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Do marmosets care to share? Oxytocin treatment reduces prosocial behavior toward strangers

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ABSTRACT

Cooperatively-breeding and socially-monogamous primates, like marmosets and humans, exhibit high levels of social tolerance and prosociality toward others. Oxytocin (OXT) generally facilitates prosocial behavior, but there is growing recognition that OXT modulation of prosocial behavior is shaped by the context of social interactions and by other motivational states such as arousal or anxiety. To determine whether prosociality varies based on social context, we evaluated whether marmoset donors (*Callithrix penicillata*) preferentially rewarded pairmates versus opposite-sex strangers in a prosocial food-sharing task. To examine potential links among OXT, stress systems, and prosociality, we evaluated whether pretrial cortisol levels in marmosets altered the impact of OXT on prosocial responses. Marmosets exhibited spontaneous prosociality toward others, but they did so preferentially toward strangers compared to their pairmates. When donor marmosets were treated with marmoset-specific Pro^8-OXT, they exhibited reduced prosociality toward strangers compared to marmosets treated with saline or consensus-mammalian Leu^8-OXT. When pretrial cortisol levels were lower, marmosets exhibited higher prosociality toward strangers. These findings demonstrate that while marmosets show spontaneous prosocial responses toward others, they do so preferentially toward opposite-sex strangers. Cooperative breeding may be associated with the expression of prosociality, but the existence of a pair-bond between marmoset partners appears to be neither necessary nor sufficient for the expression of spontaneous prosocial responses. Furthermore, high prosociality toward strangers is significantly reduced in marmosets treated with Pro^8-OXT, suggesting that OXT does not universally enhance prosociality, but, rather OXT modulation of prosocial behavior varies depending on social context.

Introduction

Altruistic or egalitarian sharing of resources is one of the foremost properties of human social relationships (Fehr and Fischbacher, 2003; Henrich et al., 2001). The notion that other species display prosocial behavior—response patterns and choices that imply an understanding and concern for the existence, benefit, and welfare for other individuals—is an alluring idea. Spontaneous prosocial behavior has been observed in children as young as 3 years of age and even younger if one includes helping behaviors (Fehr et al., 2008; Warneken et al., 2011; Warneken and Tomasello, 2007). While prosocial behavior appears to be ubiquitous among human cultures, the biological and social processes underlying this behavioral system and its occurrence across other primates are not fully characterized. Nonhuman primates have diverse social structures and cognitive abilities, therefore examining the presence and context of prosocial behavior across primate taxa will elucidate new insights for the origins, functions, and outcomes of prosocial behavior. Studies examining prosocial behavior across primates have found evidence both for and against the expression of spontaneous prosocial behavior in chimpanzees (*Pan troglodytes*) (Horner et al., 2011; Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008), Old-World monkeys (OWM) (Chang et al., 2011; Massen et al., 2010), and New-World monkeys (NWM) (Burkart et al., 2007; Cronin et al., 2009, 2010; Lakshminarayanan and Santos, 2008; Skerry et al., 2011; Stevens, 2010). The expression of spontaneous prosocial behaviors depends on a variety of contextual features such as the nature of the task and differences in cognitive, motivational, and social characteristics between partners (reviewed in Cronin, 2012).

In mammals, oxytocin [OXT] is an important neuropeptide that modulates many social processes. OXT facilitates the establishment and maintenance of social bonds between parents and their offspring (Feldman et al., 2007; Kendrick, 2000) and pair-bonds between mates (Feldman, 2012; Young and Wang, 2004). OXT is involved in the regulation of complex social behavior (Heinrichs et al., 2009; Insel, 2010), including increased cooperation and trust in humans (Baumgartner et al., 2008; De Dreu et al., 2010; Kosfeld et al., 2005). Chimpanzees with higher levels

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of urinary OXT both share food more often and groom more frequently than individuals with lower urinary OXT (Crockford et al., 2013; Wittig et al., 2014), and, importantly, these food-sharing and OXT effects were specific to dyads that shared an existing bond (Crockford et al., 2013). Furthermore, macaque monkeys that received inhaled OXT displayed increased social attention and made more prosocial choices (Chang et al., 2012). With regard to these general facilitative effects of OXT, there is also growing recognition that under certain social and environmental contexts OXT may reduce, instead of enhance, prosocial responses, and that these differential effects of OXT may vary across species (Bethlehem et al., 2014; De Dreu, 2012; Ebitz and Platt, 2013; van Anders et al., 2013). Arousal, anxiety, stress, and their physiological correlate, cortisol, are also known to interact with OXT to influence the quality of social behavior. Consequently, the effect of OXT on social behavior may act in concert with the hypothalamic–pituitary–adrenal (HPA) axis (Heinrichs et al., 2003; Parker et al., 2005; Qiao et al., 2014). This suggests that OXT and cortisol function as interacting neuroendocrine mechanisms that may underlie some of the divergent effects of OXT on prosocial behavior (Bethlehem et al., 2014).

Marmoset monkeys are an exemplary species for exploring the connections among prosocial behavior, social relationships, and neuroendocrine systems. Marmosets exhibit high social tolerance and cooperation, including monogamous pair-bonding, cooperative parenting, and food sharing (Rylands, 1993). Many of these patterns are sensitive to neuropeptide manipulations. For instance, OXT administration increases tolerance for food sharing between fathers and offspring (Saito and Nakamura, 2011), alters pair-bond affiliative behavior (Smith et al., 2010), and reduces sociosexual behavior with strangers in marmosets (Cavanaugh et al., 2014). Additionally, marmosets (*Callithrix* sp.) possess a modified nucleotide sequence in the OXT gene that yields a structurally-distinct peptide sequence for OXT (Pro^8-OXT), relative to the consensus mammalian Leu^8-OXT and other OXT variants recently found in NWMs (Lee et al., 2011; Ren et al., 2015; Vargas-Pinilla et al., 2015; Wallis, 2012). This Pro^8-OXT variant influences patterns of sociosexual behavior in marmosets (Cavanaugh et al., 2014). Overall, the marmoset represents an important and emerging primate model for elucidating links between OXT and prosocial behavior.

Burkart and colleagues (Burkart et al., 2007) have previously shown that marmosets exhibit spontaneous prosocial behavior toward kin and nonkin, but there was no systematic evaluation of whether prosociality differed when the recipient was a long-term pairmate or an unfamiliar opposite-sex partner. Since OXT affects sociosexual components of pair relationships in marmosets (Cavanaugh et al., 2014; Smith et al., 2010), we expected that OXT would also influence 'other-regarding' response tendencies to maintain pairbonds in marmosets. We therefore tested marmosets in a prosocial food sharing task with pairmates or strangers following exogenous administration of OXT ligands. In the *altruism condition*, a preferred food item was accessible only on the recipients' reward location when the donor pulled the tray (Fig. 1 and SI Video). We indexed prosocial responses in marmosets by determining whether marmosets preferentially pulled altruism trays over null trays [where no food item was present for either participant; *prosocial index* = *altruism*/(*altruism* + *null*)]. If marmosets display spontaneous prosocial behavior, then we expect to see increased prosocial responses in the presence of a recipient compared to when alone. If the existence of long-standing social relationships constitutes an important context for the expression of prosociality, then marmosets should display higher prosocial indices with pairmates relative to opposite-sex strangers. Furthermore, if OXT augments differential processing as a function of social familiarity, then we expect marmosets treated with Pro^8-OXT, but not Leu^8-OXT or an OXT-antagonist (OXTA), to show higher prosocial indices with pairmates but lower levels with strangers. Finally, because cortisol levels may modulate the effect of OXT on prosocial behavior, we evaluated whether prosocial responses of donor marmosets varied as a function of cortisol levels during testing.

Fig. 1. View of the testing apparatus. The testing apparatus was modified from an apparatus described and used in Burkart et al. (2007). The apparatus was placed in front of individual testing cages that were separated by a physical space large enough so the donor and the recipient could see each other but not engage in physical contact. The donor marmoset can pull the tray and the recipient marmoset cannot. The depicted marmosets are participating in an altruism trial where only the recipient receives the food item when the donor pulls the tray. To determine if altruism tray pulls truly reflected prosocial response tendencies, we compared altruism tray pulls with potential recipients present (pairmates or strangers) with altruism tray pulls when no recipient was present during testing.

Methods

Subjects

We tested black-tufted ear marmosets (*Callithrix penicillata*; three adult males and four adult females). Marmosets were housed as separate female–male pairs at the Callitrichid Research Center (CRC) at the University of Nebraska at Omaha (UNO). All males were previously vasectomized and females did not receive contraceptives. Colony rooms at the CRC were maintained at a temperature range of 19.0 to 22.0 °C and a 12-h:12-h light–dark cycle. All housing enclosures were wire-meshed cages (0.9 × 0.8 × 2.0 m) and equipped with branched, nest boxes, and other assorted enrichment items. All housing enclosures were furnished with barriers to prevent any visual contact between cages. Marmosets were fed Zupreem® marmoset diet between 0700 and 0900 h and given fruits and varied proteins between 1400 and 1600 h. Dietary and husbandry details at the CRC can be reviewed in Schaffner et al. (1995). The UNO/UNMC IACUC approved all procedures for this study (13-048-07), and all procedures adhere to the ethical standards and principles of the *American Society of Primatologists*.

Marmoset pairmates and strangers

Marmoset pairmates were characterized as unrelated female–male dyads that cohabitated for a minimum of 8 weeks prior to testing. This duration of cohabitation for marmosets is sufficient to elicit behavioral and social characteristics consistent with normative long-term pairbonds in marmosets (Agmo et al., 2012). One male was re-paired with another female for circumstances unrelated to experimental procedures and cohabitated for 8 weeks prior to testing; otherwise marmosets were housed with their pair-bonded partner for the duration of the project. Marmoset strangers were characterized as unfamiliar unrelated female–male testing dyads that had no visual interactions outside the testing procedures. Strangers were never pairmates in previous studies and were also participants in this study. The marmosets used in this study were not used in other concurrent or previous studies using OXT or disruption of housing conditions to prevent interference in the specificity of OXT treatments and behavioral characteristics of long-term social partners.

Apparatus and testing procedure

The apparatus consisted of two sliding trays (one above the other) where only the donor marmoset was in position to grasp and pull the trays to reward either themselves or their partner. The trays consisted of one side in which food was within reach of the donor only (*selfish*), and the adjacent side in which food was accessible only to the partner (*altruism*), or *null* trials with no food item present, but the donor was still able to pull the trays (Fig. S1). Two trays were used to ensure the donor made a decision to pull either the tray with a valued food item, the tray with no food item, or to not pull either of the two trays. Thus the marmosets could choose to pull a tray with a food item present, a null tray, or to not pull a tray. Marmosets were trained to reach criterion of 10 out of 12 correct trials (SI Methods). Once marmosets reached criterion performance on the task, testing was initiated. Each individual testing session occurred across three days with no more than 2 days in between individual testing days. Either their pairmate or a stranger was present on days 1 and 3, and on day 2 the donor marmoset was tested alone with the recipient's testing cage present. For any testing session, the recipient on day 1 and day 3 was always the same individual marmoset. On each testing day, the donor marmoset performed 12 individual testing trials consisting four of each tray conditions (Table S1). Each trial started after an experimenter showed the preferred food item to the marmoset in each of the four possible tray food areas, and then placed the food on the appropriate tray position. After the food item was placed, the experimenter simultaneously pushed both trays within reach of the donor. Donors were allowed to make only one choice per trial. If the tray with the food item was pulled it was scored as a correct tray pull, and trays pulled without the food item were scored as incorrect tray pulls. If 30 s elapsed without a successful tray pull, the trial was scored as a 'no pull.' For the null tray conditions (where both trays had no food items present), all tray pulls were scored. In both selfish and altruism trials, donor marmosets were given an option to pull a tray with and without a food item. The overall duration of an individual testing session with access to the trays ranged from ~4 to 10 min.

Each marmoset served as a donor under four treatment conditions (Leu^8-OXT, Pro^8-OXT, OXTA, and a saline control) and tested with their pairmate, strangers, and alone. Strangers were opposite-sex partners with whom they have no visual familiarity with outside of testing. All marmosets were tested in every OXT condition as a donor and recipient roles as both a pairmate and strangers. The order of OXT treatments were randomly counter-balanced in the study. All testing sessions were video recorded. Tray pulls were scored in real time by experimenters blind to treatment conditions. Marmosets were initially tested with their pairmates across all OXT conditions. After a ~2 month period, marmosets were retrained to criteria and then marmosets were tested with strangers across all OXT conditions. After another ~2 month period, marmosets were again retrained to criteria and were tested with counterbalanced pairmates and strangers across all OXT conditions to minimize over-administration of OXT treatments and prevent any order or learning effect for differences in tray pulling by partner affiliation (SI Methods). Marmosets had high familiarity with all experimenters prior to testing.

Oxytocin administration

Pro^8-OXT (synthesized by Anaspec, Fremont, CA) and Leu^8-OXT (Sigma-Aldrich: and also synthesized and provided by Dr. Maurice Manning, Medical College of Ohio, University of Toledo) were administered intranasally following procedures used in marmosets previously (Cavanaugh et al., 2014; Smith et al., 2010). Each animal received 50 μg (~25 IU) of OXT/100 μl saline solution ~30 min before the beginning of each testing session. This yielded a dose between 91 and 142 μg/kg depending on the weight of the individual marmosets across the duration of the experiment (~350–550 g). Intranasal administration of OXT in humans and macaques leads to increases in OXT concentrations in both plasma and CSF (Dal Monte et al., 2014; Striepens et al., 2013). The OXTA (L-368,899; provided by Dr. Peter Williams, Merck) is a non-peptide antagonist with high affinity for OXT receptors (Manning et al., 2012; Williams et al., 1994). The OXTA is readily absorbed after oral administration and survives passage through the gut, crosses the blood–brain barrier, and is present in both CSF and brain areas known to contain neurons with OXT receptors (Boccia et al., 2007). The OXTA was administered orally at a dose of ~20 mg/kg in a preferred food item ~90 min before testing. To control for handling effects associated with the intranasal administration, animals receiving OXTA were manually restrained and received 100 μl of intranasal saline ~30 min before testing.

Urine collection and cortisol assay

Aluminum trays were placed under individual testing cages following OXT administration and during testing sessions to collect urine samples. Marmosets were allowed to freely urinate on their tray. The urine samples were collected from the tray and were centrifuged and transferred into a clean microcentrifuge tube and stored at −20 °C until assayed using an enzyme immunoassay (EIA) previously developed and validated for marmoset urine (Smith and French, 1997). The urine samples were collected immediately following testing and resulted from urination just before or during testing. Thus, these samples characterize 'pretrial' cortisol levels because urine sampling reflects total circulating hormones levels since the last time the bladder was emptied. Testing occurred between 1030 and 1230 h. Inter-assay coefficients of variation (CV), determined from high (250 pg/well) and low (31.75 pg/well) concentration pool samples ran on each plate, were 10.3% and 18.8%, respectively. Intra-assay CVs for the high and low pools were 5.8% and 4.3%, respectively. Urinary cortisol concentrations in each sample were adjusted for variable fluid intake and output by correcting for urinary creatinine concentration (μg/mg creatinine) (French et al., 1996).

Statistical analyses

We measured the frequency (%) of correct altruism tray pulls by donor marmosets. In addition to reporting frequency of tray pulls, we controlled for the potential propensity for donor marmosets to pull trays regardless of the presence of a food item by creating an outcome variable that takes into account pulling of both altruism and null tray conditions ***'Prosocial index' = [altruism/(altruism + null)] * 100%***. Values closer to 100% reflect donor marmosets *preferentially* pulling trays in the altruism condition; values near 50% reflect marmosets pulling trays *randomly or showing no prosocial preference* regardless of tray condition; and the values below 50% reflect a decreased proportion of overall altruism tray pulling, or 'asocial'. Thus, values significantly greater than 50% reflect a preferentially altruistic prosocial index. We compared individually-grouped means of prosocial responses (% altruism tray pulls and prosocial index) across testing sessions for subjects tested with their pairmate, multiple strangers, and alone across OXT treatments. For the ANOVAs and *t*-tests (SPSS 22), we used only the five individual marmosets tested with both their pairmate and strangers since the measures were repeated-design (one female was substituted for another during the course of the experiment, see Marmoset Pairmates and Strangers). All paired-sample *t*-tests were two-tailed. The one-sample *t*-tests were compared to the prosocial index $\mu = 50\%$, which reflects no preference between altruism and null trays. For calculating effect size estimates, η^2 was used for ANOVAs. For the pairwise comparions between paired-samples or one-sample *t*-tests, Cohen's *d* effect size estimates were measured where *d* was calculated by the mean difference divided by the standard deviation of differences (in the case of one-sample tests,

the mean difference was between the group mean and the comparison value of a prosocial index of 50%) (Lakens, 2013).

To evaluate the effect of cortisol on the relationship between the prosocial index, social relatedness of the partner, and OXT, we employed multi-level modeling (MLM) (HLM 6.08). MLM functions similarly to traditional hierarchical regression, but one of the primary advantages of MLM is the ability to account for non-independent (repeated treatments and dyads) and missing data (whether marmosets provided urine samples during each of the testing sessions ($n = 146$) (Raudenbush and Bryk, 2002). This enables us to examine the effect of cortisol on tray pulling and the effect of OXT and social partner on tray pulling when controlling for differences in cortisol. We nested individual testing sessions ($n = 240$), within recipient social relatedness ($n = 19$), and within individual marmosets ($n = 7$) (Fig. S2). In addition to estimated coefficients (β and b), we calculated proportional reduction in prediction error (PRPE) for variables and tested between level model comparisons ($\Delta\chi^2$) (see SI Methods).

Results

Spontaneous prosocial responses in marmosets

Saline-treated marmoset donors displayed spontaneous prosocial responses toward others, but these responses varied as a function of social relatedness ($F(2,8) = 11.63$, $p = 0.004$, $\eta^2 = 0.74$). Specifically, marmosets pulled altruism trays more frequently in the presence of a stranger than in the presence of their pairmate (paired-samples t-test: $t(4) = 3.92$, $p = 0.02$, $d = 1.75$), and at higher rates than when tested with a stranger compared to alone (paired-samples t-test: $t(4) = 5.71$, $p = 0.01$, $d = 2.55$) (Fig. 2A). When donors were tested with their pairmate, donors did not pull the tray more frequently than they did when tested alone (paired-samples t-test: $t(4) = -1.55$, $p = 0.20$, $d = 0.69$). This finding demonstrates that marmosets show spontaneous prosocial behavior in the form of increased altruistic tray pulling, and this effect was strongest toward opposite-sex strangers.

Saline-treated marmoset donors also expressed a preferentially altruistic prosocial index toward strangers (one-sample t-test: $t(4) = 3.89$, $p = 0.02$, $d = 1.70$), but less of an altruistic preference for their pairmate (one-sample t-test: $t(4) = 2.03$, $p = 0.11$, $d = 0.91$), or when alone (one-sample t-test: $t(4) = 1.49$, $p = 0.21$, $d = 0.66$) (Fig. 2B). This finding suggests the highest altruistic tray pulling preference among donors was when tested with strangers. Marmosets expressed a higher level of prosocial index toward a stranger compared to alone (paired-samples t-test: $t(4) = 2.80$, $p = 0.05$, $d = 1.25$), but not a higher prosocial index toward their pairmate when compared to alone (paired-samples t-test: $t(4) = 1.73$, $p = 0.78$, $d = 0.77$); additionally, there was no significant difference in prosocial index comparing between strangers and pairmates (paired-samples t-test: $t(4) = 0.32$, $p = 0.16$, $d = 0.14$). In cases of null trials when no food item was present on either of the two trays, there were no significant differences based on the presence of a partner, though the effect was marginally significant ($F(2,8) = 3.59$, $p = 0.08$, $\eta^2 = 0.47$).

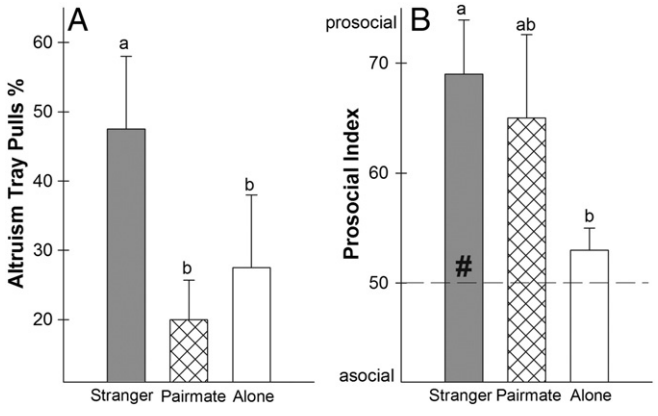

Fig. 2. Prosocial responses in saline-treated marmosets. (A) Altruism tray pulling % (group means + SEM) in donor marmosets treated with saline. (B) Prosocial index (group means + SEM) in donor marmosets treated with saline. Donor marmosets show higher altruism tray pulling when recipient is an opposite-sex stranger compared to their pairmate or when alone, indicating spontaneous prosocial behavior toward strangers. Different letters indicate $p < 0.05$; paired-samples t-test. $^{\#}p < 0.05$ for one-sample t-test compared to $\mu = 50\%$, which reflects no preferential altruism tray pulling in the prosocial index, indicated by a dashed line. ($n = 5$ individual donors).

Oxytocin treatments and prosocial responses in marmosets

Relative to saline-controls, OXT treatments modified these prosocial tendencies in marmosets, but only in cases when donors were tested with strangers. In marmosets treated with OXT, the frequency of altruism tray pulling in the presence of strangers was reduced by Pro^8-OXT (paired-samples t-test: $t(4) = 3.28$, $p = 0.03$, $d = 1.47$), but not Leu^8-OXT (paired-samples t-test: $t(4) = 0$, $p = 1.00$, $d = 0.00$), or OXTA (paired-samples t-test: $t(4) = 1.21$, $p = 0.28$, $d = 0.54$) when compared to marmosets treated with the saline control (Fig. 3A). While the effect of Pro^8-OXT resulted in a larger reduction of altruism tray pulling than Leu^8-OXT and OXTA compared to the saline-treated donors, Pro^8-OXT treatments resulted in only a marginal reduction compared to Leu^8-OXT (paired-samples t-test: $t(4) = 2.24$, $p = 0.08$,

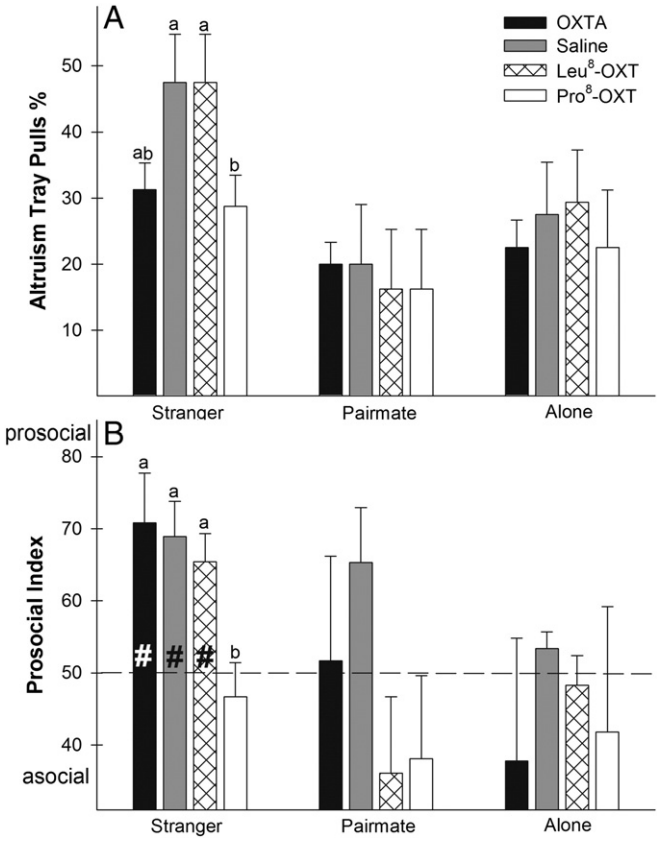

Fig. 3. Oxytocin treatment and social relatedness influence prosocial responses in marmosets. (A) Altruism tray pulls % (group means + SEM) for donor marmosets treated with saline, Leu^8-OXT, and Pro^8-OXT. Pro^8-OXT reduces altruism tray pulling for the stranger. (B) Prosocial index (group means + SEM) for donor marmosets treated with saline, Leu^8-OXT, and Pro^8-OXT. Marmosets treated with saline and Leu^8-OXT show preferential altruism tray pulling for strangers, and Pro^8-OXT reduces preferential tray pulling for strangers. Different letters indicate $p < 0.05$ for paired-samples t-test. $^{\#}p < 0.05$ for one-sample t-test compared to $\mu = 50\%$, which reflects no preferential altruism tray pulling in the prosocial index, indicated by a dashed line. ($n = 5$ individual donors).

$d = 1.00$) and showed no difference from OXTA (paired-samples t-test: $t(4) = 0.53$, $p = 0.35$, $d = 0.23$). When tested with their paimate, OXT treatment did not influence altruistic tray pulling compared to saline treated donors ($t(4)$s < 0.74, ps > 0.50, ds < 0.33).

Donors who received saline, Leu^8-OXT, and OXTA treatment showed a preferentially altruistic prosocial index toward strangers (one-sample t-tests: $t(4)$s > 3.03, ps < 0.04, ds > 1.35). Conversely, donors who received Pro^8-OXT treatments did not show a preferentially altruistic prosocial index toward strangers (one-sample t-test: $t(4) = -0.70$, $p = 0.52$, $d = 0.31$). The prosocial index toward pairmates was not significantly different from 50% for saline or any OXT treatment (one sample t-tests: $t(4)$s < 2.00, ps > 0.12, ds < 0.89). Compared to saline treatment, donor's prosocial index toward strangers was reduced when donors were treated with Pro^8-OXT (paired-samples t-test: $t(4) = 3.01$, $p = 0.04$, $d = 1.35$), but not Leu^8-OT (paired-samples t-test: $t(4) = 0.44$, $p = 0.69$, $d = 0.20$), or OXTA (paired-samples t-test: $t(4) = -0.17$, $p = 0.87$, $d = 0.08$) (Fig. 3B). Null tray pulling did not differ based on OXT treatment ($F(3,12) = 0.96$, $p = 0.45$, $\eta^2 = 0.29$), and there was no significant OXT by partner interaction $F(3,24) = 1.63$, $p = 0.18$, $\eta^2 = 0.19$). Taken together, these findings demonstrate that for both prosocial measures Pro^8-OXT treatment leads to the strongest reduction in prosocial responses toward opposite-sex strangers, while OXT treatments did not significantly alter prosocial responses toward pairmates. A summary of individual tray pulling data can be found in Table S2.

Cortisol and oxytocin interact to influence prosocial index in marmosets

MLM analyses revealed that pretrial cortisol levels modulated prosocial indices in donor marmosets. Donor marmosets with lower cortisol levels exhibited a preferentially altruistic prosocial index toward strangers compared to when no recipient was present ($\beta = -0.29$, $b = -0.45$, $t(16) = -2.39$, $p = 0.01$), or compared to when their pairmate was present ($\beta = -0.17$, $b = -0.47$, $t(16) = -2.04$, $p = 0.06$) (Fig. 4). Alternatively, donor marmosets with higher cortisol levels did not exhibit a preferentially altruistic prosocial index toward either their pairmate or stranger. These findings demonstrate that changes in cortisol levels differentially affect donor's prosocial index toward strangers and pairmates independent of OXT treatment. Specifically, marmosets with lower cortisol levels engaged in greater 'other-regarding' responses toward strangers. And while there is an increase in the prosocial index for donor's with higher cortisol (compared to lower cortisol) tested alone or with their pairmates, these donor's prosocial indices are at levels associated with non-prosocial preferences (i.e., not different from 50%).

Furthermore, OXT treatments and HPA activity interact to affect prosocial responses. When accounting for differences in cortisol levels of the donor marmoset, donors treated with OXT ligands (Pro^8 and Leu^8) show reduced prosocial responses compared to when treated with saline control ($\beta = -0.26$, $b = -8.71$, $t(16) = -3.60$, $p < 0.01$) (Fig. 5). Specifically, marmosets treated with saline and Leu^8-OXT exhibited their highest levels of prosociality toward strangers, whereas marmosets treated Pro^8-OXT exhibited lower levels of prosociality toward strangers compared to saline. When tested with their pairmates, however, marmosets show an overall reduced prosocial index, especially for Leu^8-OXT ($\beta = -0.16$, $b = -11.29$, $t(16) = -2.12$, $p = 0.05$). Overall, OXTA treatment did not affect marmoset prosociality compared to saline and agonists when accounting for cortisol ($\beta = -0.06$, $b = -1.48$, $t(16) = -0.75$, $p = 0.46$). Collectively, both cortisol and OXT modulate the expression of prosociality in marmosets, and, importantly, these differences are tied to the relationship with the recipient. What is more, the differences in prosociality toward recipients were greatest when cortisol levels were lowest in donor marmosets, suggesting that cortisol may modulate the effect of OXT on prosocial behavior toward others. A summary of MLM data is shown in Table S3.

Discussion

Marmosets show spontaneous prosocial responses toward partners in a food-sharing task, confirming previous observations that marmosets exhibit some degree of 'other-regarding preferences' (Burkart et al., 2007). Marmosets are considered socially monogamous and cooperative breeders, and, consequently, we anticipated higher prosocial responses toward pairmates when tested in our prosocial task, relative to levels of prosociality when tested with opposite-sex strangers. However, we surprisingly found the opposite pattern of responses. Marmosets expressed higher prosocial responses toward strangers, especially when levels of cortisol in donor marmosets were lower. Neuropeptide treatment modified this prosociality toward strangers, but in a social- and ligand-specific fashion. That is, Pro^8-OXT (and to a lesser degree OXTA), but not Leu^8-OXT, reduced prosociality toward strangers. OXT treatment did

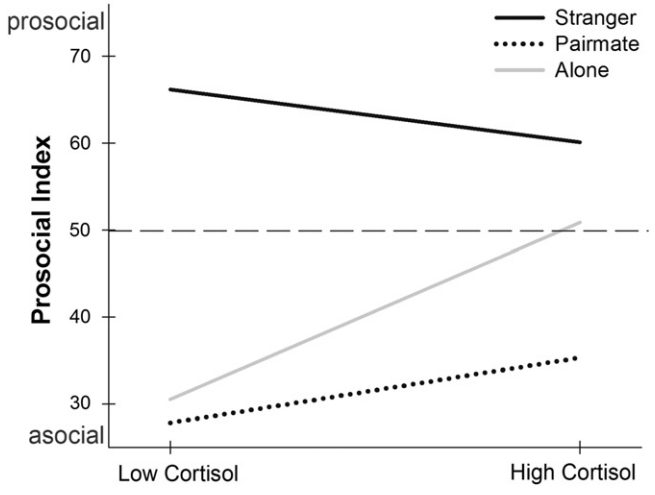

Fig. 4. Modulation of prosocial index by cortisol. (A) Modeled/adjusted means of prosocial index for donor marmosets exhibiting high and low quartiles of excreted cortisol during individual testing sessions, controlling for differences across OXT treatment. Differences based on relationship with the partner are greatest when cortisol is lowest. Specifically, donor marmosets with lower cortisol show their highest prosocial index toward strangers, while donor marmosets with higher cortisol show no preferentially altruistic prosocial index based on the presence of their partner ($n = 146$ cortisol samples; $n = 7$ individual donors). Dashed line indicates $\mu = 50\%$, which reflects random or non-preferential tray pulling in the prosocial index.

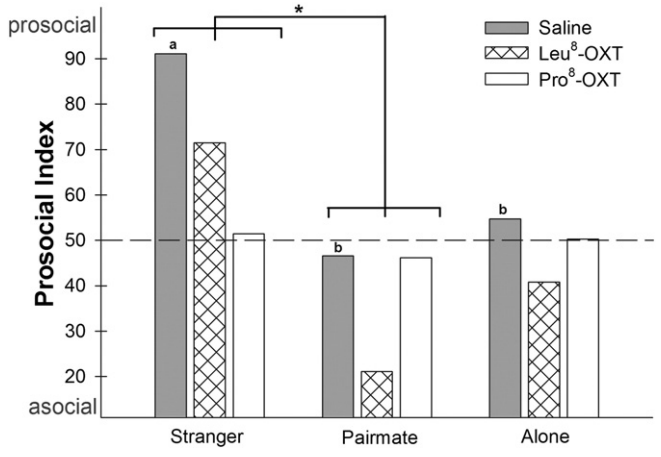

Fig. 5. Modulation of prosocial index by oxytocin controlling for cortisol. Modeled/adjusted means of prosocial index during testing with strangers, pairmates, and alone following treatments of OXT ligands and saline. Data account and control for variation in excreted cortisol levels. Saline treated marmosets showed a higher prosocial index, especially toward strangers and differential effects of OXT ligands on prosocial index toward pairmates and strangers. ($n = 240$ testing sessions; $n = 7$ individual donors). Dashed line indicates $\mu = 50\%$, which reflects random non-preferential altruism tray pulling in the prosocial index. Different letters of asterisk indicate significant differences $p < 0.05$.

not alter prosocial responses toward pairmates. These findings support the view that OXT modulation of prosociality varies depending on the flexible nature of social relationships.

Among the highly varied primate social systems, cooperative breeding (e.g., in marmoset and human families) has been proposed as a specific strategy that sets the stage for increased prosociality (Burkart et al., 2009). In both wild and free-ranging captive settings, adult male and female callitrichine primates (marmosets and tamarins) share food with others extensively, most often by adults to infants, but sharing (and tolerated stealing) also occurs among adults members of the social group (Feistner and McGrew, 1989). In controlled trials of 'altruistic' sharing, Burkart and colleagues demonstrated that prosocial sharing occurs among both related family group members and unrelated opposite-sex partners (Burkart et al., 2007). However, there was no explicit comparison between altruistic tray pulling for pairmates versus strangers, which may be a key distinction in evaluating the motivational origins of 'other-regarding preferences', especially in cooperatively-breeding primates. Tamarins (*Saguinus*), a closely-related cooperative-breeding NWM, do not show spontaneous prosocial behavior in food sharing tasks toward either their long-term pairmates or strangers (Cronin et al., 2009; Stevens, 2010; but see Cronin et al., 2010). And, conversely, both macaques and chimpanzees, two non-cooperative breeding species, do show evidence of spontaneous prosocial behavior (Horner et al., 2011; Massen et al., 2010). Comparing prosociality across studies is limited due to important and nuanced differences in methodology. However, in a recent study of standardized prosociality experiments across a wide range of primate species (including humans), the extent of allomaternal care provided the strongest explanation for the distribution of proactive prosocial behavior across primate species (Burkart et al., 2014). So while cooperative breeding may be associated with the expression of prosociality, the established relationships upon which this social system is predicated, e.g., male–female pair-bonds, appear to be neither necessary nor sufficient for the expression of spontaneous prosocial behavior toward close social partners in nonhuman primates.

Social monogamy and the associated social bias toward familiar partners can arise from multiple social and behavioral mechanisms, and studies with prairie voles have particularly highlighted the importance of partner preference in the maintenance of social bonds, along with intolerance/avoidance of opposite-sex strangers (Resendez and Aragona, 2013). Within marmoset social groups, pairmates likewise exhibit high rates of social interactions, including huddling, close proximity, grooming, temporal coordination of activities, and especially relevant for the present study, high rates of food sharing (Agmo et al., 2012; Schaffner et al., 1995). Cooperatively-breeding callitrichine primates also exhibit higher social tolerance for, and opportunistic behavioral strategies with, opposite-sex strangers, especially in the absence of their pairmate. For instance, both adult male and female wild marmosets engage in extra-group sociosexual behavior during the course of intergroup encounters (Digby, 1999; Lazaro-Perea, 2001; Nievergelt et al., 2000); and socially-bonded adult tamarins and marmosets participate in high rates of opportunistic social and sexual interactions with opposite-sex strangers when the established partner is absent, and social indifference or aggression toward the opposite-sex stranger when the partner is present (Inglett et al., 1990; Ross and French, 2011). In this fashion, the nature of social monogamy in callitrichine primates may more closely resemble the opportunistic strategies associated with partner fidelity in both female (Gangestad et al., 2010) and male (Buss, 2013) humans, and less like the nature of pair relationships in prairie voles, which are characterized by high social selectivity for partners (Rodriguez et al., 2013). Accordingly, the fundamental social processes underlying the behavioral regulation of monogamy (such as prosociality), may be differentially modified by neuroendocrine systems in socially or species-specific way.

The patterns of prosocial behavior in marmosets treated with OXT appear to deviate from the general facilitative effect of OXT on prosociality. This is an important consideration, as there is a growing recognition that OXT does not have a unidirectional valence in modulating social behavior; i.e., enhanced universal prosociality (van Anders et al., 2013). Rather, the effect of OXT on modulating social behavior appears to be shaped by the nature of the social context during social interactions, and OXT is likely involved in general processing of social stimuli (Bartz et al., 2011; Bethlehem et al., 2014; De Dreu, 2012). Furthermore, others have argued that prosociality is not always an adaptive response. OXT mediates social processing and social vigilance, and in some instances an asocial response may be appropriate (Ebitz and Platt, 2013). We have previously demonstrated ligand- and context-specificity associated with OXT treatments in the sociosexual components of pair relationships in marmosets that are consistent with the present findings. Specifically, treatment of marmosets with Pro^8-OXT, but not Leu^8-OXT, resulted in reduced rates of sociosexual behavior with an opposite-sex stranger in both males and females, and reduced time spent with the stranger in females (Cavanaugh et al., 2014). Together, these data suggest that Pro^8-OXT treatment modifies social behavior in marmosets by potentially reducing interest in opposite-sex strangers in multiple realms, including food sharing and sociosexual behavior. The reduced prosociality toward strangers in marmosets treated with Pro^8-OXT may reflect a distinctive component of social behavior in marmosets. That is, OXT may play a role in socially-monogamous relationships in marmosets by reducing prosociality toward opposite-sex strangers.

There is growing evidence that HPA activity and OXT signaling represent interacting neuroendocrine systems that modulate prosocial behavior toward others. OXT and anxiety facilitate human social approach behavior (Preckel et al., 2014; Radke et al., 2013) and alter perception of social stress (Domes et al., 2007; Eckstein et al., 2014). In voles, glucocorticoid treatment inhibits social-bond formation, but only for voles who had already established social bonds (DeVries et al., 1995). Likewise, voles with lower sociability exhibit increased anxiety and HPA activity during social preference tests and display fewer OXT neurons in the paraventricular nucleus of the hypothalamus (Qiao et al., 2014). Marmosets also show higher cortisol responses with increased social instability (Smith et al., 2011), and the presence of a pairmate can buffer marmoset stress-responses during isolation (Rukstalis and French, 2005; Smith et al., 1998). In cases where social interactions or social reward are perceived as aversive or anxiety-provoking, individuals will be less likely to behave prosocially (Bethlehem et al., 2014), and this effect is modulated by OXT (Eckstein et al., 2014). Furthermore, capuchin monkeys treated with OXT during a food-sharing task show increased social distance from their partner, suggesting that OXT may modulate food-sharing or other cooperative behavior by modulating social interest or anxiety (Brosnan et al., 2015). Thus, the overall high prosociality in marmosets toward strangers may be a reflection of strangers' social attractiveness or interest, and the reduction in prosociality toward strangers following OXT treatment may result from modifying the perceived intensity of arousal, aversion, or indifference toward unfamiliar social stimuli.

While this study elucidates interesting social contexts for which OXT and cortisol modify prosocial behavior, there are some limitations that merit future investigation. First, it is important to incorporate additional measures and features of sociality, which will help identify important stimulus and motivational states that regulate social decision making. Moreover, the current uncertainty between circulating central and/or peripheral concentrations and activation of OXT following OXT treatments may be a limitation of this study. OXT may also exert different peripheral effects on nonsocial factors such as metabolic and appetite regulation (Blevins et al., 2014). It is also known that the duration of OXT treatment may account for the differential effects on social behavior (Huang et al., 2014). Specifically, differences in social preferences were found between relatively acute and chronic OXTA administration in marmosets (Cavanaugh et al., 2014; Smith et al., 2010). Finally, there are likely differences in dosing effects of OXT (Peters et al., 2014), where

Leu^8-OXT may serve as a small, but still biologically-relevant, dose of OXT compared to Pro^8-OXT. Notwithstanding these potential limitations, and the small sample size of individual marmosets, the prosocial behavior following OXT treatments appears to be socially-specific, suggesting that cues from the social partner may be influencing prosocial behavior within the marmoset dyads, which is an important consideration given the varying context- and socially-specific findings from other OXT studies in primates (Brosnan et al., 2015; Cavanaugh et al., 2014; Chang et al., 2012; Smith et al., 2010; Wittig et al., 2014).

Conclusions

To most convincingly illuminate both the adaptive function and core neural mechanisms that underlie prosocial behavior, it is important to study the effects of OXT across many diverse environments and across a wide range of organisms. For instance, marmosets and macaques, primates with distinct species-typical social behavior, both express spontaneous prosocial behavior; but OXT differentially regulates prosocial behavior in a species-specific way. Marmosets treated with OXT show decreased food-sharing with strangers (this study), while macaques treated with OXT show increased food-sharing with strangers (Chang et al., 2012). These differences in how OXT modifies prosocial behavior may reflect differences in social or motivational contexts. Therefore, while there may be shared neuroendocrine mechanisms shaping prosocial behavior across primate species, it remains imperative to consider the exceptionally diverse species-typical functions of behavior when evaluating the sway and significance of neuroendocrine mechanisms underlying complex social behaviors.

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