



## Original Article

# Monetary sacrifice among strangers is mediated by endogenous oxytocin release after physical contact

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**Abstract**

Humans frequently sacrifice resources to help others—even strangers. The proximate mechanisms inducing such sacrifices are not well understood, and we hypothesized that touch might provoke a sacrifice of money to a stranger. We found that touch significantly elevated circulating oxytocin (OT) levels but only when it was followed by an intentional act of trust. Touch followed by trust increased monetary sacrifice by 243% relative to untouched controls. We also found that women were more susceptible than men to OT release and monetary sacrifice after touch. This suggests that touch draws on physiologic mechanisms that support cooperative behaviors in humans.

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**1. Introduction**

This article provides evidence for a proximate and manipulable mechanism, touch, that motivates anonymous sacrifice to a stranger. The experiment reported here was prompted by two observations. First, humans touch each other, including strangers, a substantial amount. Field (2001) calls touch a “human universal.” Types of touch include handshaking, caressing, kissing, and hugging. In a now classic study, touch by waitresses was shown to increase tips even though service was not judged to be better relative to those who were not touched (Crusco & Wetzel, 1984). Similarly, students checking out books at a library who were touched reported a more favorable view of service; this was especially true for women (Fisher, Rytting, & Heslin, 1976). Although these findings have been replicated and extended, touch does not always produce increased cooperation (Bohm & Hendricks, 1997). In a study related to that reported here, Kurzban (2001) has shown that men who were instructed to

touch each other’s arms during a common-pool monetary contribution experiment marginally increased contributions compared to controls ( $p=.10$ ). Touch also plays a role in postconflict reconciliation in human and nonhuman primates (Weaver & de Waal, 2003).

The second motivating observation is that the neuropeptide oxytocin (OT) has been shown to rise when individuals are intentionally shown trust via monetary transfers. Indeed, those with higher OT levels showed increased monetary sacrifice (Zak et al., 2005a). Because repetitive stroking has been shown to induce OT release in animals (Carter, 2006; Lund, 2002; Odendaal & Meintjes, 2003), we hypothesized that touch might be a physiologic mechanism connecting OT to sacrifice. Based on this notion, we designed an experiment to examine if endogenous OT could be manipulated through touch and if this would affect monetary sacrifice to a stranger.

A brief review of the evolutionary motivation for the sacrifice of resources will put our study in context. Models of kin selection, as proposed by Hamilton and extended by others (Hamilton, 1964; Grafen, 2007), show that sacrifice to family members can be fitness-enhancing. Sacrifice to strangers may be a misapplication of sacrifice meant for kin. However, as illustrated by a recent diary study in and

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around Boston, MA, USA, an average of 1.3% of household income was given to nonrelatives, and an average of 20.3 person-days was spent helping nonrelatives during a year (Schervish & Havens, 2002). It seems unlikely that such a large amount of giving is a mistake.

Sacrifice also can be explained by reciprocal altruism (Trivers, 1971) in which the giver expects a future return from the receiver. The substantial individual contributions to charitable organizations, which, in the United States, approached \$200 billion in 2005 (Giving USA, 2006) rather than to individuals suggests that reciprocation is not a primary motivating factor. Indirect reciprocity—giving to one person in the expectation of return from a different person—can explain some of the sacrifice of resources to strangers (Alexander, 1987; Nowak & Sigmund, 2005). However, this mechanism relies on reputation and does not explain anonymous giving that is the focus of this article.

Alternatively, multilevel or group selection models predict that altruistic giving to nonkin can be supported as an evolutionarily stable strategy (Sober & Wilson, 1999). These models typically require that free riders are directly punished or excluded from the group (Panchanathan & Boyd, 2004). Strong reciprocity, another multilevel selection theory, predicts that people share with reciprocators and punish defectors even in one-shot settings (Gintis, 2000; Bowles & Gintis, 2004), but whether this theory offers a new explanation for these behaviors is not uncontroversial (Burnham, & Johnson, 2005). Nevertheless, group selection theories cannot explain anonymous sacrifice of resources to others in one-shot interactions without punishment unless the “group” includes all possible others.

Sexual selection, rather than natural selection, may motivate altruistic sacrifice, an idea that can be traced to Zahavi & Zahavi (1997); Darwin (1871); Miller (2000) and others. Because sharing of resources is a highly-valued behavior for a long-term mate (Buss, 1994), public displays of the sacrifice of resources, especially by males, may help attract a mate (Glazer & Konrad, 1996). Economics experiments by anonymous participants reveal greater monetary sacrifice than predicted by models of narrow self-interest (Camerer, 2003), but the evidence for gender asymmetries in monetary sacrifice is mixed (Andreoni, Harbaugh, & Vesterlund, 2007; Eckel & Grossman, *in press*). The gender asymmetry most consistently found in monetary cooperation experiments is that men engage in more costly punishment of noncooperators than women; this occurs even when noncooperators will not be interacted with again. This behavior has been traced to the functioning of testosterone (Zak, et al., 2005b) and activation in mesolimbic reward regions of the brain (Singer et al., 2006). Costly punishment and other sacrificial behaviors can be signals of mate quality that may be maladaptive in anonymous settings (Buss, 2006; Hausken & Hirshleifer, 2004).

It is possible that some combination of these evolutionary mechanisms explains one-shot anonymous sacrifice to a stranger, or that giving is due to confusion. Andreoni (1995)

found that about one half the variation in public good contributions is due to confusion, with the other half due to “kindness” or a motivation to cooperate. Replications and extensions of this research find that 40–50% of monetary sacrifice is due to a desire to reciprocate (Andreoni et al., 2007).

If the kindness motivation for sacrifice is correct, then (i) this mechanism should be manipulable, and (ii) there should be an associated physiologic substrate. The physiologic mechanisms that motivate intentional sacrifice are important when seeking to understand how cooperation—especially among strangers—is sustained (De Waal, 2008a). Recent neuroscientific research has revealed that charitable giving, relative to keeping money for oneself, differentially activates mesolimbic reward regions of the human brain (Harbaugh, Mayr, & Burhart, 2007; Moll et al., 2006). Furthermore, studies of monetary sacrifice directed to other people have revealed a role for OT. Exogenous OT infusion has been shown to increase monetary transfers to a stranger that denote trust (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005) and raise generosity in a task to split a sum of money (Zak, Stanton, & Ahmadi, 2007). Recent human brain imaging research has revealed that regions rich in OT receptors are statistically more active in cooperative monetary tasks with people rather than during interactions with a computer that makes random decisions (Zak et al., 2006; Krueger et al., 2007).

As discussed above, repeatedly stroking a rodent’s belly has been shown to provoke OT release. Unfortunately, in humans, the relationship between touch and OT release is inconsistent. A small study by Wikstrom et al. (2003) found that 30 min of Swedish massage did not raise peripheral OT. A study of 25 women also did not find that massage raised OT, though OT did trend upward (Turner, Altemus, Enos, Cooper, & McGuinness, 1999). Similarly, two related studies that included 10 minutes of hugging by a partner did not find an acute effect on OT levels, although self-reported history of partner warm contact was associated with higher basal OT (Grewen, Girdler, Amico, & Light, 2005; Light, Grewen, & Amico, 2005). Interestingly, a small study of people petting dogs showed that 15 min spent petting a dog raised OT in both the humans and the dogs (Odendaal & Meintjes, 2003).

To test the relationship between physical contact, OT, and sacrifice, we designed an experiment with touch and monetary transfers. Sacrifice to a stranger was quantified using the anonymous “trust game” (Berg, Dickhaut, & McCabe, 1995) from experimental economics (see Methods below). The trust game uses intentional monetary transfers from one person to another to measure trust (Smith, 1998). Transferred money grows at a defined rate. The second person can either keep the transfer or return some of it to the person who initially demonstrated trust. The return transfer is often called “trustworthiness” or “reciprocity.” We prefer to call this a “sacrifice” because the second person is under no obligation to return any money nor has any monetary

<b>MASSAGE Followed by the Trust Game (MT)</b>					
Blood Draw 1	Survey	Massage	Wait for Others' Messages	Trust Game	Blood Draw 2
15 minutes	15 minutes	15 minutes	45 minutes	10 minutes	15 minutes
<b>REST Followed by the Trust Game (RT)</b>					
Blood Draw 1	Survey	Rest	Wait for Others' Messages	Trust Game	Blood Draw 2
15 minutes	15 minutes	15 minutes	45 minutes	10 minutes	15 minutes
<b>MASSAGE Alone (M)</b>					
Blood Draw 1	Survey	Massage	Wait for Others' Messages	Blood Draw 2	
15 minutes	15 minutes	15 minutes	45 minutes	15 minutes	

Fig. 1. Timeline for each of the three treatments in the experiment.

incentive to do so in the identity-masked one-shot protocol we used (see Methods). Specifically, the experiment tested if touch would increase monetary sacrifice by a person who had been trusted relative to a person who has been trusted but not touched. In addition, we hypothesize that the release of OT will be altered through touch and will predict monetary sacrifice.

## 2. Methods

### 2.1. Subjects

Ninety six students (mean age 22.3 years, S.D. 9.1) from University of California, Los Angeles (UCLA) (Los Angeles, CA, USA) participated in the study. Participants were randomly assigned to one of three groups: Massage and Trust (MT,  $n=42$ ), Rest and Trust (RT,  $n=30$ ), or Massage only (M,  $n=24$ ). Females comprised 53% of the sample and were nearly equally balanced across groups M (54%), MT (51%) and RT (53%). Sessions had between 8 and 14 participants to ensure anonymity. One subject was dropped from the study when he became queasy after the first blood draw. The study was approved by the Institutional Review Boards of UCLA and Claremont Graduate University. All subjects gave written informed consent prior to participation. Collected data masked subjects' identities using a random numeric code. Each experimental session began at 10 a.m. and lasted about 1.5 h.

### 2.2. Touch protocol

The effect of touch was implemented in a controlled manner by using massage therapists to touch participants. Three female licensed massage therapists participated in all the massage treatment sessions. Participants in the M and MT groups received a 15-min moderate pressure (Swedish) massage of their backs with their clothing on and shirts

lifted up to the shoulders in a semiprivate room. The massage therapists were instructed to minimize talking to the subjects. Participants were informed in advance that the massage therapists were asked not to converse with them. At the time of recruitment, participants were told that the experiment would evaluate “relaxation and decision making.” Those in the RT group were asked to rest for 15 min in the same rooms used by the other subjects who received massages. RT and MT sessions were run on separate days so that RT subjects were unaware that other participants received massages; during RT sessions, no massage tables were present.

### 2.3. Blood draw

After consent, all subjects had 20 ml of blood drawn by a licensed phlebotomist from an antecubital vein. Two 8-ml EDTA whole-blood tubes and one serum-separator tube were drawn while maintaining a sterile field and using a Vacutainer. Those in the MT and RT groups had a 20-ml second blood draw immediately following their decision in the trust game following the protocol in Zak, Kurzban, and Matzner (2005b). Participants were prompted to make their decisions serially so that the decision and blood draw were temporally close. This design recognizes OT's short half-life, and seeks to capture participants' physiologic states during their decisions. Participants in the M group received a second 20-ml blood draw following massage and after completing several surveys (see below). Fig. 1 shows the timeline of the experiment.

After phlebotomy, each tube was immediately placed on ice. The tubes were then placed in a refrigerated clinical centrifuge and spun at 1500 rpm for 12 min. Plasma or serum were withdrawn from these tubes and placed into 2-ml microtubes with screw caps. These tubes were immediately placed on dry ice and then transferred to a  $-70^{\circ}\text{C}$  freezer until analysis.

## 2.4. Trust game

We used a variant of the game developed by Berg et al. (1995), in which participants were given the opportunity to send a given amount of money, provided by the experimenter, to another participant. In the variant of the trust game used in this experiment, dyads of physically separated strangers in a large lab were randomly formed. Each person in a dyad received a \$10 endowment, framed to compensate the participants for their time and the two needle sticks to obtain blood samples. In each dyad, subjects were randomly assigned to the role of decision maker (DM) 1 or DM2, and both were fully informed of the structure of their one-time interaction through a series of examples. After instruction, DM1 was prompted by computer to send an integer amount of his or her \$10 to the DM2 in the dyad; whatever was sent was subtracted from DM1's account and tripled in DM2's account. Subsequently, DM2 was informed by computer of the tripled transfer he or she received and the total in his/her account and then was prompted to sacrifice some amount by making a return transfer to DM1. What DM2 sends to DM1 is not tripled and is removed from DM2's account. The DM1 to DM2 transfer is considered a signal of trust (Smith, 1998). The Nash equilibrium of the subgame predicts DM2's sacrifice to DM1 is zero, i.e., the subgame considers more money to be better than less and disregards the initial DM1 to DM2 transfer.

After massage or rest, those in the MT and RT groups played one round of the trust game as either DM1 or DM2 with random assignment. Subjects were informed that they would only make a single decision. There was no deception of any kind. All instructions and decisions in the trust game were done by computer at partitioned stations. DMs in the trust game could not communicate with each other.

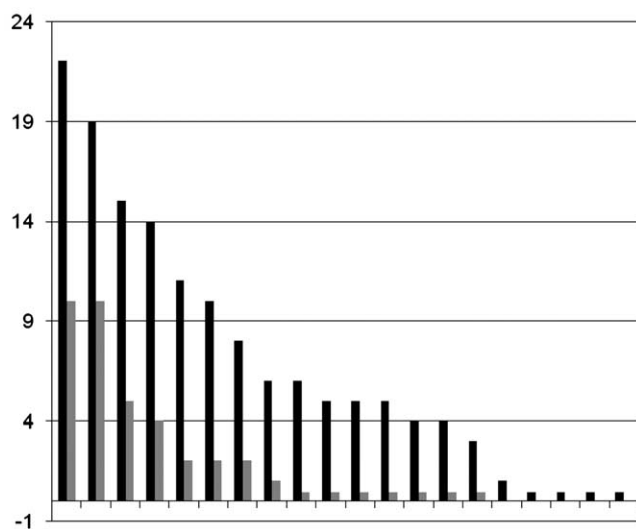


Fig. 2. Money sacrificed by DM2s in the MT group (black bars) and RT group (gray bars). The amount received by each group was the same. The maximum returned was \$22 by a participant in the MT group. Eleven participants sacrificed nothing, four (11%) of these were in the MT group, and 11 (20%), in the RT group.

## 2.5. Assays

OT was assayed using a competitive ELISA kit from Assay Designs (Ann Arbor, MI, USA). The inter- and intra-assay coefficients of variations were 7.48% at 484.68 pg/ml and 10.2% at 494.63 pg/ml (10 replicates). The assays were performed at the Endocrine Core Laboratory of the Yerkes National Primate Research Center at Emory University (Atlanta, GA, USA).

## 2.6. Surveys

Several survey instruments were included to examine the role of personality factors affecting OT release and behavior. These include the Affective Intensity Measure (AIM, Larson & Diener, 1987), social desirability using the Personal Reaction Inventory (PRI, Snyder, 1987), attachment styles (Fraley, Waller, & Brennan, 2000), as well as demographic and general attitude questions taken from Zak et al. (2005b).

## 2.7. Statistical analysis

Basal OT levels are highly variable since, like most physiologic systems, tight regulation is unnecessary absent a direct stimulus (Gimpl & Fahrenholz, 2001). As a result, all our analyses use the change in OT so that differences in basal levels do not drive the results.

Data were analyzed using Stata 9 (College Station, TX, USA) (StataCorp, 2005) for regression and correlation analysis. Statistics for *t* tests, paired *t* tests, and analysis of variance were obtained using Excel. Paired *t* tests were used to compare pre- and posttreatment OT values in group comparisons. Behavioral differences were assessed using standard *t* tests. DM2s who received a null trust signal were dropped from the behavioral analysis since there was no opportunity to sacrifice from the DM1 transfer (Zak et al., 2005b).

## 3. Results

### 3.1. Oxytocin

There was no change in OT in the M group who received massages but did not play the trust game [average basal OT=187.3 pg/ml (S.D. 131.0), average postmassage OT=189.5 pg/ml (S.D. 127.7), two-tailed paired *t* test,  $p=.62$ ,  $n=24$ ]. OT increased among subjects who received massages and played the trust game [DM1s and DM2s; average basal OT=192.4 pg/ml (S.D. 119.6), average post-massage OT=221.5 pg/ml (S.D. 126.0), two-tailed paired *t* test,  $p<.0001$ ,  $n=40$ ]. OT levels in the control RT group who rested and then played the trust game fell [DM1s and DM2s; average basal OT=256.9 pg/ml (S.D. 177.1), average post-massage OT=223.3 pg/ml (S.D. 156.9), two-tailed paired *t* test,  $p=.006$ ,  $n=27$ ].

### 3.2. Behavior

The behavioral results correlate with the physiologic changes seen across treatment groups. Fig. 2 shows a histogram

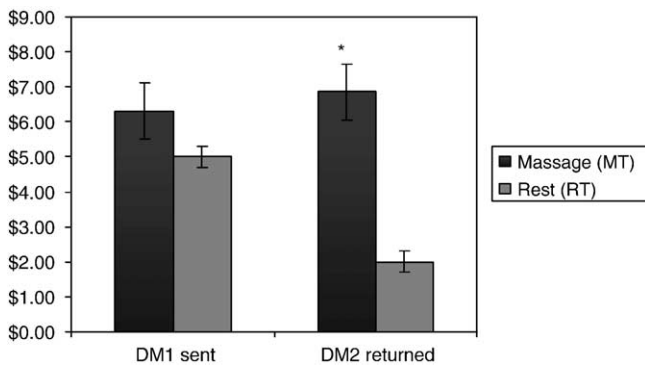


Fig. 3. The amount DM1 sends in the trust game with standard error bars. There is no statistical difference between the amount sent by DM1s to DM2s ( $p=.27$  two-tailed  $t$  test,  $n=33$ ), but DM2s in the message group sacrifice \$4.85 more on average than those in the rest group when asked to send money back to DM1s (DM2 behavior different at  $p=.006$ , two-tailed  $t$  test,  $n=32$ ).

of DM2 behavioral data. Trust by DM1s (the DM1 to DM2 transfer) in the MT group averaged \$6.30 (S.D. 3.05), while trust by DM1s in the RT group averaged \$5.00 (S.D. 3.44), though this is not statistically different (two-tailed  $t$  test,  $p=.27$ ,  $n=33$ ). Conversely, DM2s in the MT group reciprocated the trust shown in them by sacrificing to the DM1 in their dyad an average of \$6.85 (S.D. 6.40), while DM2s in the RT group only sacrificed an average of \$2.00 (S.D. 2.92). This occurred even though RT and MT DM2s received the same average amount of money from DM1s (Fig. 3). DM2 behavior across groups is statistically different (two-tailed  $t$  test,  $p=.006$ ,  $n=33$ ). On a percentage basis, DM2s in the MT group sacrificed 243% more

of their money than DM2s in the RT group (38% vs. 11%, two-tailed  $t$  test  $p=.007$ ,  $n=33$ ).

### 3.3. Oxytocin and behavior

In the MT group, a positive correlation was found between the signal of trust DM2s received and the change in their OT ( $r=.43$ , one-tailed  $t$  test,  $p=.03$ ,  $n=19$ ). That is, the more money DM2s who were massaged received, the greater the change in their OT. The linear relationship between the change in OT and the signal of trust is not seen in DM2s in the RT group (one-tailed  $t$  test,  $p=.10$ ,  $n=13$ ). For DM1s, the change in OT did not correlate with the amount of money sent in the MT group (one-tailed  $t$  test,  $p=.19$ ,  $n=21$ ) or in the RT group (one-tailed  $t$  test,  $p=.06$ ,  $n=14$ ).

Consistent with our hypotheses, the change in OT also correlated with the monetary sacrifice of DM2s in both the MT and RT groups (Fig. 4). A least-squares regression for DM2s' monetary sacrifice, controlling for the amount DM2s received from DM1s, showed that the change in OT predicts the sacrificed money (one-tailed  $t$  test,  $p=.04$ ,  $n=32$ ). Since the change in OT is highest for those who were massaged and participated in the trust game, replacing the change in OT with a binary message indicator shows that having been massaged is predicted to increase the average amount of monetary sacrifice by nearly \$5, even after controlling for the money that DM2s received (coeff=4.94, one-tailed  $t$  test  $p=.01$ ).

Because the OT data are inherently noisy, we confirmed the relationship between monetary sacrifice by DM2s and the change in OT (controlling for money received by DM2s) using a median regression. A median regression

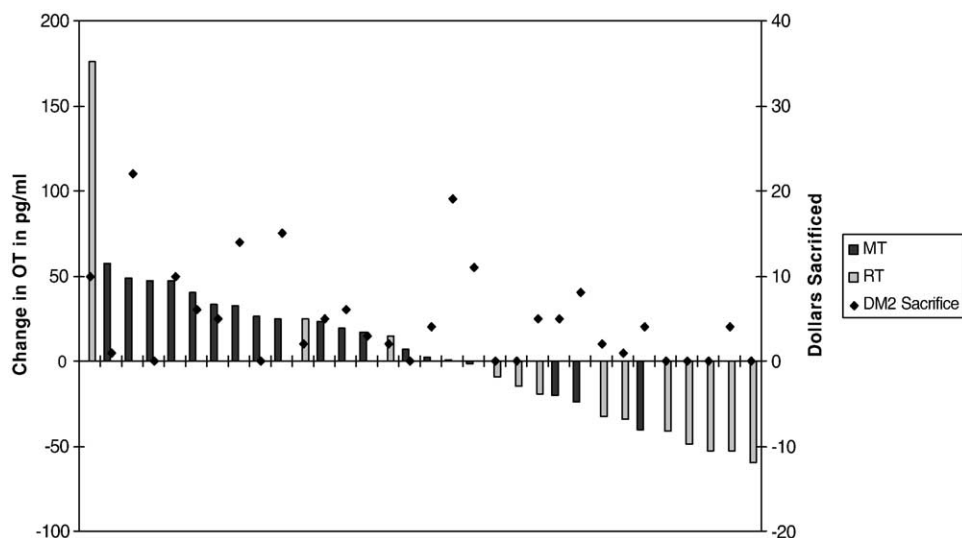


Fig. 4. The change in OT predicts the amount of monetary sacrifice in DM2s ( $r=.37 > 0$ , one-tailed  $t$  test  $p=.02$ ,  $n=32$ ). This is noteworthy because the receipt of the signal of trust is correlated with the change in OT ( $r=.42 > 0$ , one-tailed  $t$  test  $p=.01$ ,  $n=32$ ). In RT DM2s, money received predicts money sacrificed ( $r=.47 > 0$ , one-tailed  $t$  test  $p=.05$ ,  $n=13$ ) as does change in OT ( $p=.002$ , one-tailed  $t$  test). Yet, money received by DM2s in the MT group does not predict monetary sacrifice ( $r=.07$ , one-tailed  $t$  test  $p=.40$ ,  $n=19$ ). Rather, whether subjects were massaged or not has strong predictive power (one-tailed  $t$  test  $p=.01$ ). The scatter plot shows the relationship between the change in OT and the amount of money sacrificed by DM2s to DM1s. The subject with the highest change in OT is a male in the control RT group. Excluding this subject increases the  $p$  values when comparing the MT and RT groups; all other analyses also maintain significance.

(also known as a quartile regression) estimates the median of the dependent variable conditional on the values of the independent variable, by minimizing the sum of the absolute residuals (Gould & Rogers, 1994). Using a median regression, the change in OT continues to be significantly associated with monetary sacrifice (one-tailed  $t$  test,  $p=.05$ ). Secondly, the change in OT in DM2s is not biased by being massaged. An ordinary least squares (OLS) regression for the change in OT for DM2s as a function of the money they received and a binary massage indicator shows that it is the trust signal that is associated with OT release (two-tailed  $t$  test,  $p=.035$ ,  $n=32$ ), not massage (two-tailed  $t$  test,  $p=.177$ ,  $n=32$ ).

### 3.4. Gender and personality traits

There was no overall gender difference in monetary sacrifice by DM2s (one-tailed  $t$  test,  $p=.26$ ,  $n=32$ ). Pooling all three groups (MT, M, RT,  $n=96$ ), basal OT was negatively associated with the change in OT ( $r=-.28$ , two-tailed  $t$  test  $p=.007$ ). Yet, in the MT group, we found that higher basal OT predicted a larger change in OT after receiving a signal of trust (two-tailed  $t$  test  $p=.046$ ,  $n=19$ ). This suggests that massage and receipt of a signal of trust changed OT release patterns.

Associating demographic, affect, and personality traits with basal OT for all participants, we found that women were more susceptible to the massage prime [female mean basal OT=235.6 pg/ml (S.D. 114.2), male mean basal OT=179.5 pg/ml (S.D. 159.4), two-tailed  $F$  test of difference,  $p=.05$ ; correlation of basal OT and gender  $r=.19>0$  by one-tailed  $t$  test  $p=.027$ ,  $n=94$ ]. No other variables predicted OT release. Participants in the MT and M groups were not happier, less anxious, or more trusting of strangers than those in the RT group.

## 4. Discussion

Our primary finding can be restated as follows: the average monetary transfer received by DM2s (MT and RT) was \$17.36, while the average monetary sacrifice in the RT group was \$2, the average sacrifice in the MT group was \$6.85, and this difference was predicted by DM2s' change in OT. Because massaged participants subsequently sacrificed to strangers who showed trust in them but were not part of the decision to, or execution of, massage, we interpret the change in OT as a proximate mechanism that supports monetary sacrifice. The unexpected receipt of a massage, followed by a stranger showing one trust, appears to motivate monetary sacrifice through their joint effects on OT. In several studies, OT release has been associated with higher ventromedial dopamine (Liu & Wang, 2003) providing a possible proximate motivation for monetary sacrifice.

DM2s in our study—and especially those who received massages—appeared to be showing gratitude towards the

DM1s who trusted them. Adam Smith (1790), in “The Theory of Moral Sentiments” argued that gratitude drove sacrifice, “That whatever appears to be the proper object of gratitude, appears to deserve reward” (p. 94). That massage, not by DM1, but by another person, appears to induce participants to manifest monetary sacrifice toward a stranger is surprising. This result is subtle because massage alone does not raise OT. The inconsistent effect of one episode of touch causing the release of OT in humans and other animals has also been found by other groups (Turner et al., 1999; Wikstrom et al., 2004; Light et al., 2005; Grewen et al., 2005).

A possible explanation for our results is that participants in the MT group might be showing gratitude to the researchers by seeking to please them (Bonnie & De Waal, 2004; de Waal, 2006; de Waal, 2008). The blinded design sought to mitigate this effect and the lack of a difference in behavior or OT activity between DM1s in the MT and RT groups are evidence against this. Indeed, the behavior of DM1s compares well to other studies using the trust game (Camerer, 2003). It appears that massage “primed” MT DM2s' brains to respond to a signal of trust with OT release (the cellular mechanisms of OT priming have been identified by Ludwig et al., 2002). The change in OT is 16% higher among MT DM2s compared to RT DM2s, even though both received statistically identical signals of trust. In addition, RT DM2s were less willing to sacrifice money than typically observed in other trust games (Camerer, 2003).

Using both a within-subjects and between-subjects design provided two sets of control conditions. The RT condition replicated and confirmed Zak et al. (2005b) using a within-subjects design, showing that the receipt of signals of trust by DM2s is associated with endogenous OT release. A single task was used because of the possible compounding effect on OT from the receipt of multiple signals of trust, and the inhibition of OT release due to signals of distrust (Zak et al., 2005a). The interpretation of the brain mechanism associated with sacrifice should be taken with some caution; although in rodents, central and peripheral OT release coordinate during physiologic challenge (Wotjak et al., 1998), this correlation in humans is to date unknown. Another possible confound is the stress of the blood draws, as moderate stress has been shown to raise OT in women (Carter, 2006). Since every group received two blood draws, stress alone cannot explain group OT differences, and the M group had no change in OT at all. As a second check on stress and behavior, we also measured the rapidly releasing stress marker adrenocorticotrophic hormone (ACTH) for all subjects. There was no difference in DM2 ACTH after the second blood draw for those in the MT group relative to those in the M ( $p=.23$ ) and RT ( $p=.15$ ) groups. Lastly, neither estradiol levels nor female subjects' phases of their menstrual cycle, as measured by estradiol and progesterone, were associated with OT changes or monetary sacrifice (Appendix).

Our finding that women DM2s showed a stronger priming effect from massage may have evolved from mammalian attachment mechanisms in which offspring grasping at the mother's breast induces OT release absent suckling (Mathiesen, 2001; Uvnas-Moberg, 1998). A principal characteristic of mammals is maternal sacrifice of time, energy, and resources towards the rearing and protection of their offspring. Massage and trust seem to be drawing on this mechanism and together facilitate a monetary sacrifice—although, in our experiment, sacrifice toward a stranger rather than to offspring.

This experiment indicates that OT is a blunt instrument in its effect on the sacrifice of resources. That is, its manipulation outside the dyadic exchange setting substantially enhanced monetary sacrifice by DM2s within a dyad. Our finding echoes others that have shown that subtle changes of setting affect the sacrifice of money. For example, Haley & Fessler (2005) demonstrated that the use of stylized eyespots on a computer desktop increased unilateral transfers in the Dictator Game, meant to measure altruism, by 55%. Similarly, priming subjects to think about God or civic duty increased Dictator Game allocations from 73% to 129% (Shariff & Norenzayan, 2007). In our experiment, the subgame DM2s play is the dictator game; thus, we provide additional evidence that choices in this game are manipulable.

The massage prime not only increased sacrifice of money, the amount of sacrifice was predicted by the change in OT. This suggests a role for emotions in sustaining cooperation as others have noted (Fessler & Haley, 2003; Hirshleifer, 1987; Frank, 1988), as high densities of OT receptors are found in brain regions associated with emotions (Gimpl & Fahrenholz, 2001; Verbalis, 1999). Our results cannot resolve which evolutionary model best explains reciprocity in a one-shot setting, but they do show that women are more susceptible to the touch prime. Our findings for OT indicate that the physiologic mechanisms that play a central role in maternal behaviors seem to have been exapted for broader use, including inducing reciprocity. If future research supports our findings, it suggests that the deployment of a reproductive hormone in the service of cooperation with strangers is quite a feat for a simple nine amino acid peptide.

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### Appendix

Table A1. We show that personality traits between groups do affect the results by reporting the  $p$ -values for two-tailed  $t$  tests between groups for the psychological batteries used

	AIM	Attachment anxiety	Attachment avoidance	PRI
MT vs. RT	.99	.25	.39	.59
MT vs. M	.98	.60	.15	.30
RT vs. M	.97	.19	.62	.60

Table A2. This table reports correlations of personality traits and basal OT ( $p$  values for two-tailed  $t$  tests in parentheses)

	AIM	Attachment anxiety	Attachment avoidance	PRI
MT OT	.11 ( $p=.55$ )	.19 ( $p=.31$ )	-.11 ( $p=.54$ )	.014 ( $p=.92$ )
M OT	.03 ( $p=.90$ )	.22 ( $p=.33$ )	.20 ( $p=.38$ )	.08 ( $p=.71$ )
RT OT	.20 ( $p=.35$ )	-.07 ( $p=.73$ )	.30 ( $p=.13$ )	-.014 ( $p=.94$ )

With the inclusion of the AIM, the two attachment measures, and the PRI in the least-squares regression for DM2's monetary sacrifice (pooling the RT and MT samples and including a binary group indicator and controlling for the trust signal each subject received), none of the trait measures was significant (two-tailed  $t$  tests: AIM  $p=.54$ ; attachment anxiety  $p=.75$ ; attachment avoidance  $p=.54$ ; PRI  $p=.47$ ). Similarly, eight questions on whether subjects thought others were generally trustworthy and honest were unrelated to DM1 or DM2 behavior or the change in OT.

Because estrogens up-regulate OT receptors, and progesterone inhibits OT uptake by its receptor (Grazzini, Guillon, Mouillac, & Zingg, 1998), we assayed estradiol (Diagnostic Systems Laboratories, Webster, TX, USA) and progesterone (Diagnostic Products Corporation, Los Angeles, CA). We then built indicators for the follicular and luteal phases of the menstrual cycle for women (follicular: estradiol >median value of 16.93, and progesterone <3 ng/ml; luteal: progesterone >3 ng/ml). With the inclusion of these measures in the least squares regression for the amount of money DM2 returns (pooling the MT and RT groups), no effect was found ( $p=.20$ ;  $p=.46$ ), while the massage binary variable maintains significance in both cases with nearly identical  $p$  values in the baseline regression. Estradiol itself was unrelated to sacrifice ( $p=.375$ ) when put in the regression with the change in OT, while the change in OT maintained the same level of significance as it did without the additional variable. Gender was not significant for either DM1 ( $p=.18$ ) or DM2 behavior ( $p=.52$ ). We also tested if body mass index (BMI) affected the results since estrogens are synthesized in peripheral fat (Larsen, Kronenberg, Melmed, & Polonsky, 2003). Including BMI for the DM2 regression of monetary sacrifice had no effect on the results ( $p=.89$ ).

## References

- Alexander, R. (1987). *The biology of moral systems*. Aldine Transaction.
- Andreoni, J. (1995). Cooperation in public goods experiments: Kindness or confusion? *American Economic Review*, 85, 891–904.
- Andreoni, J., Harbaugh, W. T., & Vesterlund, L. (2007). Altruism in experiments. In S. Durlauf, & L. Blume (Eds.), *The New Palgrave Dictionary of Economics*, (2nd ed.). Houndmills, UK: Palgrave MacMillan.
- Berg, J., Dickhaut, J., & McCabe, K. (1995). Trust, reciprocity, and social history. *Games and Economic Behavior*, 10, 122–142.
- Bohm, J. K., & Hendricks, B. (1997). Effects of interpersonal touch, degree of justification, and sex of subject on compliance with a request. *Journal of Social Psychology*, 137, 460–469.
- Bonnie, K. E., & De Waal, F. B. M. (2004). Primate social reciprocity and the origin of gratitude. In R. A. Emmons, & M. E. McCullough (Eds.), *The psychology of gratitude* (pp. 213–229). Oxford: Oxford University Press.
- Bowles, S., & Gintis, H. (2004). The evolution of strong reciprocity: Cooperation in heterogeneous populations. *Theoretical Population Biology*, 65, 17–28.
- Burnham, T. C., & Johnson, D. D. P. (2005). The biological and evolutionary logic of human cooperation. *Analyse & Kritik*, 27, 113–135.
- Buss, D. M. (1994). *The Evolution of Desire: Strategies of human mating*. Basic books.
- Buss, D. M. (2006). Strategies of human mating. *Psychological Topics*, 15, 239–260.
- Camerer, C. F. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton, NJ: Princeton University Press.
- Carter, C. S. (2006). Biological perspectives on social attachment and bonding. In C. S. Carter, et al. (Eds.), *Attachment and bonding: A new synthesis* (pp. 85–100). Cambridge, MA: MIT Press.
- Crusco, A., & Wetzel, C. G. (1984). The Midas touch: The effects of interpersonal touch on restaurant tipping. *Personality and Social Psychology Bulletin*, 10, 512–517.
- Darwin, C. R. (1871/2000). *The descent of man, and selection in relation to sex*. Adamant Media Corporation.
- de Waal, F. B. M. (2006). *Primates and philosophers: How morality evolved*. Princeton: Princeton University Press.
- de Waal, F. B. M. (2008a). In P.J. Zak, (Eds.), *Moral markets: The critical role of values in the economy*. Princeton, NJ: Princeton University Press.
- de Waal, F. B. M. (2008b). Putting the altruism back into altruism: The evolution of empathy. *Annual Review of Psychology*, 59, 279–300.
- Eckel, C. & Grossman, P. (in press). Men, women and risk aversion: Experimental evidence. In C. Plott, & V. Smith, (Eds.), *Handbook of experimental economics results*. New York: Elsevier.
- Fessler, D. M. T., & Haley, K. J. (2003). The strategy of affect: Emotions in human cooperation. In P. Hammerstein (Ed.), *Genetic and cultural evolution of cooperation* (pp. 7–36). Cambridge, MA: MIT Press.
- Field, T. (2001). *Touch*. Cambridge, MA: MIT Press.
- Fisher, J. D., Rytting, M., & Heslin, R. (1976). Hands touching hands: Affective and evaluative effects of interpersonal touch. *Sociometry*, 39, 416–421.
- Fraley, R. C., Waller, N. G., & Brennan, K. A. (2000). An item response theory analysis of self-report measures of adult attachment. *Journal of Personality and Social Psychology*, 78, 350–365.
- Frank, R. H. (1988). *Passions within reason: The strategic role of the emotions*. New York: W.W. Norton & Company.
- Gimpl, G., & Fahrenholz, F. (2001). The oxytocin receptor system: Structure, function, and regulation. *Physiological Reviews*, 81, 629–683.
- Gintis, H. (2000). Strong reciprocity and human sociality. *Journal of Theoretical Biology*, 206, 169–179.
- Giving USA. (2006). *The annual report on philanthropy for the year 2006*. Giving institute.
- Glazer, A., & Konrad, K. A. (1996). A signaling explanation for charity. *American Economic Review*, 86, 1019–1028.
- Gould, W., & Rogers, W. H. (1994). Quantile regression as an alternative to robust regression. *Proceedings of the Statistical Computing Section*. Alexandria, VA: American Statistical Association.
- Grafen, A. (2007). Detecting kin selection at work using inclusive fitness. *Proceedings of the Royal Society B: Biological Sciences*, 274, 713–719.
- Grazzini, E., Guillon, G., Mouillac, B., & Zingg, H. H. (1998). Inhibition of oxytocin receptor function by direct binding of progesterone. *Nature*, 392, 509–512.
- Grewen, K. M., Girdler, S. S., Amico, J., & Light, K. C. (2005). Effects of partner support on resting oxytocin, cortisol, norepinephrine, and blood pressure before and after warm partner contact. *Psychosomatic Medicine*, 67, 531–538.
- Haley, K. J., & Fessler, M. T. (2005). Nobody's watching? Subtle cues affect generosity in an anonymous economic game. *Evolution and Human Behavior*, 26, 245–256.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology*, 7, 1–16.
- Harbaugh, W. T., Mayr, U., & Burghart, D. R. (2007). Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science*, 316, 1622–1625.
- Hausken, K., & Hirschleifer, J. (2004). The truthful signaling hypothesis: An explicit general equilibrium model. *Journal of Theoretical Biology*, 228, 497–511.
- Hirschleifer, J. (1987). On the emotions as guarantors of threats and promises. In J. Dupré (Ed.), *The latest on the best: Essays on evolution and optimality* (pp. 307–326). Cambridge: MIT Press.
- Kosfeld, M., Heinrichs, M., Zak, P., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature*, 435, 673–676.
- Kurzban, R. (2001). The social psychophysics of cooperation: Nonverbal communication in a public goods game. *Journal of Nonverbal Behavior*, 25, 241–259.
- Larsen, P. R., Kronenberg, H. M., Melmed, S., & Polonsky, K. S. (2003). *Williams Textbook of Endocrinology*, (10th ed.). Philadelphia, PA: Saunders.
- Larson, R. J., & Diener, E. (1987). Affect intensity as an individual difference characteristic: A review. *Journal of Research in Personality*, 21, 1–39.
- Light, K. C., Grewen, K. M., & Amico, J. A. (2005). More frequent partner hugs and higher oxytocin levels are linked to lower blood pressure and heart rate in premenopausal women. *Biological Psychology*, 69, 5–21.
- Liu, Y., & Wang, Z. X. (2003). Nucleus accumbens oxytocin and dopamine interact to regulate pair bond formation in female prairie voles. *Neuroscience*, 121, 537–544.
- Ludwig, M., Sabatier, N., Bull, P. M., Landgraf, R., Dayanithi, G., & Leng, G. (2002). Intracellular calcium stores regulate activity-dependent neuropeptide release from dendrites. *Nature*, 418, 85–89.
- Lund, I., Yu, L., Uvnas-Moberg, K., et al. (2002). Repeated massage-like stimulation induces long-term effects on nociception: Contribution of oxytocinergic mechanisms. *European Journal of Neuroscience*, 16, 330–338.
- Matthiesen, A. S., Ranskjø-Arvidson, A. B., Nissen, E., & Uvnas-Moberg, K. (2001). Postpartum maternal oxytocin release by newborns: Effects of infant hand massage and sucking. *Birth*, 28, 13–19.
- Miller, G. (2000). *The mating mind: How sexual choice shaped the evolution of human nature*. London, Heineman: Doubleday.
- Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. Human fronto-mesolimbic networks guide decisions about charitable donation. *Proceedings of the National Academy of Sciences of the USA*, 103(42), 15623–15628.
- Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, 437, 1291–1298.
- Odendaal, J. S. J., & Meintjes, R. A. (2003). Neurophysiological correlates of affiliative behaviour between humans and dogs. *Veterinary Journal*, 165, 296–301.
- Panchanathan, K., & Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature*, 432, 499–502.



- Schervish, P. G., & Havens, J. J. (2002). The Boston area diary study and the moral citizenship of care. *Voluntas: International Journal of Voluntary and Nonprofit Organizations*, 13, 47–71.
- Shariff, A. F., & Norenzayan, A. (2007). God is watching you: Supernatural agent concepts increase prosocial behavior in an anonymous economic game. *Psychological Science*, 18, 803–809.
- Singer, T., Seymour, B., O’Doherty, J., Klaas, E. S., Dolan, J. D., & Frith, C. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature*, 439, 466–469.
- Smith, A. (1790). *The theory of moral sentiments*, (6th ed.). London: A. Millar.
- Smith, V. L. (1998). The two faces of Adam Smith. *Southern Economic Journal*, 65, 2–19.
- Snyder, M. (1987). *Public appearances/private realities: The psychology of self-monitoring*. New York: W. H. Freeman and Company.
- Sober, E., & Wilson, D. S. (1999). *Unto others: The evolution and psychology of unselfish behavior*. Cambridge: Harvard University Press.
- StataCorp (2005). *Stata Statistical Software: Release 9*. College Station, TX: StataCorp LP.
- Trivers, R. L. (1971). Evolution of reciprocal altruism. *Quarterly Review of Biology*, 46, 35–57.
- Turner, R. A., Altemus, M., Enos, T., Cooper, B., & McGuiness, T. (1999). Preliminary research on plasma oxytocin in normal cycling women: investigating emotion and interpersonal distress. *Psychiatry*, 62, 97–113.
- Uvnas-Moberg, K. (1998). Oxytocin may mediate the benefits of positive social interaction and emotions. *Psychoneuroendocrinology*, 23, 819–835.
- Verbalis, J. (1999). The brain oxytocin receptor(s)? *Frontiers in Neuroendocrinology*, 20, 146–156.
- Weaver, A., & de Waal, F. B. M. (2003). The mother-offspring relationship as a template in social development: Reconciliation in captive brown capuchins (*Cebus apella*). *Journal of Comparative Psychology*, 117, 101–110.
- Wikstrom, S., Gunnarsson, T., & Nordin, C. (2003). Tactile stimulus and neurohormonal response: A pilot study. *International Journal of Neuroscience*, 113, 787–793.
- Wotjak, C. T., Ganster, J., Kohl, G., Holsboer, F., Landgraf, R., & Engelmann, M. (1998). Dissociated central and peripheral release of vasopressin, but not oxytocin, in response to repeated swim stress: New insights into the secretory capacities of peptidergic neurons. *Neuroscience*, 85, 1209–1222.
- Zahavi, A., & Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. Oxford: Oxford University Press.
- Zak, P. J., Kurzban, R., & Matzner, W. (2005a). Oxytocin is associated with human trustworthiness. *Hormones and Behavior*, 48, 522–527.
- Zak, P. J., Borja, K., Matzner, W., & Kurzban, R. (2005b). The neuroeconomics of distrust: Sex differences in behavior and physiology. *American Economic Review Papers and Proceedings*, 95, 360–364.
- Zak, P. J., Kurzban, R., & Matzner, W. (2004). The neurobiology of trust. *Annals of the New York Academy of Sciences*, 1032, 224–227.
- Zak, P. J., Park, J., Ween, J. & Graham, S. (2006). An fMRI study of interpersonal trust with exogenous oxytocin infusion. Society for Neuroscience Program No. 2006-A-130719-SfN
- Zak, P. J., Stanton, A. A., & Ahmadi, S. (2007). Oxytocin increases generosity in humans. *Public Library of Science ONE*, 2(11), e1128.