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Original Article

OXYTOCIN AND COOPERATION: COOPERATION WITH NON-KIN ASSOCIATED WITH MECHANISMS FOR AFFILIATION

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Abstract:
Animal models have shown oxytocin to be causally associated with parental and alloparental investment, and effects of administered oxytocin in humans suggest it is also associated with cooperative behaviors directed at adult non-kin. Oxytocin appears to mediate cooperative behaviors by acting on the HPA axis to reduce anxiety, allowing for the expression of approach and helping behaviors. An observational study of 44 young adult males in St. Petersburg, Russia, found no association between circulating basal endocrine measures (oxytocin, cortisol, and testosterone) and prosocial behaviors measured by self-report altruism and empathy scales. Frequency of helping behavior and emotional empathy scores were significantly correlated. The study did find emotional empathy significantly associated with fatherhood, and helping behavior significantly associated with marital status, suggesting that affiliative and helping behaviors are expressed through similar pathways. Testosterone varied significantly between ethnic and non-ethnic Russians, but did not vary with marital status or presence of children.

Keywords: Plasma oxytocin, Cortisol, Testosterone, Allocooperation, Prosocial behavior, Stress, Kin selection, Reciprocal altruism, Empathy, Parental behavior, Humans

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Introduction

Cooperative behavior puzzles evolutionary biologists, since it appears to contradict the theory that selection occurs at the level of the individual. Any individual willing to cooperate with others should find it is the victim of cheaters willing to accept the individual's cooperation yet offering nothing in return, adversely impacting the individual's fitness, or reproductive success (RS). Hamilton's theory of inclusive fitness (1964), in which cooperation towards one's close kin is selected because it increases the individual's total fitness, and Trivers' theory of reciprocal altruism (1971), in which an individual will cooperate with non-kin when it can expect future cooperation in return, have been offered as solutions to widely observed cooperative behaviors in a number of species. Oxytocin is an attractive candidate for a proximate endocrine pathway mediating cooperation described by these two theories.

Prosocial behavior directed at unrelated conspecifics (allocooperation), is a precondition for social life and can be carefully defined as both any instance of asymmetric or symmetric cooperation, and a predisposition to approach unknown individuals and cooperate prior to a history of known interactions. Prosocial behavior runs the gamut from common helping behaviors such as donating time, money, or labor (e.g. holding the bus or elevator, helping change a tire, giving money to charity, etc.), to potentially fitness-reducing examples of altruism such as donating blood, risking life and limb in the service of others, or adopting unrelated offspring (D. Y. Lee, Lee, & Kang, 2003). As critics have noted, a predisposition to allocooperation is a necessary condition for the development of reciprocal altruism (Field, 2001).

Parental behaviors directed at offspring are easily explained through inclusive fitness, but this is not so for alloparenting (or parental care directed toward unrelated young), a widespread practice across multiple taxa (Brown, 1998; Komdeur, 2006; Riedman, 1982; Wisenden, 1999). The prevalence of alloparental behavior demonstrates that mechanisms facilitating kin selection follow a rule-of-thumb, rather than strict kin discrimination, hence allowing for risk of exploitation by non-kin. Models suggest that strict genetic kin recognition mechanisms are inherently unstable, since, if a recognizable marker confers a fitness advantage it becomes increasingly common until it can no longer serve as a marker of kin (Dawkins, 1989; Rousset & Roze, 2007). In many species cooperation that can be explained by kin selection appears to follow a rule of thumb based on learned cues, proximity toward conspecifics, or other social recognition markers (Mateo, 2004). The same spandrel mechanism that allows alloparental investment can serve as a conduit for the expression of allocooperation in general. In other words, the *rule of thumb* allows for *errors* that exploit adaptive neuroendocrine mechanisms ultimately giving rise to altruism, and in equilibrium, reciprocal cooperation.

Oxytocin (OT), a neuropeptide that plays a key role in parturition and lactation, is an attractive candidate as a proximate endocrine mechanism regulating the expression of allocooperation in humans. Animal models have demonstrated that OT is causally associated with parental behaviors including alloparental care, and paternal investment, and pair bonding among monogamous rodent species (Olazabal & Young, 2006). Among socially monogamous prairie vole males, alloparental behavior is significantly reduced by OT antagonists (Bales, Kim, Lewis-Reese, & Carter, 2004); and, although female house mice often spontaneously kill unrelated young, administration of OT acts directly on the central nervous system to reduce infanticidal behavior (McCarthy, 1990). OT is tied to the expression of normative social behaviors in adults across species, and administered OT promotes parental behaviors among promiscuous rodent species, while OT antagonists inhibit such behaviors in monogamous species (Cho, DeVries, Williams, & Carter, 1999; Witt, Winslow, & Insel, 1992).

In humans, OT appears to play an important role in mother-infant bonding, and evidence suggests that there is a rise in OT in children after a structured interaction with a caregiver (Feldman, Weller, Zagoory-Sharon, & Levine, 2007; Fries, Ziegler, Kurian, Jacoris, & Pollak, 2005; Levine, Zagoory-Sharon, Feldman, & Weller, 2007). Early environments, both pre and post-utero, appear to affect OT expression. The OT delivery system in rats is disrupted by pre-natal stress, leading to deficits in adult social behaviors that are restored by administered OT (P. R. Lee, Brady, Shapiro, Dorsa, & Koenig, 2007), and the secretion of OT is reduced in human children who suffered severe neglect in infancy (Fries et al., 2005). If an individual's early environment is a good indicator of its future adult environment, it would be evolutionarily adaptive to be predisposed to allocooperation in a stable environment, but not in an unpredictable environment, and this could be regulated by OT expression.

Human studies with intranasally administered OT have found that it encourages trust and empathic generosity in economic games, facilitates the reading of emotions, and interacts with social bonding to reduce stress by lowering cortisol (Cort) levels (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007; Heinrichs, Baumgartner, Kirschbaum, & Ehlert, 2003; Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005; Zak, 2007). Administered OT leads to both reduced activation of the amygdala and persistent trusting behaviors, measured by monetary transfers, even when faced with repeated breaches of trust (Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008). OT is a known anxyolitic, acting on the hypothalamic-pituitary-adrenal axis to inhibit Cort release (Gimpl & Fahrenholz, 2001; Neumann, 2002), presumably inhibiting the stress response by reducing activity in the amygdala. This may then allow for the expression of prosocial approach behavior leading to allocooperation (Kirsch et al., 2005).

Oxytocin is released from the posterior pituitary into the central and peripheral nervous system, as well as directly from peripheral tissues such as the uterus, testis, and heart. OT levels appear coordinated in the central and peripheral nervous system of rats, and peripherally administered OT has been found to cross the blood-brain barrier. In humans, changes in plasma endocrine levels mirror changes in cerebrospinal fluid following central administration of neuropeptides similar to oxytocin, so peripheral measures from human plasma are an acceptable if imperfect substitute for other more intrusive measurements (Bartz & Hollander, 2006; Born et al., 2002; Carter et al., 2007; Gimpl & Fahrenholz, 2001).

This study examined whether basal OT, peripherally measured in plasma, acts as a conduit for allocooperation in humans, and hypothesized that the two would be significantly correlated, and that both would be inversely correlated with Cort. The primary hypothesis was that OT, by downregulating Cort, inhibits the stress response allowing the expression of allocooperation. A secondary hypothesis was that testosterone might be inversely correlated with both OT and allocooperation, since both pair bonding and infants, strongly associated with OT, tend to inhibit testosterone expression in males (Gray, Yang, & Pope, 2006; McIntyre et al., 2006). There is a significant literature linking helping behaviors in humans to empathic concern (Davis, 1994), so behavioral scales were chosen that measured both past frequency of helping behavior and empathic concern, with the assumption that the two would be strongly correlated, and would provide a broader measure of allocooperation than that offered by one-shot monetary transfers in economic games.

Methods

To examine the hypothesis that OT acts as a developmentally mediated proximate mechanism for allocooperation in humans, an observational study was conducted at L.G. Sokolov Hospital, Central Medical Unit #122, in St. Petersburg, Russia on 45 male subjects. Only males were observed to avoid significant differences in peripheral OT associated with sex. One of the best-known functions of the hormone is milk ejection and uterine contraction, and it appears to stimulate mid-cycle luteinizing hormone release (Gimpl & Fahrenholz, 2001). Subjects were administered an expanded 60-point Self-Report Altruism Scale, (Johnson et al., 1989; Rushton, Chrisjohn, & Fekken, 1981) and the 30-item Multi-Dimensional Emotional Empathy Scale, (Caruso & Mayer, 1998), followed by an 18 mL blood draw to measure circulating OT, Cort, and testosterone levels. One individual was removed from final analysis after declining to participate in the blood draw, leaving a final $N = 44$. Subjects were compensated $20.00 for their participation. Within a week of the blood draw, a subset of 11 subjects (25%), was also interviewed using an expanded In-Depth Adult Attachment Interview, the AAI (analyzed separately; George, Kaplan, & Main, 1996), and compensated an additional $10.00. The study lasted up to two hours for the forty-four participants participating in blood draw and behavior scales.

Russia is a useful environment to study these questions due to the recent history of economic scarcity and political turmoil surrounding the collapse of the Soviet Union, exemplified by a two-thirds decline in real income, and a sharp drop in life expectancy in the early 1990s (Chen, Wittgenstein, & McKeon, 1996; Notzon et al., 1998). The study focused on young adult males, with most subjects falling within 18-35 years of age to control for sex and age differences in endocrine expression. The age range (mean±SD age, 25.023±6 years) ensures subjects' early environment was affected by Russia's recent tumultuous changes, both the economic scarcity and the political chaos leading to the collapse of the Soviet Union in 1991. Four subjects fell outside of the 18-35-age range: two subjects were 37, one was 38, and one was 46 years of age. Subjects were divided between ethnic and non-ethnic Russians to examine environmental differences related to ethnicity and culture.

Endocrine measures

All scales and blood draws occurred during a three-week period in late summer 2006, and were administered between the hours of 10AM and 2PM to minimize the effect of daily rhythm in concentrations of OT (Forsling, Montgomery, Halpin, Windle, & Treacher, 1998). All blood draws occurred within fifteen minutes of the behavioral scales and within three minutes of seating for the draw in an attempt to measure basal levels. The blood was drawn by a nurse-phlebotomist at Central Medical Unit #122, into chilled K-3 9ml EDTA polypropylene tubes (Monovette, Sarstedt, Germany, # 02.1066.001; Corway, St. Petersburg). Immediately after the draw, 500 KIU of aprotinin was added per mL of sample as a protease inhibitor. The sample was then centrifuged at room temperature at 1,000x*g* for 10 minutes, aliquoted, and stored at –35ºC until ready for shipment.

The serum was shipped on dry ice to the University of Chicago and stored at –35ºC until it was assayed for testosterone, Cort, and OT in the Mateo lab at the University of Chicago's Institute for Mind and Biology. The serum was assayed for testosterone using a polyclonal anti-testosterone antibody and testosterone-HRP obtained from UC Davis. This EIA process has been validated in the Mateo lab for linearity and recovery for human serum. Cort was assayed using a Corti-Cote RIA kit (ICN Biomedicals, Costa Mesa, CA). The serum samples were assayed for OT using Assay Design's RIA Oxytocin Enzyme Immunoassay Kit (#901-153; Ann Arbor, MI). OT was extracted according to the procedure outlined in the Oxytocin Enzyme Immunoassay kit, except for clarification in a room temperature centrifuge at 14,000x*g*. The high and low intra-assay CVs for the OT plates were 1.29% and 2.45% respectively, calculated using percent bound.

Prosocial behavior measures

Subjects were administered an expanded 60-item version of the Self-Report Altruism scale, which has held up to peer evaluation and been successfully tested across a variety of cultures and countries (Johnson et al., 1989; Rushton et al., 1981), including five additional and three modified questions appropriate for Russia. A total of eight questions were negatively worded and reverse-scored in the final analysis to increase validity of the scale, and one was removed due to lack of salience for the Russian experience. Questions range from the mundane: "I have delayed an elevator," to the dramatic: "I have saved someone's life." Respondents mark the frequency of behavior for each question: never, once, more than once, often, very often, with responses measured as a Likert scale from one to five. Altruism scores were computed by reverse-scoring the eight negatively worded questions, then adding all 60 questions and calculating the mean for comparison across scales.

Following the Self-Report Altruism scale, subjects were administered the 30-item Multi-Dimensional Emotional Empathy Scale (Caruso & Mayer, 1998). This scale was chosen because it measures emotional, non-cognitive responses, so the correlation to the Self-Report Altruism Scale is neither obvious nor expected. The scale includes items ranging from "Certain pieces of music can really move me," and "I don't cry easily," to "I feel good when I help someone out." Questions are measured one to five, from strongly disagree to strongly agree. Six of the questions were reverse-scored in the original scale. Empathy scores were computed by reverse-scoring negatively worded questions, then adding all 30 questions and calculating the mean for comparison. Internal consistency for both scales was calculated using coefficient alpha.

Data analysis

Data were analyzed using Intercooled Stata 10.0 for Macintosh using primarily non-parametric statistics. OT and testosterone were log-transformed for normality. The relationship between Likert scales, and Likert scales and endocrine measures was analyzed using Spearman's *rho*. Pearson's r was used to determine relationship among normal-transformed variables. Student's t-test and Mann-Whitney U (z) were used to analyze variance of means across categorical variables, while ordered logistic regression (ologit z) was used to control across multiple variables.

Results

The study found no direct association between prosocial behavior and basal endocrine measures, listed in Table 1.

Table 1: Summary statistics and spearman correlates of basal endocrine levels and prosocial behavior scores ($N = 44$)

	Self-report Altruism M±SD: 2.5±0.41, Min/Max: 1.85/3.75	**Emotional Empathy** M±SD: 3.4±0.44, Min/Max: 2.33/4.37
Oxytocin (pg/mL ÷ 8, concentration factor) M±SD: 4.06±1.07, Min/Max: 2.14/6.62	*rho* = 0.03, p = 0.86	*rho* = -0.18, p = 0.25
Testosterone (ng/mL *100, dilution factor) M±SD: 24.76±11.26, Min/Max: 10.2/67.7	*rho* = 0.08, p = 0.62	*rho* = -0.04, p = 0.8
Cortisol (ug/dL) M±SD: 7.69±2.37, Min/Max: 2.6/12.16	*rho* = 0.17, p = 0.26	*rho* = 0.18, p = 0.23

OT and Cort were negatively correlated as predicted ($N = 44$, $r = -0.19$, $p = 0.23$), but not significantly so. However, a subset of individuals aged 18-26 (the age of volunteers for the AAI), exhibited a strong negative relationship between OT and Cort (Fig.1: $N = 32$, $r = -0.33$, $p = 0.07$). This was confirmed through ordered logistic analysis ($z = -2.49$, $p = 0.01$), controlling for testosterone and age. The older-aged 27-46 subset exhibited a positive, but non-significant relationship between OT and Cort ($N = 12$, $r = 0.15$, $p = 0.64$), as seen in Fig.1. Similarly, testosterone was negatively associated with age (*z* = -2.05, *p* = 0.04), controlling for OT and Cort, but only for the 27 to 46 subgroup. As with testosterone, this raises questions about the relationship between OT and Cort as the individual ages, suggesting that the anxiolytic effect of OT diminishes with age.

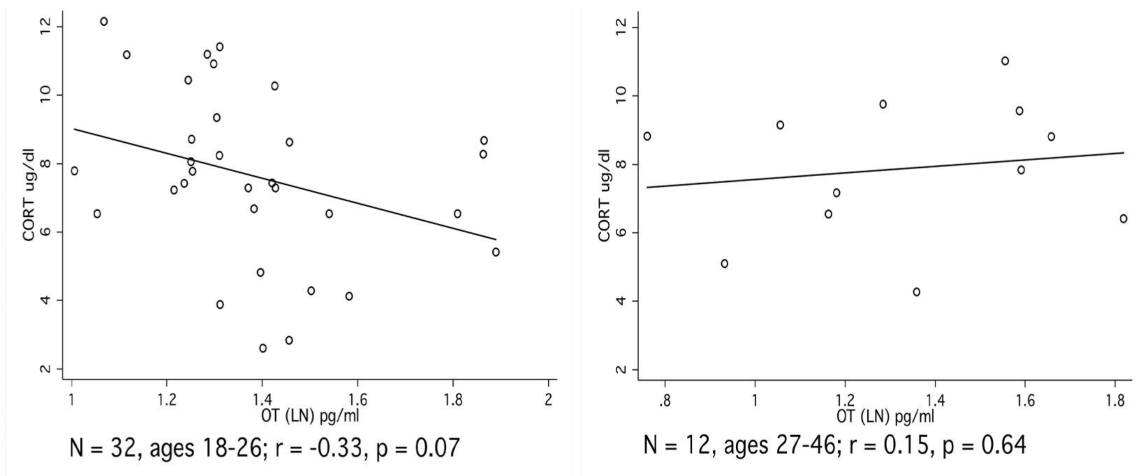

Fig. 1: Cortisol and log-transformed oxytocin, with regression line, by age group

The study did find a significant positive correlation between emotional empathy and helping behavior for the total population (*N* = 44, *rho* = 0.44, *p* = 0.003). Emotional empathy is a strong predictor of helping behavior as measured in the two scales, confirming the link between empathy and allocooperation (Davis, 1994). Further, the fact that the empathy scale measured emotional affect and the altruism scale measured frequency of behavior suggests that individuals are predisposed to allocooperation in a manner that influences cognitively mediated behavior. The alpha reliability for the Expanded Self-Report Altruism Scale scores was 0.92 (mean±SD altruism, 2.5±0.41), and for the Emotional Empathy Scale scores was 0.86 (mean±SD empathy, 3.4±0.44).

Although prosocial behavior was not associated with endocrine measures, it was significantly associated with marital status and fatherhood, suggesting that affiliative and helping behaviors are expressed through similar pathways. Helping behavior was significantly associated with marital status (Fig.2: *N* = 44, *z* = -2., *p* = 0.05), but not children (*N* = 43, *z* = -1.46, *p* = 0.14); whereas empathy was significantly associated with children (Fig.3*:* *N* = 43, *z* = -2.09, *p* = 0.04), but not marital status (*N* = 44, *z* = -1.79, *p* = 0.07). This relationship was complicated by age, which was significantly associated with altruism (*N* = 44, *rho* = 0.48, *p* = 0.001) and empathy (*N* = 44, *rho* = 0.36, *p* = 0.02), as well as marital status (*N* = 44, *z* = -3.99, *p* = 0.001) and children (*N* = 43, *z* = -3.51, *p* = 0.001).

Helping behavior varied significantly by age group (18-26 (*N* = 32) vs. 27-46 (*N* = 12): *z* = -2.003, *p* = 0.045), but empathy did not suggesting that empathy remains stable over time, whereas frequency of helping behavior tends to increase with experience. However, the effect of age and experience was strongest in questions relating to material resources, such as donations to charity (z = -2.419, p = 0.016), and owning a car to sacrifice a parking spot (z = -2.026, p = 0.043), or yield one's right-of-way (z = -2.066, p = 0.039), and did not show an effect in stronger challenges to fitness such as physically defending another's honor (z = 1.161, p = 0.246), or saving another's life (z = -0.420, p = 0.675). Ordered logistic regression demonstrated that age (but not age group) was a significant predictor for frequency of helping behavior when controlling for marital status ($z = 1.98$, $p = 0.05$) and presence of children ($z = 2.34$, $p = 0.02$), but not a significant predictor for empathy, when controlling for marital status ($z = 1.40$, $p = 0.16$) or children ($z = 1.21$, $p = 0.23$). Presence of children did approach significance for empathy when controlling for age group ($z = 1.80$, $p = 0.07$), strengthening the hypothesis that children have an effect on empathic concern linked to prosocial behavior beyond the effect of age.

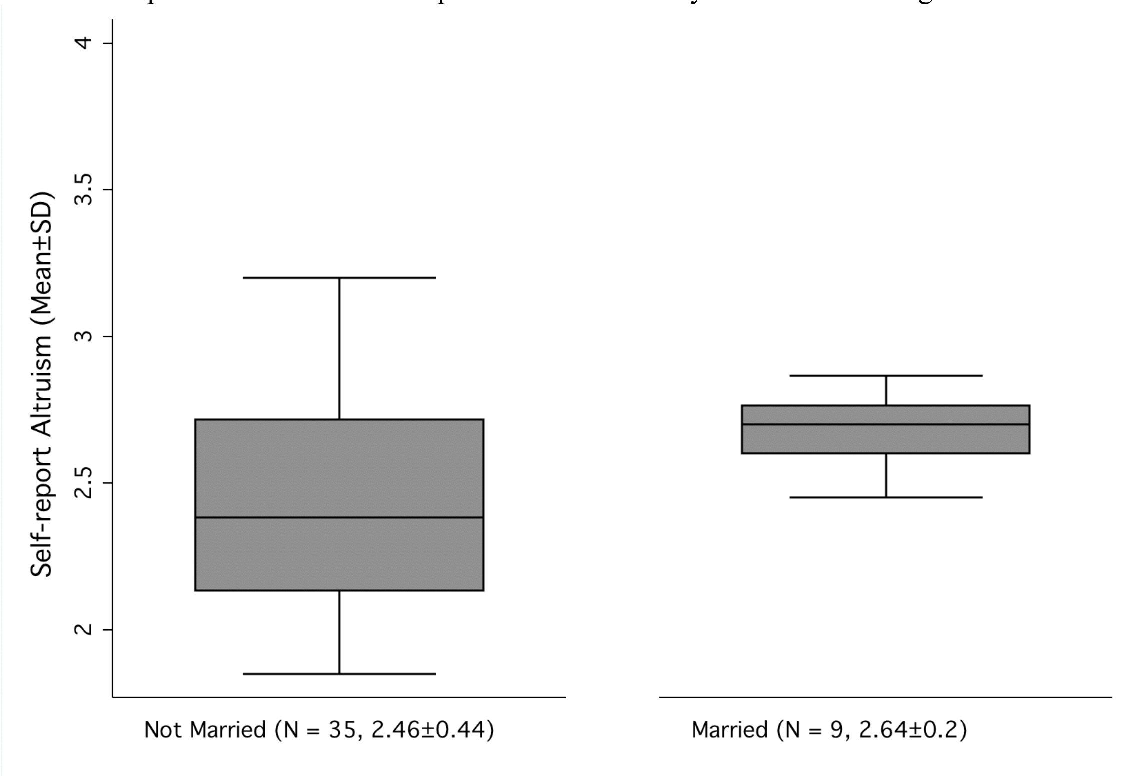

Fig.2: Married adult males in Russia reported higher helping behavior scores than their unmarried counterparts; Mann-Whitney $z = -2$, $p = 0.05$

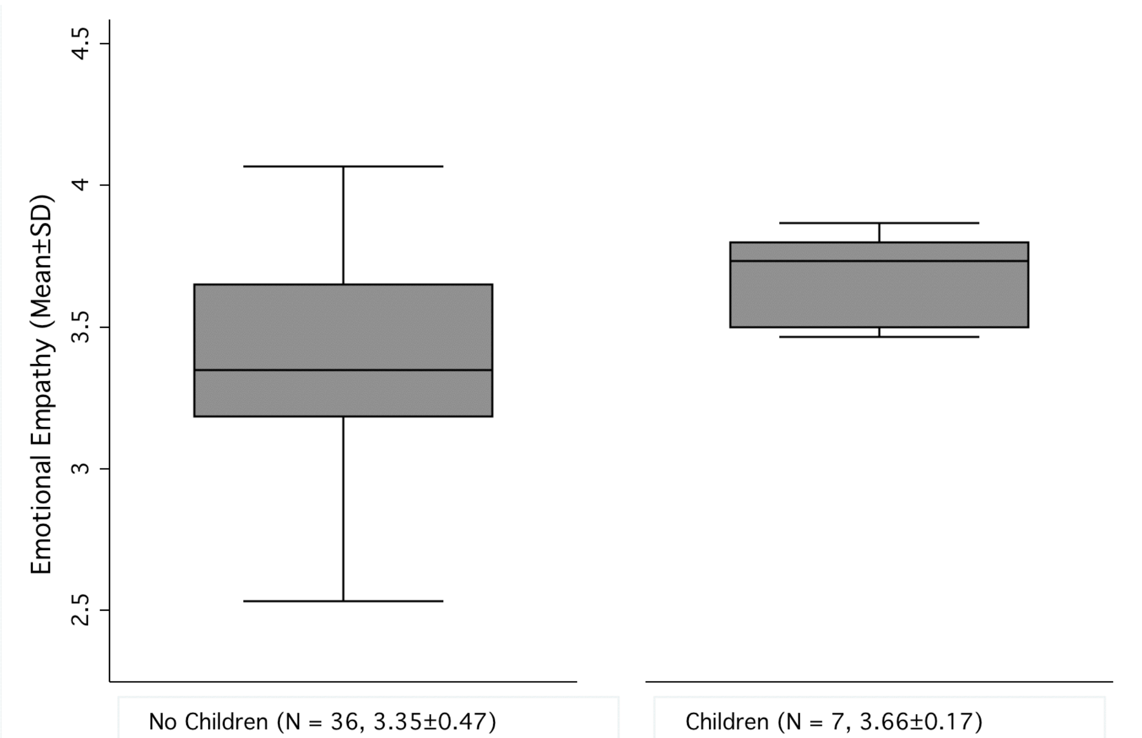

Fig.3: Adult male fathers in Russia reported higher emotional empathy scores than their childless counterparts; Mann-Whitney z = -2.09, p = 0.04

One unusual endocrine finding merits reporting. There was a strong association between testosterone and ethnicity: non-ethnic Russian minorities exhibited significantly higher basal levels of testosterone than their ethnic Russian counterparts (two-tailed $t = -2.27$, $p = 0.03$), and this relationship held after controlling for age and occupation (ologit $z = 2.42$, $p = 0.02$). There was also a relationship between occupation (comparing blue collar/clerical to students/doctors) and testosterone (two-tailed $t = -1.95$, $p = 0.06$), that gained significance controlling for age (ologit $z = 2.46$, $p = 0.01$).

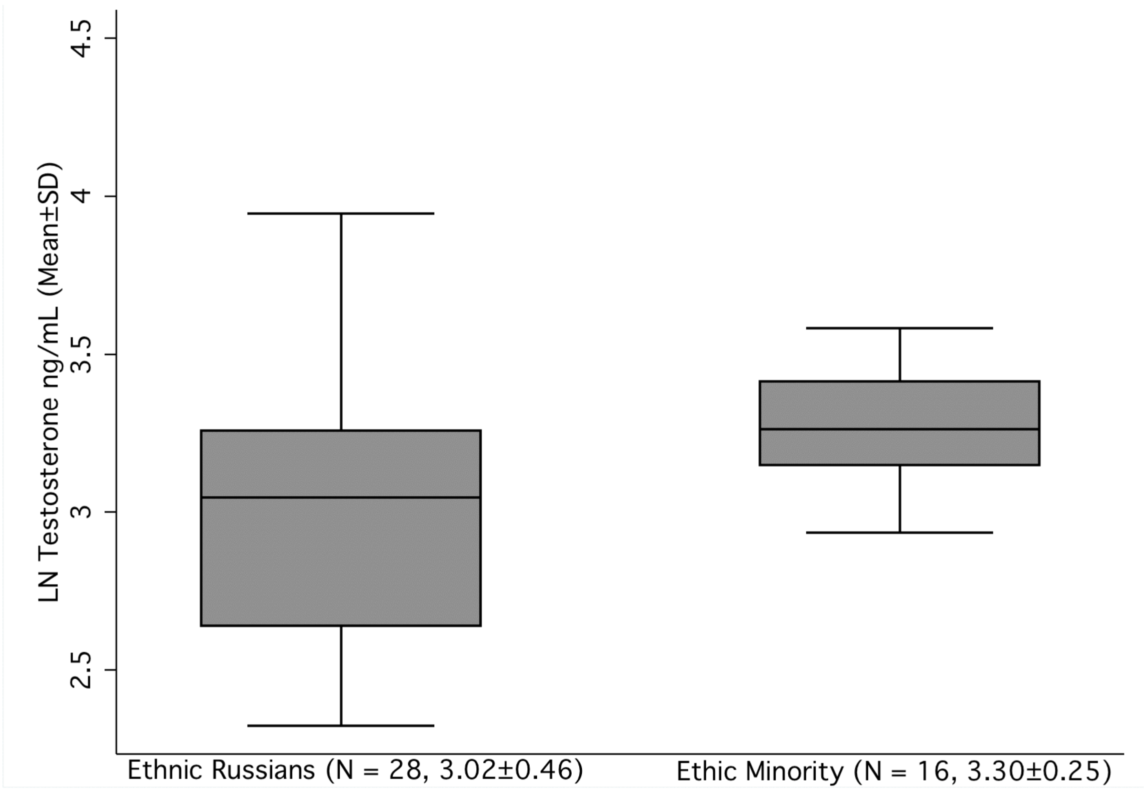

Fig.4: Self-described ethnic minorities in Russia exhibited higher concentrations of basal testosterone, measured in plasma, than their ethnic Russian counterparts; Mann-Whitney $z = -2.48$, $p = 0.01$

Discussion

Contrary to expectations, the basal endocrine measures of OT, Cort, and testosterone were not associated with either frequency of helping behavior or emotional empathy (Table 1). However, helping behavior was associated with marital status (Fig.2), and emotional empathy was associated with presence of children (Fig.3), two conditions that have been linked to OT expression. Animal models have shown OT to be causally associated with both parental and alloparental investment, and pair bonding (Lim & Young, 2006; Olazabal & Young, 2006), and experiments with human subjects have shown increased rates of prosocial behavior, measured through monetary transfers, associated with intra-nasally administered OT (Kosfeld et al., 2005; Zak, 2007). There is only limited evidence associating endogenous OT levels with prosocial behavior in humans (Zak, Kurzban, & Matzner, 2005), and this study failed to replicate those findings.

The main limitations were the observational nature of the present study relying on a single blood-draw to measure endocrine levels. Although multiple plasma measures would have established a more rigorous baseline for observation in this study, observed changes in behavior linked to OT have mostly followed potent infusion with OT, so a possible explanation for why the findings did not reject the null hypothesis is that basal endocrine concentrations are not sufficient to promote allocooperative behavior. Instead what must be examined is acute endocrine response with measurements taken prior to and following an experimental challenge. Positive social contact can lead to a burst of oxytocin, and it is this elevated endocrine level that is necessary to bind with oxytocin receptors and affect mood and behavior (Uvnas-Moberg, 1998). Future research must examine the effect of socially induced acute OT response and a range of prosocial behaviors to make a compelling case for OT as a proximate endocrine mechanism for allocooperation.

It has been suggested that OT mediates cooperative behaviors by acting on the HPA axis to lower glucocorticoid levels and reduce activity in the amygdala, allowing for the expression of approach and helping behaviors (Kirsch et al., 2005). This study did not find a relationship between basal Cort levels and prosocial behavior; it did, however, find the expected inverse relationship between Cort and OT among younger, but not older subjects (Fig.1). The amplitude of arginine vasopressin release, a neuropeptide similar to oxytocin, decreases with age in males, but OT release does not appear to vary with age (Forsling et al., 1998), so further research will need to examine the effect of age on both basal and acute OT secretion and Cort response. There is also a number of studies that have found discrepancies in the relationship between Cort and OT related to depression, social isolation, and early separation from parents, so it is possible one of these conditions played a role in the observed differences by age group, but this seems unlikely (Grippo, Cushing, & Carter, 2007; Meinlschmidt & Heim, 2007; Taylor et al., 2006).

OT also appears to act on the fusiform face area to improve individuals' empathic ability to read affective mental states and respond appropriately (Domes et al., 2007). Although basal OT and empathy were not associated in this study, we did confirm the hypothesis that emotional empathy is a strong predictor of helping behavior, and empathy was strongly associated with the presence of children, suggesting a role for OT.

While pair bonding and parental care have been causally associated with OT, romantic involvement and fatherhood have been associated with reduced testosterone in human males (Gray, Parkin, & Samms-Vaughan, 2007). This study did not find an association between basal testosterone, prosocial behavior, marital status, or children, so, as with Cort and OT levels, response levels merit further examination.

Testosterone did vary significantly between ethnic Russians and ethnic minorities, primarily from the Caucasus, but this might have varied due to social competition associated with migration and ethnic rivalry, social status associated with occupation, since students and doctors were overrepresented among ethnic minorities that participated in the study, or genetic differences similar to those found between East Asian and European samples (Heald et al., 2007; Jakobsson et al., 2006; Van Houten & Gooren, 2000).

The study findings do support the hypothesis that reciprocal altruism and kin selection are connected, since the presence of children and marriage showed a strong correlation with allocooperation. Rather than encouraging reduced cooperation, pair bonding and child rearing were tied to increased levels of allocooperation. The present results do not rule out but do call into question oxytocin as a proximate mechanism, and indicate that an experimental design measuring pre and post endocrine levels is needed to examine the relationship between acute OT response levels and allocooperation. An examination of acute oxytocin levels following a tactile stimulus is the next step for investigation, and a manipulation involving a standardized interaction of fathers grooming their children followed by a cooperation challenge is underway to build on the present study.

Conclusion

This observational study found no association between circulating basal endocrine measures (OT, Cort, and testosterone) and prosocial measures of emotional empathy and frequency of helping behavior. However, as expected, emotional empathy was a significant predictor of frequency of helping behavior, and the former was associated with fatherhood, and the latter with marital status, suggesting that affiliative behaviors causally associated with OT and helping behaviors are expressed through similar pathways. Testosterone varied significantly between ethnic and non-ethnic Russians, but did not vary by marital status or presence of children. Contrary to experimental findings with centrally administered OT, the study finds no evidence for the hypothesis that frequency of quotidian prosocial behavior and basal OT are positively correlated, and limited but compelling evidence that affiliative and prosocial behaviors operate along similar pathways.

References

Bales, K. L., Kim, A. J., Lewis-Reese, A. D. & Carter, C. S. (2004). Both oxytocin and vasopressin may influence alloparental behavior in male prairie voles. *Hormones and Behavior, 45*(5), 354-361.

Bartz, J. A. & Hollander, E. (2006). The neuroscience of affiliation: Forging links between basic and clinical research on neuropeptides and social behavior. *Hormones and Behavior, 50*(4), 518-528.

Baumgartner, T., Heinrichs, M., Vonlanthen, A., Fischbacher, U. & Fehr, E. (2008). Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. *Neuron, 58*(4), 639-650.

Born, J., Lange, T., Kern, W., McGregor, G. P., Bickel, U. & Fehm, H. L. (2002). Sniffing neuropeptides: a transnasal approach to the human brain. *Nature Neuroscience, 5*(6), 514-516.

Brown, K. M. (1998). Proximate and ultimate causes of adoption in ring-billed gulls. *Animal Behaviour, 56*(6), 1529-1543.

Carter, C. S., Pournajafi-Nazarloo, H., Kramer, K. M., Ziegler, T. E., White-Traut, R., Bello, D., et al. (2007). Oxytocin: Behavioral associations and potential as a salivary biomarker. *Annals of the New York Academy of Sciences, 1098* (Oral-Based Diagnostics), 312-322.

Caruso, D. R. & Mayer, J. D. (1998). A Measure of emotional empathy for adolescents and adults. Unpublished empathy scale. University of New Hampshire.

Chen, L. C., Wittgenstein, F. & McKeon, E. (1996). The upsurge of mortality in Russia: Causes and policy implications. *Population and Development Review, 22*(3), 517-530.

Cho, M. M., DeVries, A. C., Williams, J. R.,& Carter, C. S. (1999). The effects of oxytocin and vasopressin on partner preferences in male and female prairie voles (Microtus ochrogaster). *Behavioral Neuroscience, 113*(5), 1071-1079.

Davis, M. H. (1994). *Empathy: a social psychological approach*. Madison, Wis.: Brown & Benchmark Publishers.

Dawkins, R. (1989). *The selfish gene* (New ed.). Oxford ; New York: Oxford University Press.

Domes, G., Heinrichs, M., Michel, A., Berger, C. & Herpertz, S. C. (2007). Oxytocin improves "mind-reading" in humans. *Biological Psychiatry, 61*(6), 731-733.

Feldman, R., Weller, A., Zagoory-Sharon, O. & Levine, A. (2007). Evidence for a neuroendocrinological foundation of human affiliation: Plasma oxytocin levels across pregnancy and the postpartum period predict mother-infant bonding. *Psychological Science, 18*(11), 965-970.

Field, A. J. (2001). *Altruistically inclined? : the behavioral sciences, evolutionary theory, and the origins of reciprocity*. Ann Arbor: University of Michigan Press.

Forsling, M. L., Montgomery, H., Halpin, D., Windle, R. J., & Treacher, D. F. (1998). Daily patterns of secretion of neurohypophysial hormones in man: Effect of age. *Experimental Physiology, 83*(3), 409-418.

Fries, A. B. W., Ziegler, T. E., Kurian, J. R., Jacoris, S. & Pollak, S. D. (2005). Early experience in humans is associated with changes in neuropeptides critical for regulating social behavior. *Proceedings of the National Academy of Sciences of the United States of America, 102*(47), 17237-17240.

Gimpl, G. & Fahrenholz, F. (2001). The oxytocin receptor system: Structure, function, and regulation. *Physiological Reviews, 81*(2), 629-683.

Gray, P. B., Parkin, J. C. & Samms-Vaughan, M. E. (2007). Hormonal correlates of human paternal interactions: A hospital-based investigation in urban Jamaica. *Hormones and Behavior, 52*(4), 499-507.

Gray, P. B., Yang, C. F. J., & Pope, H. G. (2006). Fathers have lower salivary testosterone levels than unmarried men and married non-fathers in Beijing, China. *Proceedings of the Royal Society B-Biological Sciences, 273*(1584), 333-339.

Grippo, A. J., Cushing, B. S. & Carter, C. S. (2007). Depression-like behavior and stressor-induced neuroendocrine activation in female prairie voles exposed to chronic social isolation. *Psychosomatic Medicine, 69*(2), 149-157.

Hamilton, W. D. (1964). The genetical evolution of social behavior I and II. *Journal of Theoretical Biology, 7*(1), 1-16, 17-32.

Heald, A. H., Patel, J., Anderson, S. G., Vyas, A., Rudenski, A., Hughes, E., et al. (2007). Migration is associated with lower total, but not free testosterone levels in South Asian men. *Clinical Endocrinology, 67*(5), 651-655.

Heinrichs, M., Baumgartner, T., Kirschbaum, C. & Ehlert, U. (2003). Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biological Psychiatry, 54*(12), 1389-1398.

Jakobsson, J., Ekstrom, L., Inotsume, N., Garle, M., Lorentzon, M., Ohlsson, C., et al. (2006). Large differences in testosterone excretion in Korean and Swedish men are strongly associated with a UDP-glucuronosyl transferase 2B17 polymorphism. *Journal of Clinical Endocrinology and Metabolism, 91*(2), 687-693.

Johnson, R. C., Danko, G. P., Darvill, T. J., Bochner, S., Bowers, J. K., Huang, Y. H., et al. (1989). Cross-cultural assessment of altruism and its correlates. *Personality and Individual Differences, 10*(8), 855-868.

Kirsch, P., Esslinger, C., Chen, Q., Mier, D., Lis, S., Siddhanti, S., et al. (2005). Oxytocin modulates neural circuitry for social cognition and fear in humans. *Journal of Neuroscience, 25*(49), 11489-11493.

Komdeur, J. (2006). Variation in individual investment strategies among social animals. *Ethology, 112*(8), 729-747.

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature, 435*(7042), 673-676.

Lee, D. Y., Lee, J. Y., & Kang, C. H. (2003). Development and validation of an Altruism Scale for Adults. *Psychological Reports, 92*(2), 555-561.

Lee, P. R., Brady, D. L., Shapiro, R. A., Dorsa, D. M. & Koenig, J. I. (2007). Prenatal stress generates deficits in rat social behavior: Reversal by oxytocin. *Brain Research, 1156*, 152-167.

Levine, A., Zagoory-Sharon, O., Feldman, R. & Weller, A. (2007). Oxytocin during pregnancy and early postpartum: Individual patterns and maternal-fetal attachment. *Peptides, 28*(6), 1162-1169.

Lim, M. M. & Young, L. J. (2006). Neuropeptidergic regulation of affiliative behavior and social bonding in animals. *Hormones and Behavior, 50*(4), 506-517.

Mateo, J. M. (2004). Recognition systems and biological organization: The perception component of social recognition. *Annales Zoologici Fennici, 41*(6), 729-745.

McCarthy, M. M. (1990). Oxytocin inhibits infanticide in female house mice (Mus domesticus). *Hormones and Behavior, 24*(3), 365-375.

McIntyre, M., Gangestad, S. W., Gray, P. B., Chapman, J. F., Burnham, T. C., O'Rourke, M. T., et al. (2006). Romantic involvement often reduces men's testosterone levels - but not always: The moderating role of extrapair sexual interest. *Journal of Personality and Social Psychology, 91*(4), 642-651.

Meinlschmidt, G. & Heim, C. (2007). Sensitivity to intranasal oxytocin in adult men with early parental separation. *Biological Psychiatry, 61*(9), 1109-1111.

Neumann, I. D. (2002). Involvement of the brain oxytocin system in stress coping: interactions with the hypothalamo-pituitary-adrenal axis. In *Vasopressin and Oxytocin: from Genes to Clinical Applications* (Vol. 139, pp. 147-162). Amsterdam: Elsevier Science Bv.

Notzon, F. C., Komarov, Y. M., Ermakov, S. P., Sempos, C. T., Marks, J. S. & Sempos, E. V. (1998). Causes of declining life expectancy in Russia. *Jama-Journal of the American Medical Association, 279*(10), 793-800.

Olazabal, D. E. & Young, L. J. (2006). Species and individual differences in juvenile female alloparental care are associated with oxytocin receptor density in the striatum and the lateral septum. *Hormones and Behavior, 49*(5), 681-687.

Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology, 57*(4), 405-435.

Rousset, F. & Roze, D. (2007). Constraints on the origin and maintenance of genetic kin recognition. *Evolution, 61*(10), 2320-2330.

Rushton, J. P., Chrisjohn, R. D., & Fekken, G. C. (1981). The altruistic personality and the Self-Report Altruism Scale. *Personality and Individual Differences, 2*(4), 293-302.

Taylor, S. E., Gonzaga, G. C., Klein, L. C., Hu, P. F., Greendale, G. A. & Seeman, T. E. (2006). Relation of oxytocin to psychological stress responses and hypothalamic-pituitary-adrenocorticaI axis activity in older women. *Psychosomatic Medicine, 68*(2), 238-245.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology, 46*(1), 35-57.

Uvnas-Moberg, K. (1998). Oxytocin may mediate the benefits of positive social interaction and emotions. *Psychoneuroendocrinology, 23*(8), 819-835.

Van Houten, M. E. & Gooren, L. J. G. (2000). Differences in reproductive endocrinology between Asian men and Caucasian men: a literature review. *Asian Journal of Andrology, 2*(1), 13-20.

Wisenden, B. D. (1999). Alloparental care in fishes. *Reviews in Fish Biology and Fisheries, 9*(1), 45-70.

Witt, D. M., Winslow, J. T. & Insel, T. R. (1992). Enhanced social interactions in rats following chronic, centrally infused oxytocin. *Pharmacology Biochemistry and Behavior, 43*(3), 855-861.

Zak, P. J. (2007). Oxytocin increases generosity in humans. *PLoS ONE, 2*(11), e1128.

Zak, P. J., Kurzban, R. & Matzner, W. T. (2005). Oxytocin is associated with human trustworthiness. *Hormones and Behavior, 48*(5), 522-527.

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