Oxytocin reduces food sharing in capuchin monkeys by modulating social distance

Sarah F. Brosnan [a,b,c,*], **Catherine F. Talbot** [a,b], **Jennifer L. Essler** [a],
Kelly Leverett [a], **Timothy Flemming** [a,b], **Patrick Dougall** [a],
Carla Heyler [a] **and Paul J. Zak** [d]

[a] Language Research Center, Georgia State University, Atlanta, GA 30034, USA
[b] Department of Psychology, Georgia State University,
P.O. Box 5010, Atlanta, GA 30302, USA
[c] Neuroscience Institute and Department of Philosophy,
Georgia State University, Atlanta, GA 30302, USA
[d] The Center for Neuroeconomic Studies, Claremont Graduate University,
Claremont, CA 91711, USA
[*] Corresponding author's e-mail address: sarah.brosnan@gmail.com

Abstract

Recent evidence indicates that oxytocin plays an important role in promoting prosocial behaviour amongst humans and other species. We tested whether oxytocin affected cooperation and food-sharing in capuchin monkeys, a highly cooperative New World primate. Subjects received either 2IU oxytocin or an inert adjuvent intranasally prior to each session. Oxytocin influenced food sharing in capuchins in ways we did not anticipate. Recipients were less likely to passively acquire food from possessors when either individual had received OT than in the control, and also spent less time in proximity to their partner. Passive food sharing requires proximity, and oxytocin decreased the capuchins' typical congregating behaviour, apparently resulting in decreased sharing. We propose that the likely mechanism for increased social distance is the known anxiolytic effect of oxytocin. Our results indicate a need to consider how oxytocin affects the context of interactions and interacts with modes of sociality unique to each species.

Keywords

oxytocin, anxiolytic, prosocial, social distance, food sharing, cooperation, capuchin monkey, *Cebus apella*, *Sapajus apella*.

1. Introduction

Oxytocin (OT), and hormones that interact with OT, are important in the regulation of mammalian social behaviours, including maternal care, pair bonding and other aspects of sociality (Gimpl & Fahrenholz, 2001; Carter & Keverne, 2002; Young & Wang, 2004; Kosfeld et al., 2005; Lim & Young, 2006; Carter et al., 2008; Morhenn et al., 2008; Ross et al., 2009; Wittig et al., 2013). Recent evidence indicates that human brains have evolved to utilize OT to affect social behaviours in addition to maternal and mate relationships. Prominent among these is the role of OT in eliciting prosocial interactions with strangers, including trust (Kosfeld et al., 2005) and trustworthiness (Zak et al., 2005), generosity (Zak et al., 2007), sacrifice (Morhenn et al., 2008), gratitude (Barraza et al., 2013) and donations to distal others through charities (Barazza et al., 2011). In humans, OT appears to motivate behaviours typically called moral (Zak, 2011, 2012). It does this, in part, by down-regulating stress responses associated with interacting with others (Insel, 1997; Kirsch et al., 2005; Baumgartner et al., 2008) and enhancing the experience of empathy (Barazza & Zak, 2009; Bartz et al., 2010a), the latter potentially being important in other species, including capuchin monkeys (de Waal et al., 2008). OT infusion in humans does not inhibit cognitive abilities (Kosfeld et al., 2005; Zak et al., 2007), and recent findings show that OT does not erase created in-group biases (De Dreu et al., 2010, 2012; van Anders et al., 2013). Similarly, changes in endogenous OT do not remove in-group biases when those biases are made salient via ritual (Terris et al., 2013). An emerging perspective from studies in humans is that OT increases attention to social cues that can be pro- or anti-social (Barazza & Zak, 2013). Investigating the evolutionary basis for the effect of oxytocin in capuchins is an important step to understanding the nuanced effects of OT on social behaviours.

Capuchin monkeys are an excellent species for which to study the effects of OT on social behaviour. Like humans, capuchins exhibit strong social bonds with both kin and non-kin. Females are philopatric, leading to very strong relationships between them, and male capuchins remain part of their adult social group for a large portion of their lifespan (Fragaszy et al., 2004). Additionally, capuchins are highly cooperative (Brosnan, 2010) and are one of the few non-human primates to show consistent experimental evidence of prosocial behaviour (defined in these studies as food sharing; de Waal et al., 2008; Lakshminarayanan & Santos, 2008; Brosnan et al., 2010; Jaeggi et al.,

2010). Thus, we anticipate that capuchin monkeys have evolved neurochemical signalling mechanisms to form and maintain social bonds. Tellingly, for the hypotheses tested here, these primates also engage in allomaternal care (Fragaszy et al., 2004).

In the field, capuchins participate in extensive coalitions and alliances and engage in food sharing (Perry & Rose, 1994). Coalitions are also important for group hunting and defence (Perry et al., 2003). In laboratory settings, capuchins easily work together to jointly obtain resources (Mendres & de Waal, 2000; but see Visalberghi et al., 2000) and show evidence of understanding the contingencies of these interactions. Capuchin monkeys are more successful cooperators when they can see their social partner, implying some degree of visual coordination (Mendres & de Waal, 2000) and are more likely to attempt to obtain the food when the social partner, whose help is required, is present rather than absent (Mendres & de Waal, 2000). Additionally, capuchins are sensitive to their partner's behaviour. In experimental tests in which one monkey, who receives no food, has to help another one obtain food, monkeys were more likely to help if their partner had shared the food on previous trials (de Waal & Berger, 2000; see also Brosnan et al., 2006). Partner sensitivity is apparently not something that requires learning within a new cooperative context; monkeys who could cooperate to get food that was either clumped (and therefore monopolisable) or dispersed were more likely to cooperate in the dispersed condition from the very first trial (de Waal & Davis, 2002).

Capuchins are also among the few primates to routinely share food with other adults (Feistner & McGrew, 1989; Jaeggi & van Schaik, 2011), including active food sharing (de Waal, 1997), behaviour that has been classified as prosocial for its benefit to other individuals. In experimental situations, capuchin monkeys choose options that bring food to their social partners (de Waal et al., 2008), even when their partner will receive more food (Lakshminarayanan & Santos, 2008), although this behaviour ceases when the discrepancy becomes too high (Brosnan et al., 2010). As expected, monkeys bring more food to kin and members of their social group than to strangers (de Waal et al., 2008). This behaviour is particularly notable as in experimental tests, capuchins are more consistently prosocial (e.g., more often provide food to others) in these sorts of tasks than are other nonhuman primates, including chimpanzees (Silk et al., 2005; Jensen et al., 2006; Jaeggi et al., 2010; but see Horner et al., 2011).

While emerging evidence indicates that both empathy (de Waal, 2008; de Waal et al., 2008) and moral behaviour (Flack & de Waal, 2000; Brosnan, 2011) are shared across many species, it is unknown whether the broadly prosocial effects of OT are unique to humans, as there are very few studies on how OT impacts non-human primates. While in many cases the mechanisms between humans and other species look similar, with OT decreasing anxious behaviours (Parker et al., 2005) and increasing prosocial behaviours (Smith et al., 2010; Chang et al., 2012) and willingness to food share (although this was not statistically significant; Saito & Nakamura, 2011), in some cases the effects seem to be reversed. A study of OT infusion in rhesus macaques showed a baseline preference to reward others, but an enhanced bias to reward themselves over a partner following OT treatment (Chang et al., 2012). This suggests that the effects of OT are dependent on the social context, possibly in species-specific ways. Moreover, data on OT's effect on food sharing in New World monkeys thus far come from callithrichids (Smith et al., 2010), which are often considered more prosocial than are other species (Burkart et al., 2007; Cronin et al., 2009, 2010; but see Stevens, 2010), presumably due to their cooperative breeding social structure (Jaeggi et al., 2010).

The differences across species are important; there is significant variation in the locations and densities of OT receptors across mammals. Species that are social, and especially those that pair-bond, have a greater number of OT receptors in the forebrain that modulate dopaminergic reward regions in the brain (Donaldson & Young, 2008; Ross et al., 2009). In addition, animals that are abused or neglected during early development have fewer OT receptors in the forebrain and tend to be socially withdrawn, anxious and neophobic (Meaney, 2001). For example, nursery-reared rhesus monkeys have lower levels of OT in cerebral spinal fluid and impaired social behaviours compared to those that are maternally reared (Winslow et al., 2003). The present study explored the effect of exogenous OT infusion in capuchin monkeys, a New World species notable for both cooperation (de Waal & Berger, 2000; Mendres & de Waal, 2000; de Waal & Davis, 2002; Brosnan et al., 2006; Brosnan, 2010) and prosocial behaviours with non-kin, non-mate individuals (de Waal et al., 2008; Lakshminarayanan & Santos, 2008; Brosnan et al., 2010). Capuchin social structure suggests they may have a sufficient density of OT receptors in the forebrain that they could be pharmacologically manipulated in ways that influence social behaviours. As a result, we hypothesized that exogenous OT infusion would increase food sharing by capuchins.

To test this hypothesis, we tested mother-reared, group housed capuchin monkeys from the same social group, utilizing a cooperative bar-pull task in which individuals worked together to achieve rewards for one or both members of a dyad. This allowed us to simultaneously investigate both cooperative and prosocial behaviour in the same paradigm (see Methods for details; based on de Waal & Berger, 2000). There were three barpull conditions; subjects either worked together to each receive the same reward (Mutual) or for one to receive a reward while the other did not (Prosocial; called Coop in de Waal & Berger, 2000), or the subject pulled in the tray by itself to receive a reward (Solo). In each case, subjects received a nasal spray consisting of either 2IU OT or the same volume of a placebo saline spray (Control) in a balanced design such that each pair participated in one test of each barpull condition in which both received OT, only the subject or only the partner had received OT, or neither received OT (although every monkey participating always received a nasal spray). To avoid interactions with stress (Parker et al., 2005) or glucose (Ho & Blevins, 2013), subjects had been trained to receive the spray while unrestrained (see Methods for details). Conditions were counterbalanced within each pair.

2. Methods

Subjects came from two groups of mother-reared capuchin monkeys socially living in multi-male, multi-female social groups in a large indoor-outdoor facility at the Language Research Center of Georgia State University. Subjects were always with their social group except during testing and were provided daily with multiple types of enrichment. Monkeys were tested in chambers that were permanently affixed to the indoor section of their home enclosure. Subjects were given the opportunity to voluntarily enter these chambers and participate in behavioural and cognitive testing on a daily basis (Evans et al., 2008). Subjects could choose whether or not to participate and were never food or water deprived at any time except for veterinary reasons. Running water was available ad libitum at all times, including in the testing chambers. Food, including primate chow and fresh fruits and vegetables, was provided multiple times per day independently of food rewards obtained during cognitive and behavioural testing.

We tested eight adult monkeys in every pair possible with three constraints (see Table 1). First, they were only tested with other individuals from their

Table 1.
Monkeys taking part in the study.

| Subject 1	Sex	Age (start of testing)	Group	Subject 2 (in order of testing)
Gabe	Male	11	1	Logan, Nala
Logan	Male	4	1	Gabe, Liam
Liam	Male	6	1	Logan
Nala	Female	7	1	Gabe
Griffin	Male	12	2	Drella, Lily
Drella	Male	19	2	Griffin, Wren
Lily	Female	12	2	Griffin
Wren	Female	7	2	Drella

social group (Group 1: 3 males, ages 4, 6, and 13 years, 1 female, age 7 years; Group 2: 2 males, ages 12 and 9 years, 2 females, ages 7 and 12 years), and second, they were only tested with individuals with whom they would voluntarily separate (see below). With these constraints, we tested six pairs (3MM, 3FF; some monkeys were used in two pairs; no monkey was ever used in three pairs). Monkeys who were used in two pairs completed all testing with their first partner before completing any sessions with their second partner. During testing, monkeys were separated from the other monkey in the testing chamber by a Lexan partition with five evenly spaced 5.5 cm diameter holes (three in one row, two in the second row) to allow for food sharing. The test chamber was sufficiently wide (152.4 cm) that subjects could withdraw beyond their partner's reach. Food was acquired at the side of the enclosure, beyond their partner's reach, so sharing, even passive sharing, required active transport of food to the middle partition.

Subjects were initially trained to receive an intranasal spray without any need for restraint and without a food reward. This was essential for two reasons. First, oxytocin is known to interact with stress, and the stress of restraint would thus confound results (Song et al., 1988). Second, oxytocin interacts with glucose (Ho & Blevins, 2013), which is present in many food rewards, and food rewards, even if sugar free, would potentially confound sharing results, thus it was essential that all subjects receive the nasal spray voluntarily, without the need for either restraint or reward. Training was done using positive reinforcement techniques in which subjects were initially given food rewards (sugar free juice) for allowing us to place the sprayer against their nares and, subsequently, for allowing us to spray saline. Once

training was complete the subjects were transitioned to accepting the spray without reinforcement, although on a regular basis subjects were, outside of testing times, brought in for a saline spray and given a food reward. This intermittent reinforcement allowed us to maintain their willingness to accept the spray.

All subjects received an intranasal spray of either 2IU OT or the placebo control (an identical volume of sterile saline) 30 min prior to every session, to allow the OT to transit from the sinuses to the brain (we based this on estimates of how long it takes for intranasal OT to cause behavioural effects in humans; Born et al., 2002). As there are no studies on capuchin monkeys, the OT dose was based on a dose of 0.5 IU/kg used for humans (Zak et al., 2007). Each test session consisted of six 5-min trials. Due to repeated testing, basal or post-infusion OT in blood was not obtained. Rapid changes in endogenous OT make it a poor measure for repeated interactions. Rather, we relied on the fact that pairs were randomly assigned to the treatment or control condition to infer the effects of OT on food sharing. Recent findings have shown that intranasal OT infusion reaches cerebral spinal fluid in macaques (Chang et al., 2012) and humans (Striepens et al., 2013).

Subjects had to pull in a counterweighted tray in order to receive a food reward. This was based on previous work indicating that capuchins will work together in such a context (de Waal & Berger, 2000). The tray consisted of a 76.2×15.2 cm platform with food cups mounted on either side, with their centres 27 cm from midline and 20 cm from the front of the test chamber when the tray was pulled in (see Figure 1). Monkeys could not reach their partner's food in any location. The tray could be pulled in jointly if both monkeys pulled simultaneously on two 76 cm long cords, one on each side of the tray. Following de Waal and Berger, there were three conditions; our experimental condition, in which both individuals were required to pull in the tray but only the subject got a reward (Prosocial), and two controls. In the first, both subjects were required to pull in the tray, but both got an identical reward (Mutual) and in the second, only the subject had access to pull in the tray for his or her reward (Solo). Each subject participated in one session of each barpull condition (Prosocial, Mutual, Solo) for each possible OT/saline combination (e.g. both got OT, both got saline, subject got OT/partner got saline, subject got saline/partner got OT) for a total of twelve sessions (3 barpull conditions $\times$ 4 OT conditions) per subject. Each of the 12 sessions consisted of six trials.
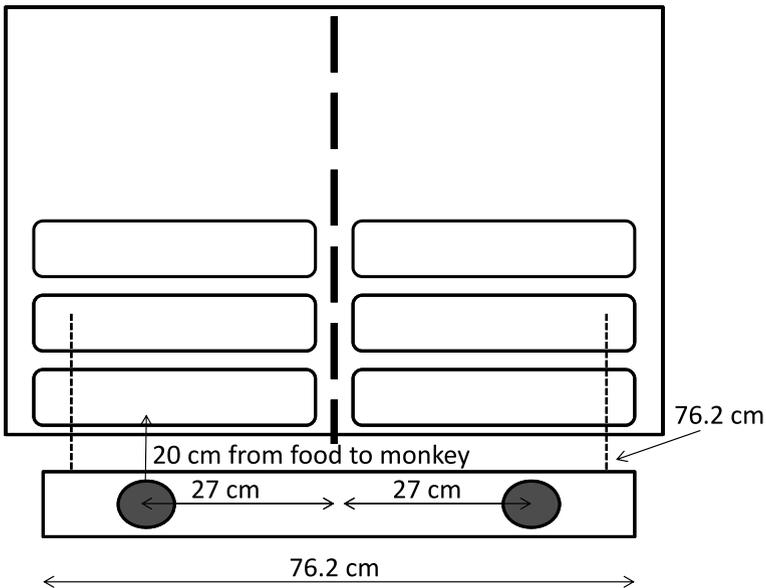
Figure 1. Diagram of the barpull apparatus. Monkeys were paired side by side, separated by a mesh partition (indicated by heavy dashed line). The tray could be pulled in by the two 76-cm pulls (indicated by light dashed line); the partner's pull was removed for the Solo condition. The centre of the food cups was 20 cm from the openings in the front of the testing chamber when the tray was fully pulled in.

All sessions were videotaped and coded by observers who did not participate in the study and were blind to the hypotheses. Each trial was coded as successful (tray pulled in) or not. Food sharing events were coded as active (possessor provided food to the receiver) or passive (receiver reached over and acquired food themselves). We also coded the location of the subject and partner in the test chamber, measuring the time spent either in proximity (within arm's reach of the middle partition) or not (beyond arms' reach). Finally, we coded the number of self-scratches by each individual in each session. Twenty-one percent of the sessions were coded by a second observer to calculate interobserver reliability. Reliability was high for whether the tray was pulled in (Cohen's $\kappa = 0.91$), for the number of sharing events (Spearman's rho correlating sharing by session: $r_s = 0.929$, $p < 0.001$), the latency to successful pull (correlating latencies by trial: $r_s = 0.848$, $p < 0.001$), and the number of self-scratches (Spearman's rho correlating number of scratches per trial: $r_s = 0.777$, $p < 0.001$).

3. Results

We measured three types of actions, i.e., pulling behaviour, sharing behaviour and social distance. Pulling and sharing behaviour were both measured with respect to the number of successful pulls, while social distance was measured as the average distance between the animals in their adjacent cages. Analyses used repeated measures ANOVAs with two conditions: Pulling and OT. Analyses were based on the mean performance of the dyad in each condition rather than the individual. Although our sample size was small ($N = 8$ individuals), previous studies with similar or smaller samples have found significant effects of OT on social behaviour ($N = 6$ individuals, Saito & Nakamura, 2011; or $N = 3$ individuals, Chang et al., 2012). Additionally, the previous study of cooperation and food sharing off of which we based our design found a significant difference between conditions with a sample of 7 pairs, each of which received 24 cooperation, 8 mutualism and 8 solo-effort trials using the same procedure we implement here (de Waal & Berger, 2000; our study involved 8 pairs who, across OT conditions, completed 24 trials of each condition).

First, we found no effect of OT on bar-pulling. The pair was more likely to succeed in pulling in the tray in the Solo and Mutual conditions than in the Prosocial condition in which one monkey did not receive food (Figure 2; $F_{3,2} = 61.793$, $p = 0.004$). However, OT did not affect pulling be-
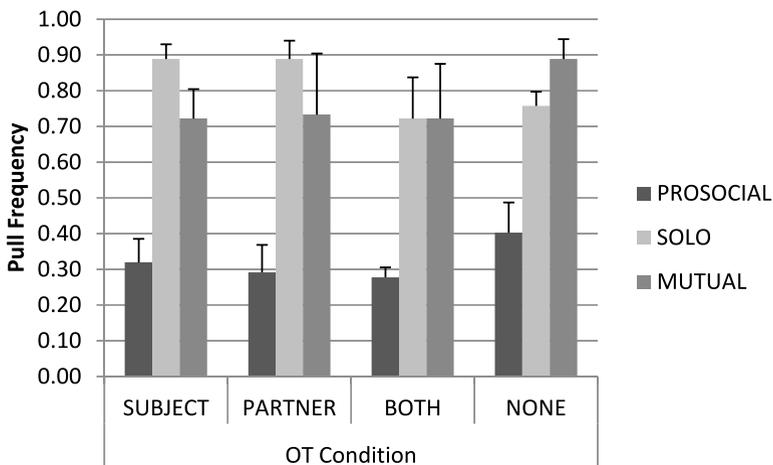
Figure 2. Frequency of successful cooperation (pulling frequency) across the oxytocin and payoff conditions.

haviour ($F_{3,2} = 0.122$, $p = 0.939$). Similarly, latency to a successful pull was strongly influenced by condition ($F_{3,2} = 40.936$, $p = 0.007$) but not OT ($F_{3,2} = 4.617$, $p = 0.183$). Interestingly pulling was faster in the Prosocial condition (mean = 3.50 s) than either Mutual (mean = 7.04 s) or Solo (mean = 10.35 s; the slowest), perhaps indicating that cooperation must occur quickly, or it does not occur at all (we did not include trials in which the pair did not succeed in our latency analysis). This may be similar to recent studies indicating that humans are most prosocial when they 'go with their gut' and make a snap decision as compared to when they carefully consider their decision (Rand et al., 2012).

Next, we examined food sharing following successful pulls. We found that OT affects sharing behaviour, albeit not in the expected way. There was no effect of either pulling condition or OT on active giving, in which the possessor actively hands food to the recipient (Figure 3: Pulling Type: $F_{3,2} = 1.597$, $p = 0.337$; OT Condition: $F_{3,2} = 1.000$, $p = 0.535$). However, active sharing was extremely rare (0.0068% of sharing events, or 23 of 3393 instances of sharing, including Giving, Taking and Collecting), and most food sharing in primates is passive, not active in nature (Jaeggi et al., 2010). Thus it is most appropriate to consider passive forms of sharing, including Taking, in which a recipient actively removed food from the possession or
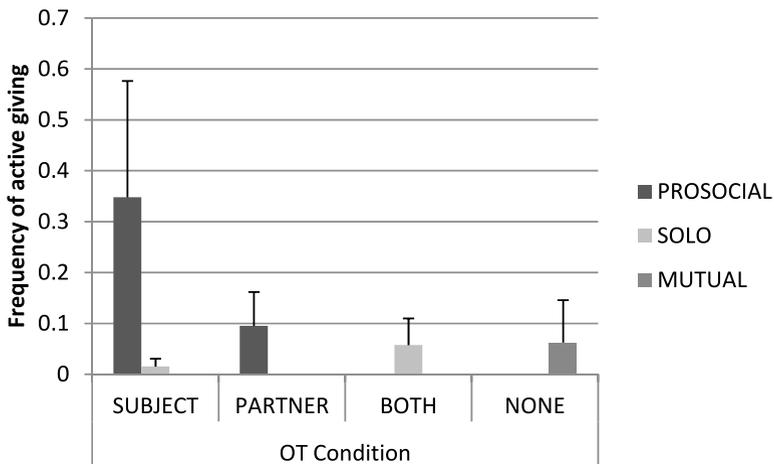

Figure 3. Frequency of active food transfer across oxytocin and payoff conditions (note that in most conditions, there were no active transfers at all).

vicinity of a possessor while within view of the possessor, and Collecting, in which the recipient removes food at some distance from the possessor.

There was no effect of Pulling Type on Taking ($F_{3,2} = 2.894$, $p = 0.199$), but there was on Collecting, with recipients collecting more food in the Solo condition than the other two conditions ($F_{3,2} = 24.071$, $p = 0.014$). This finding fails to replicate earlier findings of greater food sharing in the Prosocial condition in capuchins (de Waal & Berger, 2000), possibly emphasising the context dependence of sharing behaviour. Using a multiple regression model, we examined how food sharing (Collecting and Taking) might have been driven by particular animals or dyads. Using data on all interactions ($N = 881$), we regressed the number of pieces of food shared across dyads on the particular animals in the test, the type of test, and whether one or more animals received OT administration. Compared to Solo trials, sharing was reduced in the Prosocial condition ($\beta = -0.08$, $p = 0.008$) and was higher in the Mutual condition ($\beta = 0.10$, $p = 0.02$). The presence of any individual animal in the dyad had no effect on food sharing (p values > 0.34), although one dyad did favour each other. That dyad, Griffin and Drella, permitted more food sharing when these monkeys were tested together ($\beta = 0.09$, $p = 0.04$). Although this is anecdotal, we note that Griffin and Drella were the only males in their group and got along very well, indicating that relationship quality may influence results in studies such as these. More research on why capuchins share food in controlled settings remains to be done as this regression model only explains 5.1% of the variation in food sharing.

We additionally looked at whether OT influenced food sharing. There was a significant effect of OT on Taking (Figure 4: $F_{3,2} = 27.003$, $p = 0.036$) but not Collecting ($F_{3,2} = 6.877$, $p = 0.130$), such that there were higher levels of taking on pulls in which *neither* subject got OT than any other OT distribution. Although these results are counter intuitive given the current model for the role of OT in humans, we believe that this finding is being driven by another factor which OT affected, subjects' social distance.

Estimating a least-squares regression for the entire sample similar to the one above but without controlling for which animals were in the trial or trial type, we predicted the (active and passive) quantity of food sharing. This analysis showed that when both monkeys received OT there was reduced sharing ($\beta = -0.469 < 0$, $p = 0.03$, $N = 442$). There was the same amount of sharing when only one animal received OT as when no OT was administered. The number of pulls of the tray did not vary with OT administration
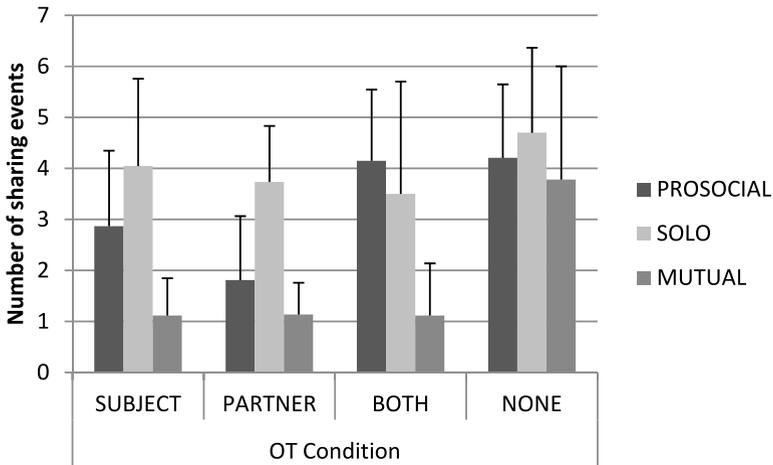
Figure 4. Frequency of taking (passive transfer in which the recipient initiates transfer) across oxytocin and payoff conditions.

for one or both animals (p values > 0.05). But, OT infusion affected the time spent within arm's reach of the centre partition, which affected the ability to share or take food ($r = 0.28$, $p = 0.001$). We found a declining linear relationship between OT and time spent by the partition. Time spent by the partition averaged 198.1 s when neither animal received OT ($p = 0.001$), 166.4 s when one received OT ($p = 0.001$), and 157.4 s when both received OT ($p = 0.001$; Figure 5). This may indicate two things. First, taking can only occur when both monkeys are close to the partition, and can reach the food. Thus, if recipients are spending less time adjacent to the partition when they are receiving OT, this explains the counterintuitive result that they receive less food when OT is present. On the other hand, possessors are not affected by OT, indicating that while OT does influence behaviour, other factors, such as one's amount of food, may override these effects.

Finally, one possible explanation for the above is that the animals were less stressed when they received OT, and so were less inclined to huddle in proximity. To explore whether the change in social distance could be related to anxiety, we looked at the number of self-scratches, a measure of stress in some non-human primates (Maestripieri et al., 1992; Troisi, 2002). To do so, we compared the amount of self-scratching by monkeys in trials in which both subjects got OT to the other trials (as the above analysis), but found that there was not a significant difference in scratching levels for either subjects
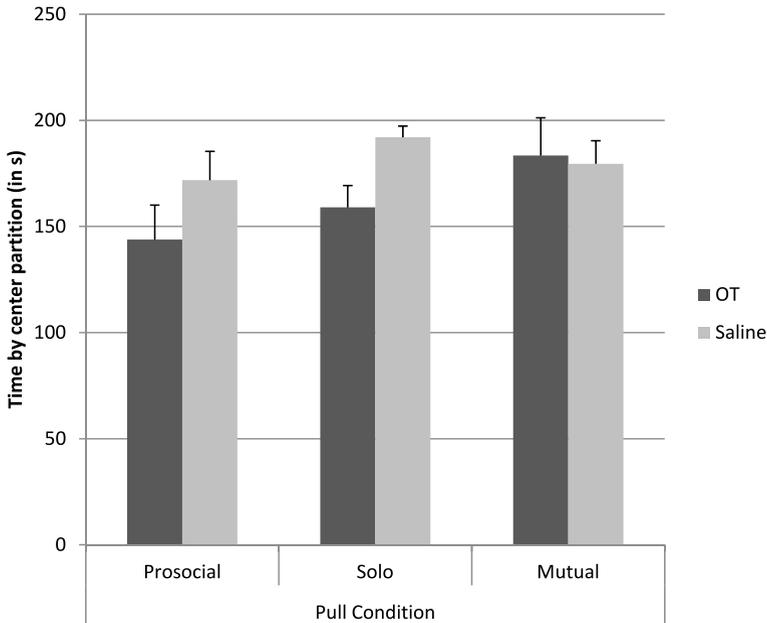
Figure 5. Time spent by the centre partition for the partner in each of the three pull conditions. Dark bars are for trial in which the subject received oxytocin; light bars are for trials in which they received the saline control.

($t = -1.255$, $p = 0.209$) or partners ($t = 0.314$, $p = 0.754$). However, of the conditions, there was only one situation in which there was a conflict between the monkeys; the individual in the partner role in the Prosocial test had to decide whether or not to pull for their partner to obtain food (partners could not pull in the Solo condition and also benefitted in the Mutual condition, and subjects always benefitted). Partners scratched significantly less often in the Prosocial condition when both monkeys received OT ($t = 2.510$, $p = 0.012$), possibly indicating that the anxiolytic effects were pronounced in situations in which there is stress, in this case due to a conflict of interest between the monkeys.

4. Discussion

Our key result is that social distance, as measured by time spent in proximity to the centre partition, is affected by OT, with partners spending less time in proximity when given the peptide. Although this is counter to some findings

among mated pairs in cooperative breeders (Smith et al., 2010), it is in line with results examining the interaction of stress and OT in non-cooperatively breeding New World monkeys (Parker et al., 2005). While our results cannot identify mechanisms, a likely explanation is that the administration of OT lowered stress responses (as indicated by the lower self-scratching levels in the partner in the Prosocial condition when both subjects received OT), thus reducing the desire for social contact (social contact itself being anxiolytic; Zak, 2012). The behaviour we observed is predicted by a recent mathematical model of collective action in which, due to nonlinear effect of stress on cooperative behaviours, reduced stress can result in less sharing (Zak & Barraza, 2013). This provides a possible reason why reduced proximity produced the counterintuitive result of decreased food sharing. Given that the majority of food sharing in capuchins, and indeed most primates, is passive, with the recipient initiating the transfer (Jaeggi et al., 2010), reduced proximity by the recipient would naturally lead to reduced food sharing if food sharing frequency is based on duration in proximity (e.g., individuals do not increase food sharing when time is restricted). These results indicate that the prosocial effects of OT may be moderated by other effects downstream from OT itself. Reduced stress and other mechanisms may then lead to the opposite results seen in other studies as well (Bartz et al., 2010b, 2011a, b; Chang et al., 2012; De Dreu et al., 2012). OT's anxiolytic effects occur through the down-regulation of amygdala activity (Kirsch et al., 2005; Gamer et al., 2010) and the inhibition of stress hormones, including epinephrine, noriephinephrine and ACTH (Bissett et al., 1967; Parker et al., 2005; Petersson et al., 2005).

Consistent with our findings, OT infusion has been shown to reduce social vigilance in rhesus macaques (Ebitz et al., 2013; Parr et al., 2013). Macaques given OT had less attention to salient social cues, for example, time spent looking at dominant monkeys' faces and at emotional faces, and thus reducing sociality. This appears to occur via an anxioloytic effect, as we posit. OT infusion had a similar effect at decreasing willingness to provide food for others at the expense of oneself in macaques (subjects serially chose whether to allocate rewards to themselves or another macaque; Chang et al., 2012). Note, however, that while reduced social vigilance and reduced anxiety undoubtedly interact, it seems more likely that our results, which are based on passive sharing rather than active provision, were driven by the latter more

than the former, as reduced social vigilance should make monkeys less inhibited in social situations and hence more likely to reach for their partner's food.

We encourage additional research to explore this link between the anxiolytic effects of OT and social behaviours, such as food sharing. Our results on self-scratching indicate that OT was anxiolytic, but this outcome was specific to the partner role in the Prosocial condition. This is the only situation in which a monkey experienced a conflict in which pulling did not benefit themselves, possibly indicating that the anxiolytic effect is more pronounced in stressful situations. However, we additionally note that while there is evidence of self-scratching as a displacement behaviour that indicates stress in non-human primates (Maestripieri et al., 1992; Troisi, 2002), to our knowledge this has not been studied in capuchins, nor is it the only possible displacement behaviour. Therefore more work is needed. Additionally, there could be other reasons besides the anxiolytic effects of OT for our results. For example, OT has been shown to be anorexigenic, especially in obese animals and for well-fed humans (Blevins & Ho, 2013; Ott et al., 2013), although we note that all food was consumed in all conditions in the current study. Thus while it is possible that there was a slight anorexigenic effect that decreased motivation to acquire food, it was not strong enough to decrease food consumption for individuals in possession of food and so we think it unlikely that this drove our subjects' behaviour.

Despite the well-documented effects of OT on prosocial behaviour in humans, prosociality may be driven by effects secondary to OT, leading to unanticipated results (Bartz et al., 2010b, 2011a, b; Chang et al., 2012; De Dreu et al., 2012). For example, a 21 day OT infusion study in adolescent male prairie voles produced reduced partner preferences (Bales et al., 2013), while 10 day OT infusion in older adult humans did not increase social behaviours, though it did raise dispositional gratitude and reduce fatigue (Barraza et al., 2013). Several brain imaging studies point to an inhibition of amygdala activity following OT infusion in humans (Kirsch et al., 2005; Petrovic et al., 2008). It will be exciting to see what future research uncovers in terms of the mechanisms of action through which OT modulates prosocial behaviours. Understanding this will increase our understanding of how OT functions and, subsequently, the underlying mechanisms and evolution of prosocial behaviour among humans and other species.

Note that our results and all of those previously discussed in New World monkeys (Parker et al., 2005; Smith et al., 2010) are based on the consensus mammalian form of oxytocin, rather than the newly discovered NWM form in which there is a proline substitution (Lee et al., 2011). The resulting amino acid change results in changes in the peptide structure, but it is as yet unknown what result this has on oxytocin expression or binding, nor how it affects behaviour differently from the consensus mammalian form used in these studies. Finally, it is unknown why this change would have evolved, and whether other species besides this clade of NWMs and tree shrews possess the mutation, meaning that it is not clear what selective pressures led to this novel form. Although we did find a significant behavioural change as the results of the OT infusion, we also cannot know for sure whether the consensus mammalian OT that we infused was actually binding to OT receptors in the NWM brain.

We also note that, consistent with other studies of OT's influences on behaviour, we had a small sample size (e.g., $N = 6$, Saito & Nakamura, 2011; or $N = 3$, Chang et al., 2012). Our social groups contained only eight adult individuals, five males and three females. Aside from the small sample size, this does not allow us to explore different effects of OT on males versus females. Human OT research has shown sex differences, with females releasing more endogenous OT after positive social stimuli displaying greater prosocial behaviours than males (reviewed in Taylor & Gonzaga, 2007; Zak, 2012). Most previous research on the influences of OT on non-human primate behaviour have used only one sex (e.g., females only; Parker et al., 2005; or males only; Saito & Nakamura, 2011; Chang et al., 2012). This is clearly an area for further research using nonhuman primates.

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