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Oxytocin is associated with human trustworthiness

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Abstract

Human beings exhibit substantial interpersonal trust—even with strangers. The neuroactive hormone oxytocin facilitates social recognition in animals, and we examine if oxytocin is related to trustworthiness between humans. This paper reports the results of an experiment to test this hypothesis, where trust and trustworthiness are measured using the sequential anonymous "trust game" with monetary payoffs. We find that oxytocin levels are higher in subjects who receive a monetary transfer that reflects an intention of trust relative to an unintentional monetary transfer of the same amount. In addition, higher oxytocin levels are associated with trustworthy behavior (the reciprocation of trust). Absent intentionality, both the oxytocin and behavioral responses are extinguished. We conclude that perceptions of intentions of trust affect levels of circulating oxytocin.

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Trust pervades nearly every aspect of our daily lives, from personal relationships to whether entire economies successfully develop (Zak and Knack, 2001). Trust occurs when one person permits another to make a decision that affects the first's welfare. While the physiological mechanisms related to some human social behaviors, e.g., aggression, are fairly well understood (Gregg and Siegel, 2001; Lee and Coccaro, 2001), the physiology of interpersonal trust is just beginning to be examined (McCabe et al., 2001; Rilling et al., 2002).

Animal models identify a prominent role for the neuroactive hormone oxytocin (OT) in facilitating various social behaviors, including social recognition (Choleris et al., 2003; Winslow and Insel, 2002), maternal attachment (Carter and Keverne, 2002; Insel and Young, 2001; Pedersen and Prange, 1979), and pair bonding (Carter, 1998; Dluzen and Carter, 1979; Insel, 1997; Insel and Shapiro, 1992). OT is a nonapeptide synthesized in the paraventricular nucleus and supraoptic nucleus of the hypothalamus and released to peripheral circulation by the neurohypophysis. OT is also secreted into the central nervous system (CNS), functioning as a neuromodulator. In human beings, accumulations of OT receptors are found in the amygdala (Loup et al., 1991), a CNS region associated with social behaviors.

Based on the behavioral literature in animals and the human neurophysiology of OT, we hypothesize that OT will be involved in trusting behaviors in humans. Specifically, we predict that when people receive a monetary transfer that is voluntary and intentional, connoting trust, peripheral OT will be higher than when people receive a monetary transfer absent an intention of trust. Behaviorally, we hypothesize that an increase in peripheral OT will be associated with trustworthy behavior (reciprocating trust). We emphasize that these hypotheses relate the effect of OT as activated by a signal of trust rather than associating basal OT with behavior.

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Laboratory studies consistently show substantial amounts of interpersonal trust in monetary exchange experiments (Fehr and Rockenbach, 2003; Fehr and Gächter, 2002; Camerer, 2003). We use a variant of the game developed by Berg et al. (1995), in which participants have the opportunity to send money provided by the experimenter to another participant. This money is tripled, and the receiving player can return all, some, or none of this money back to the player who sent the money to them.

A substantial number of researchers have used this method to assess "trust," measured by the amount that decision-maker 1 (DM1) sends to decision-maker 2 (DM2) (Smith, 1998). This transfer is considered an index of trust because the money sent to DM2 entails a cost to DM1 which can only be recouped if DM2 voluntarily reciprocates. The greater the transfer, the greater the cost to DM1, and the larger the potential for gains to cooperation. Similarly, the amount DM2 transfers to DM1 is an index of trustworthiness for parallel reasons. DM2 can only reciprocate trust by taking money out of his or her account—every dollar transferred to a DM1 reduces DM2's earnings one-to-one.

Standard economic theory (the "subgame perfect Nash equilibrium") predicts that rational self-interested individuals should never trust another person in a one-shot interaction, and if someone does trust you, you should not be trustworthy. This is because the Nash equilibrium embodies the assumption that DM2s prefer more money to less, so they should not be trustworthy (i.e., are expected to keep all the money in their accounts). DM1s, anticipating this, should never send anything to DM2s. Yet, across a large number of experiments, experimenters, and monetary stakes, DM1s consistently send substantial amounts to DM2s, and DM2s nearly always return some money to DM1s (Smith, 1998), though there is substantial individual variation in the choices made in these experiments (Camerer, 2003). Because participants typically demonstrate trust and trustworthiness in this protocol, along with substantial variability, this method is ideal for examining the hypothesis that OT is related to trustworthiness.

Methods

Participants

One hundred and fifty six students from the University of California, Los Angeles (UCLA) participated. In the Intention condition (described below), the mean (SD) age of participants was 22 (4.3), 50% female; in the Random Draw condition, the mean age (SD) was 20 (2.7), 53% female. Both groups of participants were racially diverse. In the Intention condition, we were unable to obtain sufficient quantities of blood from three participants (see below), and one participant while in the lab was viewing sexual explicit material on the Internet, which could raise OT, and was

removed. The final sample size was 96 of which 48 participants were DM2s. In the Random Draw condition (described below), three DM2s received a zero monetary transfer and were excluded from the sample because these DM2s lack behavioral variation (i.e., DM2s who receive zero always return zero to DM1s), as was one participant with an apparently anomalous OT level five standard deviations above the mean. The final sample was 38, of which 19 participants were DM2s.

Procedure

All participants earned \$10 for showing up for the experiment and were assigned an identity-masking code. There was a random assignment of one half the participants to the role of DM1 and the other half to DM2, and DM1–DM2 dyads were formed. Participants were informed of the consequences of their own decisions and that of the other DM, but could not communicate directly with the other DM. All interactions were made through a computer interface, with participants seated in partitioned stations in a large computer lab, ensuring participant anonymity. In line with lab policy, there was no deception of any kind.

When the experiment began, DM1s were asked by the software how much (if any) of the \$10 earned by showing up they would like to transfer to the DM2 in their dyad. Both DMs were advised that whatever DM1 sent to DM2 would be tripled and put into DM2's account. After all DM1s made their decisions, the DM2s were informed of how much the DM1 in their dyad sent them, as well as the total in their accounts. The software then queried DM2s to send some integer amount, including zero, from their account back to the DM1 in their dyad.

Each participant made a single decision when prompted. Immediately after each decision, they were taken into an anteroom and 28 ml of blood was drawn from an antecubital vein. The time between a participant's decision and blood draw was designed to be as close as possible to capture participants' physiologic state during the decision. After all decisions were made, the experiment ended and participants were privately paid their earnings. Each experimental session began at 1:00 PM, a time of minimum diurnal variation for most hormones. Experimental sessions lasted approximately 1.5 h.

Design

We conducted two experimental conditions, yielding a 1×2 between-subjects design. In the Intention condition, the standard trust interaction described above was implemented. In a second condition, called Random Draw, DM1 publicly pulled a numbered ball from an urn. The urn contained 11 balls numbered 0, 1, ... 10, corresponding to the set of choices DM1s could make in the Intention condition. DM1s were forced to make the monetary transfer to DM2 determined by the ball. The Random Draw

condition removed the intentional signaling element from DM1's decision, allowing us to extract the behavioral and endocrine effects of the trust signal separate from the effect of a monetary transfer from another person.

Blood draw

Following each participant's decision, he or she was brought into a private room for a blood draw. Blood draws typically occurred within 2 min of each participant's decision. A small number of participants faced longer delays (e.g., if the previous participant fainted), but there was no statistical impact of the delay time on the results. Two EDTA and two serum-separator tubes were drawn from a participant's antecubital vein maintaining a sterile field and using a Vacutainer. Following phlebotomy, each tube was immediately placed on ice. The blood was placed in refrigerated clinical centrifuges and spun at 1500 rpm for 12 min. Plasma and serum were withdrawn and placed into 2 ml centrifuge tubes with screw caps. The tubes were placed on dry ice and transferred to a -70° C freezer until ready for analysis.

Assays

Ten hormones were assayed using either radioimmunoassays (RIA) or enzyme-linked immunosorbent assays (ELISA). All tests were performed at the Endocrine Core Laboratory of the Yerkes National Primate Research Center at Emory University, Atlanta, GA. The following hormones were assayed using commercial kits from Diagnostic Systems Laboratories (Webster, TX): andrenocorticotropin hormone (ACTH) (plasma-RIA), prolactin (serum-RIA), cortisol (serum-RIA), dihydrotestosterone (DHT) (serum-RIA), testosterone (serum-RIA), estradiol (serum-RIA), beta human chorionic gonadotropin (β-hCG) (serum-ELISA). Progesterone (serum) was assayed using an RIA kit from Diagnostic Products Corporation (Los Angeles, CA). Both OT and arginine vasopressin were assayed using a competitive ELISA assay from R&D Systems (Minneapolis, MN). The inter- and intra-assay coefficients of variations were 10.7% and 12.2%, respectively, with sensitivity <4.68 pg/ml.

Survey

A 155-question survey constructed by the authors of social and developmental history, and 40 questions on affective intensity (AIM, Larsen and Diener, 1987) was administered to participants. AIM provides information on general personality traits rather than a participant's feelings during the experiment itself. For this reason, the survey was completed before participants made decisions. The survey was designed to examine whether personality traits and life events were related to hormone levels and behavior in the trust game.

Results

Behavior

In the Intention condition, the mean (SD) amount sent by DM1s from their \$10 show-up payment to DM2s was \$5.52 (\$3.13); the mean amount returned by DM2s was \$6.96 (41% of the amount received from DM1s, SD = \$6.29). In the Random Draw condition, the amount taken from DM1 and sent to DM2 was \$5.63 (\$2.65). In this condition, DM2s returned to DM1s, on average, only \$3.58 (25% of the amount received from DM1s, SD = \$3.31). Trustworthiness levels (the transfer from DM2 to DM1) across experimental conditions were statistically different from each other (F test, two-tailed, P = 0.030).

Further, as one would expect if DM2s were responding reciprocally only when the money they received was the result of an intentional act, in the Intention condition the correlation between the amount DM1s sent (trust) and the amount DM2s returned to them (trustworthiness) was 0.56 and was statistically different from zero (t test, P = 0.00001, two-tailed, N = 48). This contrasts with the Random Draw condition, in which this correlation is 0.20 and is not statistically different from zero (t test, P = 0.40, two-tailed, N = 19; see Fig. 1).

Oxytocin

Turning to our central hypothesis, in the Intention condition the mean (SD) for DM2 OT in the sample is 278.46 (182.11) pg/ml. This is 41% higher than the mean in the Random Draw condition, 197.75 (165.23) pg/ml (see Fig. 2). An ANOVA on DM2 OT levels in the Intention and Random Draw conditions shows that, consistent with our primary hypothesis, OT levels are higher when there is an intention of trust (F test, one-tailed, N = 67, P = 0.049).

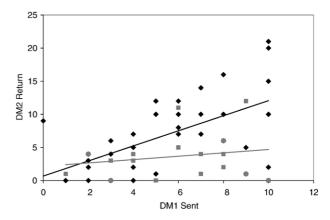


Fig. 1. The figure plots the amount returned by DM2s to DM1s (trustworthiness) when the DM1 to DM2 transfer is intentional (black), and when the initial transfer is determined by a random draw (gray) and least squares regression lines through the data. There is a statistically significant correlation between the signal of trust by DM1s and trustworthiness by DM2s in the Intention condition, but not in the Random Draw condition, indicating trustworthiness is part of a social obligation for reciprocity.

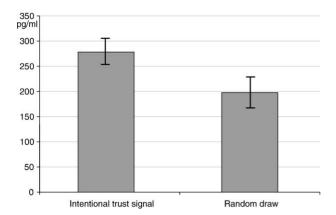


Fig. 2. OT levels and standards errors for DM2s with and without an intention to trust. In the Intention condition, DM1s voluntarily transfer money to DM2s. In the Random Draw condition, the transfer from DM1s to DM2s was determined by a public draw of a numbered ball. OT levels across conditions are statistically different at P < 0.05.

This difference occurs even though the average amount of money transferred from DM1s to DM2s did not differ between conditions (F test, two-tailed, P > 0.89).

Next, we tested our second hypothesis, whether DM2 OT levels were related to their behavior in the Intention condition. To investigate this relationship, we estimated a multiple regression model of trustworthiness (the amount returned by DM2 to DM1) as a function of the log of OT and the amount DM2 received from DM1. We use log of OT as this functional form captures the expected saturation on behavior at OT rises. Covariate control variables included age and sex. The regression was tested for normality of the errors (Jarque–Bera statistic, P=0.87) and heteroskedasticity (White χ^2 statistic P=0.0005). The latter issue required additional statistical correction. The equation was re-estimated using White's (White, 1980) heteroskedasticity-consistent covariance matrix ($R^2=0.45$, N=48).

The estimation shows that $\log(\text{OT})$ (coeff. 2.383) is statistically significant (one-tailed t test, P = 0.021). The age variable controls for possible age-related hormonal changes and because survey data show trust increasing with respondents' ages (Putnam, 2000), while the sex variable examines if a gender difference is present. Age was statistically significant, but sex was not (two-tailed t tests, P = 0.01 and P = 0.34, respectively). The statistical significance of $\log(\text{OT})$ was maintained whether or not the controls were included (without controls, coeff. = 2.543, P = 0.011, one-tailed t test). There is no overall difference in the trustworthiness of males and females in the Intention condition, as some behavioral experiments on trust have found (Croson and Buchan, 1999).

In the Random Draw condition, estimating the identical least-squares regression relating the amount DM2 returns to DM1 to log(OT) used in the Intention condition (including covariate controls), we find the coefficient of log(OT) is insignificantly different from zero (t test, one-tailed, P = 0.24). The age variable is also insignificant (t test, two-tailed, t = 0.064) but sex is significant (t test, two-tailed,

P = 0.049). An analysis of why women were more generous than men in the Random Draw condition is presented elsewhere (Zak et al., in press).

In addition to OT, we measured nine other hormones to determine if the relationship between OT and trustworthiness occurs indirectly. The other hormones measured are andrenocorticotropin hormone (ACTH), cortisol, prolactin, estradiol, testosterone, dihydrotestosterone (DHT), progesterone, arginine vasopressin (AVP), and human chorionic gonadotropin, beta subunit (β-hCG). OT is known to reduce ACTH and cortisol (Coiro et al., 1988), prolactin-releasing peptide promotes OT release (Zhu and Onaka, 2003), estradiol up-regulates the uptake of OT (Verbalis, 1999), testosterone inhibits the action of central OT (Arsenijevic and Tribollet, 1998), progesterone inhibits oxytocin binding (Grazzini et al., 1998), while AVP and OT are related peptides that differ by two amino acids. Lastly, β-hCG was measured to determine if any female participants were pregnant; none were. We find no evidence for a correlation between DM2s' OT and the levels of all but one of the other hormones in the Intention condition [two-tailed t tests of the correlation of OT and: ACTH (P = 0.82, r = -0.057), cortisol (P = 0.36, r = 0.18), prolactin (P = 0.43, r = 0.20), estradiol (P = 0.46, r = 0.19), testosterone (P = 0.81, r =0.04), DHT (P = 0.70, r = -0.06), progesterone (P = 0.70, r = -0.19)]. Only the levels of OT and AVP are statistically related (P = 0.08, r = 0.30) in DM2s. This is likely spurious as AVP is unrelated to trustworthiness (t test, two-tailed, P =0.90), and the ELISA cross-reactivity of AVP to OT is very low (<0.001%) (R&D Systems, 2001). Behaviorally, AVP is associated with aggression (Coccaro et al., 1998).

Because of evidence in rodents that estrogens increase OT binding at receptor sites, we investigated its impact on participants' behaviors. Re-estimating the least-squares regression for trustworthiness in the Intention condition including the interactive variable estradiol \times OT, statistical significance was not obtained (coefficient = -0.00001, P = 0.85, t test, two-tailed), with or without the inclusion of log(OT). These analyses suggest that OT is directly responding to the signal of trust.

We did not find endocrine evidence associated with trusting behaviors by DM1s. In particular, OT levels for DM1s in the Intention condition were unpredictive of the strength of the trust signal (r = -0.14, two-tailed t test, P = 0.33). This suggests that OT responds to signals of trust but is not associated with producing trust itself.

Survey

We also examined if trust and trustworthiness were related to developmental or personality differences independent of the experimental task by analyzing answers to survey questions. This approach follows from research in rats showing that developmental history affects the density of OT receptors in the brain (Champagne et al., 2001). Taking into account potentially spurious results due to

multiple comparisons, we report only correlations for questions asked two or more ways that all obtain statistical significance (P < 0.05). Using this criterion, only a few of the survey questions were related to participants' behaviors in the Intention condition. We find that DM1s who exhibited trust behaviorally reported that they think others are generally trustworthy and honest (4 questions). Similarly, trustworthy behavior in DM2s was largely unrelated to the survey questions, but was associated with two self-report measures of emotional lability (from 40 affect questions) and two questions on selfishness (a belief that people are selfish was negatively correlated with trustworthiness). Including these four measures singly in the least squares regression for trustworthiness as a function of log(OT), transfer received from DM1, and controls, all four questions were statistically significant (two-tailed t test, P < 0.05).

Discussion

The results of the present experiment are a first step toward understanding the role of hormones in complex human social interactions that involve trust and trustworthiness. We find, consistent with our hypotheses, that OT appears to respond to a social intention of trust and is associated with trustworthiness. When the social signal of trust is extinguished, so are the OT response and the high degree of trustworthiness seen in the Intention condition. Our results allow us to infer a causal relationship between the perceived intention behind a monetary transfer and the level of peripheral OT. At present, we cannot distinguish between the possibility that OT levels caused trustworthy behavior and the alternative that increased OT levels were caused by trustworthy behavior. We favor the first possibility, but additional work will be required before a definitive conclusion can be drawn.

The generation of trust signals by DM1s is unrelated to DM1 OT levels, while DM2s who receive a social signal of trust have an OT response. The lack of a relationship between OT and DM1 behavior is consistent with findings in the animal literature on the reactivity of OT to social cues (Carter and Keverne, 2002). Our analysis also showed that the relationship between OT and trustworthy behavior by DM2s is nonlinear. Possible explanations for this finding include significant differences in the number of participants' OT receptors (OTRs), or that OTRs may be bound by an endogenous or exogenous OT antagonist. This would reduce the feedback between OT release and release termination, resulting in variable levels of OT for the same stimulus. As discussed above, we examined a number of hormones that inhibit or stimulate OT release and uptake, but find no evidence that these affect trustworthy behavior. We leave open for future research the characterization of variations in OTR activity during the trust game.

The advantage of the "neuroeconomic" approach of this study (Zak, 2004) is that participants engage in actual social

interactions along with monetary rewards to motivate attention to task. Indeed, DM1s incurred a direct cost and bore a risk to trust another person, while DM2s incurred a cost to be trustworthy. Our findings suggest that social interactions outside the laboratory involving intentions of trust might also produce OT responses because of two features that bias the results against finding a physiologic reaction: the absence of face-to-face communication by participants, and participant anonymity. It seems likely that additional interpersonal cues would augment the endocrine response. The analysis of the survey questions supports the interpretation that the social aspect of trust, rather than personality traits, are driving the results we report.

Concern for the possible confounding effects of social interactions led us away from a design in which we drew blood both before and after each decision. This design has the advantage of directly measuring changes in OT within subjects, but introduces the confound of the additional interaction with the phlebotomist. Our use of random assignment to condition and our between-subject analysis preserves our ability to draw inferences about differences that emerge between treatments without requiring the additional blood draw.

Our results should not be interpreted as showing CNS OT activity during trusting behaviors because peripheral and CNS OT are synthesized by distinct hypothalamic cell populations. In rodents, central and peripheral OT secretion coordinate during physiologic challenge (Wotjak et al., 1998), but the relationship between peripheral OT and CNS OT in humans is unknown. Nevertheless, the findings here should be considered in light of the fMRI study of Rilling et al. (2002), who show significant activity in vetromedial regions rich in dopamine receptors during cooperative behaviors. In the prairie vole, the nucleus accumbens is dense in OT receptors (Lim et al., 2004), and OT appears to be critical for linking social signals to vertromedial reward circuits (Insel, 2003).

The results reported here provide initial evidence in humans for the role of OT in the social processes surrounding trust and trustworthiness. Because this work is a first step in understanding the complex hormonal influences on behavior, substantial additional research is required. In particular, future work should monitor hormone levels over the course of interactions, investigate different types of social interactions, and exogenously manipulate oxytocin to enable stronger causal inferences about the relationship between hormones and trusting behaviors. We hope the findings reported here will provide a foundation for work along these lines.

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