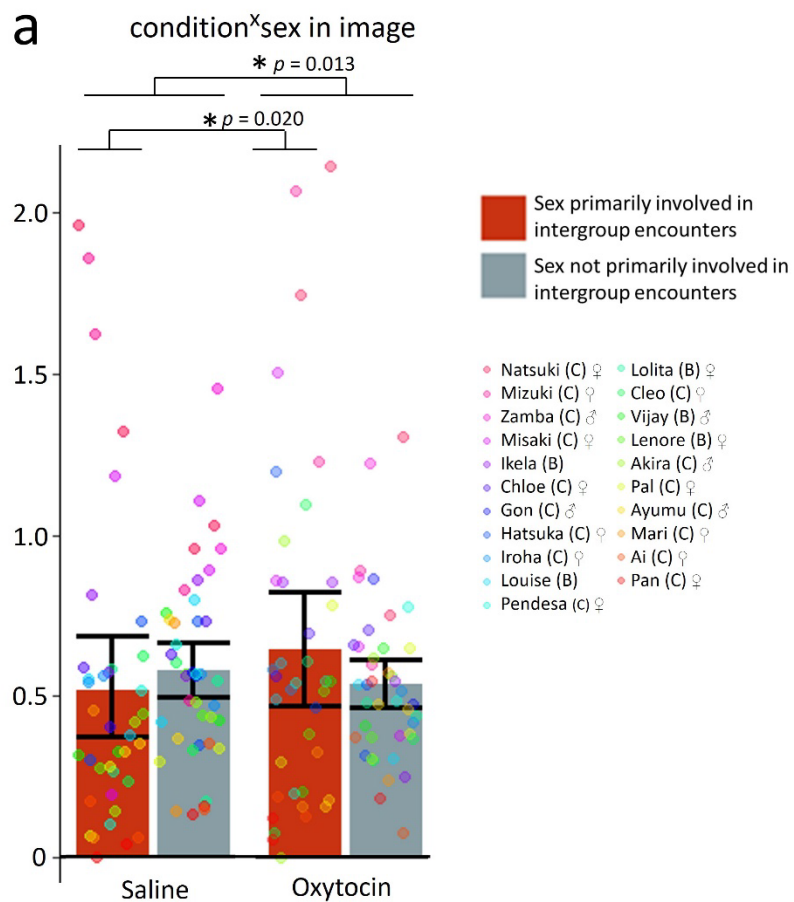
Term	Estimate	SE	$\chi^2$	$p$
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Intercept	0.27	0.10	-	-
Species * Condition * Sex in image	-0.0012	0.030	0.0016	0.97
Species * Sex in image	0.012	0.061	0.037	0.85
Species * Condition	-0.0032	0.032	0.010	0.92
Species	-0.08	0.10	0.60	0.45
Participant sex * Condition * Sex in image	-0.025	0.031	0.65	0.42
<b>Condition * Sex in photo</b>	<b>-0.066</b>	<b>0.030</b>	<b>4.79</b>	<b>0.038*</b>
Participant sex * Condition	0.0023	0.028	0.0064	0.94
Participant sex * Sex in image	0.094	0.068	1.91	0.18
Participant sex	-0.075	0.10	0.56	0.46
Day	-0.061	0.047	1.70	0.21
Image order	-0.045	0.047	0.90	0.36

409

410

411           In the model with average looking time to outgroup images per stimulus video as a  
412 response, there was a significant interaction effect between condition and sex primarily involved  
413 in intergroup encounters ( $p = 0.013$ ,  $\beta = 0.042$ ,  $SE = 0.017$ ,  $\chi^2 = 6.36$ ; Figure 4). This interaction  
414 effect was not significant in the model with looking time to ingroup images as a response ( $p = 0.67$ ,  
415  $\beta = -0.011$ ,  $SE = 0.026$ ,  $\chi^2 = 0.19$ ; Figure 4). We further investigated the former result by running  
416 follow up models for each sex category separately. In this analysis, we found a main effect of  
417 condition in looking time to the sex primarily involved in intergroup encounters ( $p = 0.020$ ,  $\beta =$   
418  $0.064$ ,  $SE = 0.026$ ,  $\chi^2 = 5.88$ ), where OT increased looking time to the outgroup images. We found  
419 no significant effect of condition in looking time to the sex which is not primarily involved in  
420 intergroup encounters ( $p = 0.23$ ,  $\beta = -0.021$ ,  $SE = 0.018$ ,  $\chi^2 = 1.45$ ; Figure 4).



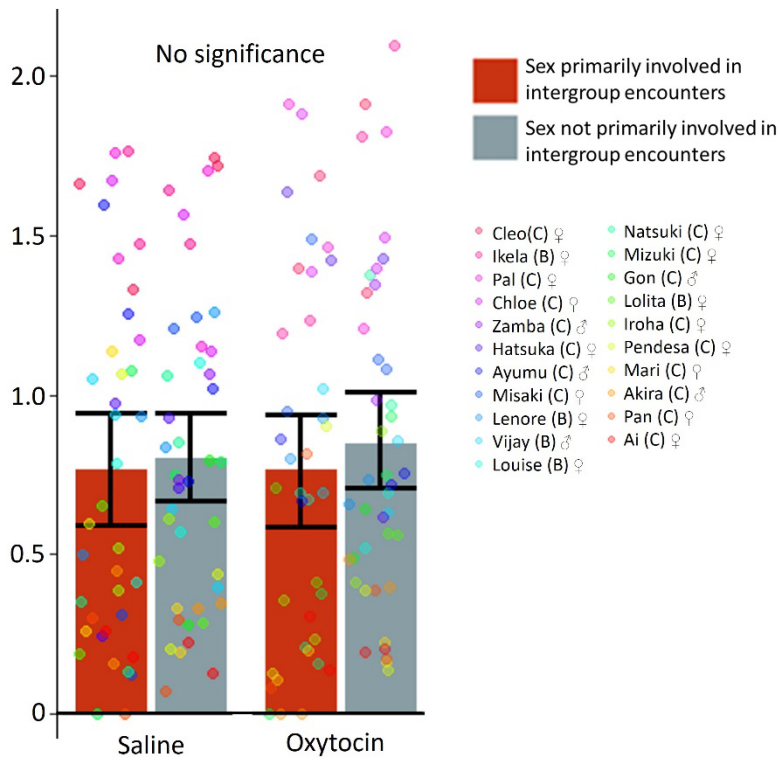


Figure 4. Mean looking time (seconds) as a function of condition and sex in image with 95% confidence intervals by group affiliation. a) Outgroup attention b) Ingroup attention. Sex primarily involved in intergroup encounters refers to male chimpanzees and female bonobos.

Table 4. Model results of attention to images by group (Sex in image represents sex primarily involved in intergroup encounters, referring to male chimpanzees and female bonobos). Full details of follow-up model can be found in supplementary material.

Response	Term	Estimate	SE	$\chi^2$	<i>p</i>
Attention to outgroup images	Intercept	0.58	0.066	-	-
	<b>Condition * Sex in image</b>	<b>0.042</b>	<b>0.017</b>	<b>6.36</b>	<b>0.013*</b>
	Participant sex	0.0023	0.063	0.0013	0.97
	Species	0.041	0.066	0.38	0.54
	Day	-0.0074	0.022	0.11	0.74
Attention to ingroup images	Intercept	0.8	0.1	-	-
	Condition * Sex in image	-0.011	0.026	0.19	0.67
	Condition	0.013	0.024	0.27	0.61
	Sex in image	-0.032	0.035	0.84	0.37
	Participant sex	-0.047	0.091	0.27	0.61
	Species	-0.045	0.1	0.2	0.66
	Day	-0.025	0.033	0.58	0.47

432 Discussion:

433           We found that OT selectively increased attention towards outgroup members of the sex  
434 primarily involved in intergroup encounters, namely, chimpanzee males and bonobos females.  
435 Thus, OT seemed to influence group-related attention in both species, while this effect was  
436 restricted to the images of a particular sex. We also found that attention was generally biased to  
437 ingroup members in both species, which is consistent with the previous study with a similar eye-  
438 tracking test design (Lewis et al., 2021) and studies in humans showing preferential attention  
439 towards ingroup members (Kelly et al., 2005; Moradi et al., 2020, 2018). While preferential looking  
440 paradigms cannot with certainty determine if the increased outgroup looking was due to higher  
441 vigilance to the outgroup or reduced interest in ingroup images, our follow-up analyses suggest  
442 that the effects were driven primarily by an increase in looking to the outgroup images and not a  
443 decrease in looking to the ingroup images. These results suggest a fundamentally common role of  
444 OT in increasing outgroup salience across species, but also suggest the existence of an additional  
445 factor, likely certain existing attentional biases and social motivations, that modified the  
446 expression of OT effect in species-relevant ways.

447           These findings support our first hypothesis, the general intergroup relations hypothesis,  
448 which predicted that OT plays a common role in supporting intergroup behaviors across species,  
449 but not the second hypothesis, the intergroup aggression hypothesis, which predicted that OT acts  
450 on competitive intergroup relations mainly in chimpanzees. More specifically, we found support  
451 for the outgroup vigilance sub-hypothesis of the general intergroup relations hypothesis, which  
452 predicted an increase in outgroup attention. Our results also supported our prediction that the sex  
453 in image mediates the effect of OT. In both bonobos and chimpanzees, attention was shifted from

ingroup images towards outgroup images more strongly for images of the sex primarily involved in intergroup encounters following OT administration. Of relevance to these results in the human literature, Egito et al. (2020) found that OT increased the salience of the racial outgroup in a threat recognition task and thereby eliminated the higher ingroup attentiveness compared to outgroup attentiveness found in the placebo condition. In this study, OT selectively increased the salience of the racial outgroup in a threat recognition task, yielding similar performance for ingroup and outgroup stimuli. Although this previous study measured response time and accuracy measures rather than eye movements, we similarly found in bonobos and chimpanzees that OT eliminated the increased baseline attention toward the ingroup (found in Lewis et al., 2021) by increasing attention toward outgroup images of the sex primarily involved in intergroup encounters. Similarly, oxytocin compared to placebo promotes attention to the eyes of outgroup members with dilating pupils (and a trend for greater attention to outgroup eyes with constricting pupils), while not significantly affecting attention to ingroup eyes in a study of trust and pupil mimicry (Kret and De Dreu, 2017; supplemental material). While we did not investigate the attention to the eyes and the previous study was not aimed at comparing group-based attention, a similar effect on outgroup attention may be responsible for these effects (and may be relate to the effects they report in the main text, which should be explored in the future). Overall, the results from bonobos, chimpanzees, and humans are generally consistent in that OT promoted outgroup salience in these species, although the effect was observed in species-relevant ways in that it was restricted to particular sexes in bonobos and chimpanzees.

There are at least two interpretations for the observed sex specificity of OT effect. First, female bonobos and male chimpanzees may be more important in the context of intergroup



encounters in these species, and thus OT may have acted on the outgroup salience of the sex more relevant to intergroup relations in each species. An alternative interpretation is that these species are more motivated to view or differentiate between ingroup and outgroup images of the sex with which they are generally more concerned (e.g. due to generally higher dominance as suggested by Lewis et al., 2021). Any effect on this existing attentional bias could therefore result in more detectable changes in viewing patterns for those sexes than the other. In either case, it is possible that the observed sex specificity in this study was driven in part by existing attentional or motivational bias interacting with the effect of OT, rather than the effect of OT *per se*.

There are several limitations that must be considered before further interpretation of results. First, while we did not find any effect of participant sex, it remains possible that with more males of each species differences would emerge. We could test only one male bonobo and only four male chimpanzees, and as noted in both species the sexes differ in their propensity to engage in intergroup encounters; thus, it remains unclear whether there is any effect of participant sex. Of particular note, two of the male chimpanzees lived in home groups with no other males, seriously limiting our ability to detect any changes OT may have in the gaze of males towards other male group members. It is worth noting that there were no significant effects based on participant sex in any models (in either interaction or main effects), including a model focused only on the chimpanzee data, though this could be due to the low sample size. Second, we had much fewer bonobos, which may have limited the detection of significant species differences. Thus, although we found similar results in terms of the effect of OT in outgroup salience, the degree of this effect might differ with a larger sample size. Third, our main results were observed only in the data with the image pairings where ingroup and outgroup faces presented matched gaze direction (see

supplementary material for the details about exclusion of the gaze unmatched data set). Finally, ape participants' attention to the stimuli was overall low, which could be a major reason for the observed overall small looking differences in the image pairings and the observed weak effects of OT in our results. In future studies, the use of dynamic instead of static images, and whole-body expressions instead of neutral faces might solve this issue, although it may add additional noise to the data. It may be interesting to compare attention to different kinds of social interaction, for example in comparing socio-positive and socio-negative interactions, as influenced by group affiliation. While these limitations pose challenges to the interpretation of our data, our results show that, at a minimum, OT affected attention to a particular outgroup sex (that primarily involved in the intergroup encounter) in bonobos and chimpanzees. In our dataset, this observed tendency did not seem to largely differ between species or sexes.

Our result is consistent with previous findings on the OT system in *Pan* for other social behaviours, where OT has generally conserved roles that act in species-relevant ways. For example, the effect of exogenous OT on eye contact in *Pan* was found to promote species-typical looking patterns enlarging known species differences (Brooks et al., 2021a) and field studies have found associations between urinary OT and social cohesion in species-typical behaviour, such as bonobo social bonding through GG-rubbing (Moscovice et al., 2019) and chimpanzee cooperation in group hunting (Samuni et al., 2018) and border patrols (Samuni et al., 2017). In these behaviours, like this study, the OT system may have common roles that are more consistent through evolution, such as in supporting social cohesion, attentional salience, and intergroup relations, but varied specific instantiations and outputs that support each species' own social tendencies.

Future work can explore this hypothesis in relation to neurophysiology of the two species, especially with regard to OT receptor distribution in the brain regions known to be affected by OT, which differ between bonobos and chimpanzees, and play a role in human vigilance and group-based behaviour, notably the insula (Grace et al., 2018; Rilling et al., 2012; Rogers-Carter et al., 2018; Staes et al., 2018; Wigton et al., 2015), ACC (Burkett et al., 2016; Grace et al., 2018; Issa et al., 2019; Rilling et al., 2012; Yamagishi et al., 2020), and amygdala (Cikara et al., 2017; Gamer et al., 2010; Lischke et al., 2012; Rilling et al., 2012; Staes et al., 2018; Stimpson et al., 2016; Vollberg and Cikara, 2018).

Our results are also generally consistent with previous literature on OT's role in outgroup behaviour in humans (de Dreu et al., 2012; Egito et al., 2020; Lischke et al., 2012). Although the aim of this study was not to test existing hypotheses for the effects of OT, such as the social salience, social approach, and general approach-avoidance hypotheses (Harari-Dahan and Bernstein, 2014; Kemp and Guastella, 2011; Shamay-Tsoory and Abu-Akel, 2016), our results do not contradict with these hypothesis. In our results, however, the increased salience (or propensity to approach) was restricted to outgroup images of the sex primarily involved in intergroup encounters; namely, OT did not consolidate the existing looking bias to the ingroup images in apes but acted more selectively on their responses to the particular outgroup sexes. Our results do not support a broad reduction in vigilance (such as suggested in Ebitz et al., 2013 and Ebitz and Platt, 2014), as attention to the outgroup sex relevant for intergroup encounters increased rather than decreased. Still, caution should be taken with regard to the specific interpretation of the changes in looking patterns due to limitations of preferential-looking designs.

In conclusion, our results show that OT modulates bonobo and chimpanzee group-based social attention, shifting attention towards outgroup individuals of the sex most engaged in intergroup encounters. Thus, OT may have a generally conserved role in supporting some hominid intergroup behavior despite their differing severity of outgroup encounters. However, the behavioural output might not be necessarily the same across the species, meaning that OT may act in species-relevant ways under the influence of existing attentional or motivational bias in each species, which may have been evolved under unique socio-ecological backgrounds of each species. The oxytocin system may therefore be crucial to our understanding of the evolution of intergroup relations and social divergence in both human and nonhuman apes.

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