When Two Become One: The Role of Oxytocin in Interpersonal Coordination and Cooperation

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Abstract

■ Cooperation involves intentional coordinated acts performed to achieve potentially positive outcomes. Here we present a novel explanatory model of cooperation, which focuses on the role of the oxytocinergic system in promoting interpersonal coordination and synchrony. Cooperation was assessed using a novel computerized drawing task that may be performed individually or cooperatively by two participants who coordinate their actions. Using a within-subject crossover design, 42 participants performed the task alone and with a partner following the administration of placebo and oxytocin 1 week apart. The data indicate that following placebo administration, participants performed better alone than in pairs. Yet, the administration of oxytocin improved paired performance up to the level of individual performance. This effect depended on the personality traits of cooperativeness or competitiveness. It is concluded that oxytocin may play a key role in enhancing social synchrony and coordination of behaviors required for cooperation. ■

INTRODUCTION

Many human and nonhuman activities are performed in cooperation and involve the coordination of voluntary acts to potentially generate benefits that could not have been brought about individually (Brosnan & de Waal, 2002). In nature, cooperation has been noted among many species in a variety of behavioral strategies, including within-group aggressive alliances, intergroup aggression and defense, and group hunting (Hall & Peters, 2008; Heinsohn & Packer, 1995; Scheel & Packer, 1991; Boesch & Boesch, 1989; Kruuk, 1972). Synchronized coordinated behaviors have also been noted in other contexts of social behaviors, such as in ritualized aggression in territorial disputes (Beecher, Campbell, & Nordby, 2000; Serpell, 1981; Schuster, 1976). In mating rituals, it has been suggested that the level of behavioral matching provides a criterion for mate selection by evoking psychological states of attraction (Spoon, Millam, & Owings, 2006; Maynard Smith, 1978).

In humans, synchronized behaviors manifest themselves in behavioral matching, whereby individuals tend to coordinate their actions and mimic the postures or actions of others with or without awareness or conscious intent (Noy, Dekel, & Alon, 2011; Richardson, Marsh, & Baron, 2007; Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007; Tognoli, Lagarde, DeGuzman, & Kelso, 2007; Sebanz, Bekkering, & Knoblich, 2006; Chartrand & Bargh, 1999; Bernieri & Rosenthal, 1991; Bernieri, 1988; LaFrance, 1979). These coordinated synchronized actions may be pleasurable and therefore may be utilized in forming and maintaining group cohesion (Sober & Wilson, 1998). Furthermore, behavioral synchrony or the ability to match and follow each other and focus attention while interacting was found to be important in mother–infant relationships and to be associated with gains in social communication (Siller & Sigman, 2002). In line with the suggested function of interpersonal synchrony in evoking prosocial emotions (Siller & Sigman, 2002; Maynard Smith, 1978), it was recently suggested that the oxytocinergic system plays a major role in the interactive reciprocity and dyadic synchronized behavior characterizing the mother–infant relationship (Feldman, Magori-Cohen, Galili, Singer, & Louzoun, 2011) as well as romantic relationships (Schneiderman, Zagoory-Sharon, Leckman, & Feldman, 2012).

Oxytocin (OT), a nine-amino-acid cyclic neuropeptide produced in the paraventricular nucleus of the hypothalamus, has a well-established role in reproduction and pair-bond formation (e.g., Carter, Grippo, Pournajafi-Nazarloo, Ruscio, & Porges, 2008). Centrally released OT has been implicated in the regulation of a wide range of social behaviors, such as social motivation and approach behaviors (Lim & Young, 2006; Witt, Winslow, & Insel, 1992) as well as the formation and expression of social memories required for the discrimination and recognition of a familiar individual (Bielsky & Young, 2004; Choleris et al., 2003; Dluzen, Muraoka, Engelmann, Ebner, & Landgraf, 2000; Ferguson et al., 2000; Popik & van Ree, 1991). In small rodents, cerebral ventricular infusions of OT lead to a general

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nonselective increase in social affiliation and a reduction in anxiety and aggression (Harmon, Huhman, Moore, & Albers, 2002; Witt et al., 1992). In addition to modulating social behaviors, OT has been implicated in reducing the physiological and psychological correlates of stress (Heinrichs, Baumgartner, Kirscbaum, & Ehlert, 2003) and in modulating the brain areas and neural circuitries involved in processing fear-related information (Petrovic, Kalisch, Singer, & Dolan, 2008; Kirsch et al., 2005).

Moreover, it has been demonstrated in humans that a single dose of intranasally administered OT is sufficient to produce a substantial increase in mental state attribution (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007), to improve accurate social perception (Fischer-Shofty, Shamay-Tsoory, Harari, & Levkovitz, 2010), and to elevate levels of "resonance" emotional empathy (Hurlemann et al., 2010). Furthermore, Zak and colleagues (2004, 2005) found that OT levels are increased after receiving a social signal of trust and that higher OT levels are associated with trustworthy behaviors. Similarly, Kosfeld and colleagues (2005) reported that the intranasal administration of OT elevates trust and affects the willingness to take social risks arising from interpersonal interactions. Likewise, OT has been found to increase trust and promote cooperative behaviors in different decision-making tasks by reducing "fear of betrayal" or betrayal aversion (De Dreu et al., 2012; Rilling et al., 2012; Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008; Kosfeld et al., 2005).

It should be considered that cooperation in these studies was assessed in economic tasks involving monetary gains and risks. These studies represent the prevailing paradigms of cooperation in humans that relay on economic decision-making tasks, where the propensity to cooperate is measured by the subjects' choices to cooperate or to act selfishly by "defecting." Thus, such tasks may inherently provoke "fear of betrayal" and OT administration may promote cooperation by reducing this fear due to its anxiolytic properties (Petrovic et al., 2008; Kirsch et al., 2005; Heinrichs et al., 2003).

Yet, it may be that OT promotes cooperation in a manner that is different from reducing "fear of betrayal." As most forms of cooperation in nature and among humans involve interpersonal coordination (Neo, 2006), and given the role of OT in pair bonding (for a review, see de Boer, van Buel, & Ter Horst, 2012) and synchrony (Feldman, 2012), it may be that OT promotes cooperation by increasing motor coordination and synchrony of actions and behaviors in a manner which is dissociated from fear of betrayal.

To test the hypothesis that OT promotes cooperation by increasing interpersonal coordination, a novel cooperative task was designed on the basis of the children's "Etch-a-Sketch" game. Utilizing this task allows the assessment of performance for a single subject with full control of all the control keys, as well as for pairs of subjects that have to cooperate by coordinating their actions in controlling the keys (see Tools section below for a full description of the task). The "Etch-a-Sketch" task was employed in the current study to evaluate the role of the oxytocinergic system in promoting cooperation by increasing interpersonal coordination and synchrony.

METHODS

Participants

Forty-two healthy men and women (age range = 23–34 years) were recruited by ads and were compensated for their participation. All participants gave their written informed consent before their participation. Exclusion criteria included medical or psychiatric illness and use of any substantial medication or other substance (including heavy smoking). All participants were instructed to avoid psychotropic substances, such as caffeine and nicotine, for at least 12 hr before the experiment. Because of the significant hormonal interactions between OT and estrogen, information regarding menstrual cycle and contraceptive pills was collected among the women. Only women who signed a form confirming that they are not pregnant were allowed to participate in the study. The study protocol was approved by Shalvata Hospital's ethics committee.

Substance Administration

A double-blind placebo (PL)-controlled within-subject crossover design was used, with participants randomly assigned into groups before the experiment for the first administration of either PL or OT (22 received first OT and 20 first PL). A single dose of 24 IU OT or PL was intranasally administered (three puffs per nostril, each puff containing 4 IU) 45 min before the task performance. The PL contained all inactive ingredients except for the neuropeptide. At the second session of the experiment, 7 days later, participants underwent the same procedure with the other substance (i.e., PL or OT). Dosage and waiting time corresponded to those previously used in experiments designed to investigate the effect of the intranasal administration of OT on behavior in humans (Domes et al., 2010; Guastella, Mitchell, & Dadds, 2008; Kirsch et al., 2005; Kosfeld et al., 2005).

Tools

The "Etch-a-Sketch" Task

This computerized task is based on the children's game "Etch-a-Sketch" in which the object is to draw on a magnetic board with the use of two handles—one controlling the up and down movement of the marker and the other controlling the left and right movement of the marker. The participants were required to trace, in the most precise manner, seven different shapes (appearing on the monitor in random order) using a marker. The marker was controlled using the keyboard's A and S keys for left

[A] and right [S] movement and the ↑ and ↓ keys for up [↑] and down [↓] movement. The task was performed under two conditions: ALONE (single subject) or as a COUPLE (a pair of participants). In the ALONE condition, one participant controlled all the keys, whereas in the COUPLE condition, the A and S keys were controlled by one participant while the ↑ and ↓ keys were controlled by the other. The shapes that appeared on the monitor were different combinations of vertical lines, horizontal lines, and diagonal lines at varying angles (see Figure 1A). In the COUPLE condition, tracing a horizontal line required that only one participant use the A and S keys, whereas tracing a vertical line required that only the other participant use the ↑ and ↓ keys. Yet, tracing a diagonal line required that both participants work together to press the two sets of keys in a coordinated and synchronized manner. For example, pressing ↑ and S created a diagonal line going from the bottom left to the upper right: /. The angle of the diagonal line was determined by the ratio of each key pressed, such that pressing more on the ↑ and less on the S key created a steeper angle.

Scoring system: Both accuracy and RT were assessed for the ALONE and COUPLE conditions.

RT: The time to complete each item.

Accuracy: As illustrated in Figure 1(B, C), correct performance was determined by the number of pixels that the traced shape created by the participants (the blue line) deviated from the original shape (the red line). The area between the two lines (colored in pink) was created by the deviation (deviation scores). Lower scores (fewer pink pixels) indicated a more accurate precision. Scores ranged between 0, representing a perfect score (flawless tracing), and tens of thousands, representing poor accuracy and a large deviation from the original shape. In the example of Figure 1C, the participants were given a score of 1612.

In the COUPLE condition, a more accurate performance (lower scores) indicated better cooperation and coordination between the participants' key pressing.

Assessment of dispositional cooperative tendencies. Cooperative dispositions were assessed using the social value orientation (SVO) to examine the possibility that the effect of OT on cooperative performance may be modulated by a personal tendency toward cooperation or competition. The SVO indicates how people allocate outcomes for themselves and anonymous others (Van Lange & Liebrand, 1991; Messick & McClintock, 1968). The items in the task require choosing between a series of nine items involving three alternative outcome distributions with points for oneself and an anonymous other (the decomposed game technique). Each item contained a cooperative (e.g., self: 520, other: 520), an individualistic (e.g., self: 580, other: 320), and a competitive choice (e.g., self: 520, other: 120). Following their selection, participants are classified as having a cooperative, individualistic, or competitive orientation; the task is internally consistent, reliable over considerable time periods, and not associated with measures of social desirability (de Kwaadsteniet, van Dijk, Wit, & de Cremer, 2006; Parks, 1994; Platow, 1994; Van Lange & Kuhlman, 1994; Eisenberger, Kuhlman, & Cotterell, 1992).

Assessment of affective state. To rule out the possibility that OT may have a general effect on mood, which in turn may affect performance of the "Etch-a-Sketch" task, the participants' mood was examined using the Depression Adjective Check List (DACL). The DACL is a 32-item self-report instrument designed to measure affective states (Lubin, 1965). This questionnaire is widely used for the evaluation of short-term mood changes (Lubin & Riesenmy, 1996) and was therefore chosen to assess mood 45 min following the substance (OT or PL) administration.

General Procedure

Before the beginning of each testing session, the participants were shown into a waiting room with five to seven other participants whom they had never met before. While waiting, they completed a consent form with the help of a doctor, who described in detail the potential side effects of OT but did not reveal the study's goal. To

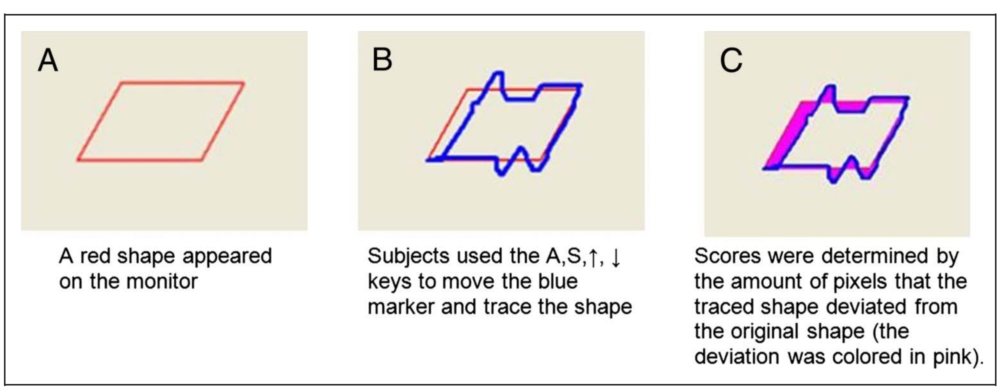

Figure 1. The "Etch-a-Sketch" task requires tracing, in the most precise manner, seven different shapes (appearing on the monitor in random order) using a marker. The marker is controlled using the keyboard's A and S keys for left [A] and right [S] movement and the ↑ and ↓ keys for up [↑] and down [↓] movement.

avoid significant interactions between the participants, the investigators did not introduce the participants to each other.

Each participant was then escorted to a separate room to receive either the intranasal OT or the PL treatment. After drug administration, the participants were asked to wait 45 min to ensure that the OT levels in the CNS had reached a plateau. During this waiting period, participants completed the SVO scale. At the end of the 45-min period, participants completed the DACL so as to track any mood changes following administration of the drug. Participants were then given the instructions for the "Etch-a-Sketch" tracing task and were asked to perform the task alone. The ALONE condition served as a baseline for basic individual motor performance and therefore it was reasoned that this condition should be performed before the COUPLE condition. Furthermore, data from a pilot study indicated that participants had more difficulties in performing the task in the COUPLE condition without any experience in manipulating the control keys on their own. Therefore, to avoid high variability in performance, participants first performed the ALONE condition.

Following performance in the ALONE condition, the participants were invited to the waiting room and the experimenter introduced each participant to her/his partner for the pair condition. The pairing of couples was planned in advance so that each participant was randomly paired with a same-sex and same-treatment partner. Although participants were not matched according to their "Etch-a-Sketch ability," as defined by their scores in the alone condition, the random design of this experiment counterbalanced such individual differences. One week later, each participant underwent the same procedure following the administration of the other substance, but with a different randomly selected same-sex, same-treatment partner.

Data Analyses

To examine the effect of treatment (OT/PL), condition (ALONE/COUPLE), and personality traits (SVO ratings of competitive, cooperative/individualistic) on performance (deviation scores and RT), a linear mixed model (LMM) was used. The LMM technique is a data analysis approach that is increasingly used in psychology to effectively address problems that general linear models, like repeated-measures ANOVA, cannot deal with (Kliegl, Wei, Dambacher, Yan, & Zhou, 2010). The LMM forte is the ability to model correctly dyadic data by handling random effects. For example, the LMM analysis was recently used to analyze consolation in dyads of chimpanzees (Fraser, Stahl, & Aureli, 2008) and contagious yawning in human dyads (Norscia & Palagi, 2011). The LMM was utilized in this study to deal with the issue of interdependence between the scores within each pair, because the LMM procedure expands the general linear model so that the data are permitted to exhibit correlated and nonconstant variability.

In the LMM analysis, we specified the following fixed effects: treatment, condition, and SVO; the interactions: Treatment × Condition and Treatment × Condition × SVO. In addition, we used the following dyadic random effects: OT dyads and PL dyads. We tested models for each combination involving the variables of interest, spanning from a single-variable model to a model including all the fixed factors and their interaction terms (full model). To select the best model, we used the Akaike's Corrected Information Criterion, and the model with a lower value of Akaike's Corrected Information Criterion was considered to be the best model.

Finally, a repeated-measures ANOVA was used to confirm that treatment did not have a general effect on mood as measured by the DACL.

RESULTS

OT Improved Cooperative Performance of the "Etch-a-Sketch" Task, but Did Not Affect Individual Performance

Utilizing an LMM, we assessed how the Treatment (OT/PL), Experimental Conditions (ALONE/COUPLE), and Social Orientation that was assessed by the SVO (cooperative, individualistic, competitive) affected performance in the "Etch-a-Sketch" task as measured by both accuracy (deviation scores) and RT (dependent variable).

Treatment, Conditions, and SVO were entered as fixed factors (including the interactions between them), and OT and PL dyads were entered as random effects (see Methods for definitions).

Accuracy

The fix effect for Conditions was found significant, $F(101.5) = 4.950$, $p = .028$, indicating that the participants' accuracy overall was better in the ALONE ($M = 639.73$, $SD = 88.60$) as compared with the COUPLE condition ($M = 784.47$, $SD = 88.60$). Although overall performance following treatment with OT ($M = 658.91$, $SD = 88.60$) was better than PL ($M = 828.13$, $SD = 88.60$), the Treatment effect did not reach significance, $F(101.5) = 3.289$, $p = .076$.

As illustrated in Figure 2, the fixed effect for the Treatment × Condition interaction was found to be significant, $F(101.5) = 9.608$, $p = .003$, suggesting that treatment had a differential effect on accurate performance of the task individually (ALONE) or cooperatively (as a COUPLE). Follow-up post hoc analysis (with correction for multiple comparisons) indicated that in the COUPLE condition accuracy was better following the administration of OT as compared with PL [$t(96) = 2.09$, $p = .039$]. Moreover, in the PL condition, the participants performed significantly more accurately individually than

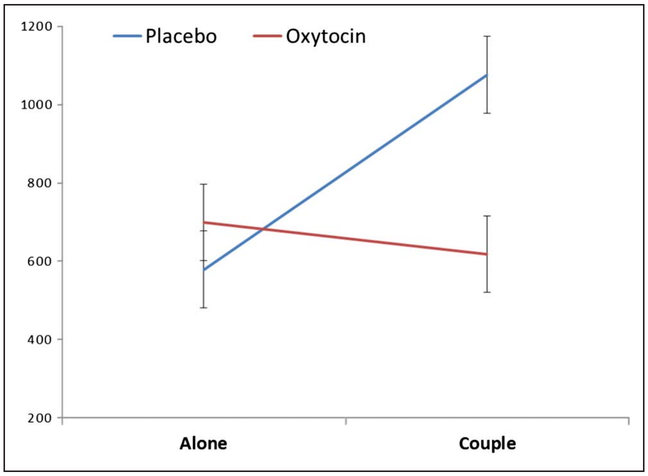

Figure 2. OT improved cooperative performance of the "Etch-a-Sketch" task but did not affect individual performance.

cooperatively as a couple [$t(96) = -3.75$, $p = .0003$]. This difference was erased by administration of OT [$t(96) = -1.71$, $p = .09$].

Furthermore, the three-way interaction Treatment × Condition × SVO was found significant, $F(101.5) = 6.455$, $p = .0019$, indicating that the OT had a differential effect depending on the social orientation of participants. Follow-up post hoc analysis (with correction for multiple comparisons) indicated that in the COUPLE condition a more accurate performance was evident following the administration of OT as compared with PL only in participants classified as competitive [$t(96) = 2.4$, $p = .018$]. On the other hand, in the ALONE condition, competitive participants were significantly more accurate in their performance following the administration of PL as compared with OT [$t(96) = -2.36$, $p = .02$].

There were no significant differences between the OT and PL conditions in the COUPLE condition in participants classified as cooperative [$t(96) = 0.02$, $p = .985$] or individualistic [$t(96) = 0.41$, $p = .682$].

Remarkably, following the administration of PL, the participants classified as competitive [$t(96) = -3.35$, $p = .00012$] and the participants classified as individualistic [$t(96) = -2.30$, $p = .023$] performed significantly less accurately in the COUPLE as compared with the ALONE condition, indicating that the COUPLE condition was particularly harder for the competitive and individualistic participants. Moreover, the participants classified as cooperative did not perform less accurately in the COUPLE as compared with the ALONE condition [$t(96) = -0.57$, $p = .572$] following the administration of OT (see Table 1).

RT

An LMM model of analyses was carried out to examine the effects of the Treatment, Condition, and SVO on RT. The analyses indicated no significant fix effect for conditions, $F(127.9) = 2.782$, $p = .098$, and treatment, $F(127.9) = 2.215$, $p = .139$, nor for the interactions Treatment × Condition, $F(127.9) = 1.683$, $p = .197$, and Treatment × Condition × SVO interaction, $F(108.7) = 6.455$, $p = .710$. Collectively these analyses suggested that treatment had no effect on the RT (see Table 1).

Table 1. Means and Standard Errors of Performance following the Administration of OT and PL in Participants Classified as Individualistic, Competitive, and Cooperative Based on the SVO

	Alone				*Couple*			
	PL		*OT*		*PL*		*OT*	
	Mean	*SE*	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*
Individual								
Deviation scores	678.97	130.74	693.16	172.50	832.13	137.61	657.14	61.74
RT	51.67	2.38	53.40	3.29	47.44	1.32196	49.18	1.64
Competitive								
Deviation scores	399.59	197.63	816.04	298.41	1467.90	565.15	494.00	134.71
RT	50.84	5.63	49.09	5.47	42.87	2.13	53.50	3.20
Cooperative								
Deviation scores	671.20	120.57	678.75	114.31	788.39	113.62	686.57	80.78
RT	48.28	2.83	48.84	2.77	46.39	2.13	47.39	1.76

Twenty-two participants were classified as individualistic, fourteen as cooperative, and six as competitive. Deviation scores represent the number of pixels that deviated from the original form. The RT measure represents the time (in seconds) to complete the task.

Speed–Accuracy Trade-off

Finally, to ensure that there was no speed–accuracy trade-off, we calculated the correlations between RT and deviation scores. These analyses indicated no significant correlation between these measures, confirming that there was no speed accuracy trade-off ($p > .05$).

Neither Sex, the Order of Drug Administration, nor the Use of Contraceptive Pills Changed the Effect of OT Administration on Performing the "Etch-a-Sketch" Task

Gender

To rule out the possibility that OT had a differential effect on performance according to sex, we carried out an LMM analyses to assess how the treatment, condition, and sex (women, men) affected deviation scores in the "Etch-a-Sketch" task (OT and PL dyads were entered as random effects). These analyses indicated that sex did not interact with treatment, $F(117.2) = 2.061$, $p = .154$. Furthermore, the three-way interaction for Sex × Condition × Treatment was found not significant, $F(117.2) = 1.538$, $p = .219$, indicating that the participants' sex did not influence the effect of OT administration on accurate performance of the task.

Contraceptive Pills

To rule out the possibility that the use of contraceptive pills may modulate the effect of OT administration on performing the "Etch-a-Sketch" task, a three-way LMM analysis was conducted, with Treatment, Condition, and Pills (on the pill, no pill, male) as the fixed effect. The three-way interaction for Pills × Conditions × Treatment was not significant, $F(117.8) = 0.154$, $p = .696$. Collectively, these analyses indicate that the participants' use of contraceptive pills did not modulate the effect of OT administration on accurate performance of the task.

Order of OT/PL Administration

To rule out the possibility that the order of treatment may modulate the effect of OT administration on performing the "Etch-a-Sketch" task, a three-way LMM analysis was conducted, with Treatment, Condition, and Order (first OT/first PL) as the fixed effect. The Order effect was not significant, $F(22.9) = 2.35$, $p = .139$, nor was the three-way interaction for Order × Conditions × Treatment, $F(114.9) = 0.054$, $p = .816$. Collectively, these analyses indicate that the order of treatment did not modulate the effect of OT administration on accurate performance of the task.

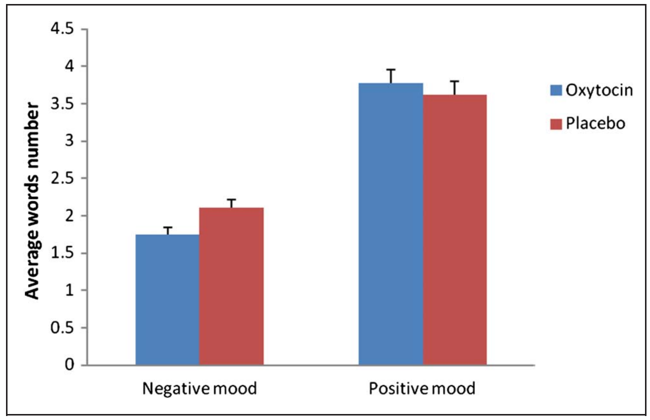

Figure 3. OT administration did not affect mood.

OT Administration Did Not Affect the Participants' Mood

DACL scores were analyzed using a two-way repeated-measures ANOVA, with Treatment and Mood (positive, negative) as the independent variables. These analyses indicated no significant main effect for Treatment, $F(1, 41) = 0.338$, *ns*. The interaction Treatment × Mood was also not significant, $F(1, 41) = 0.491$, *ns*. There was a significant main effect for Mood, $F(1, 41) = 9.464$, $p \leq .01$, indicating that the participants were generally in a positive mood (as compared with a negative mood), regardless of treatment (Figure 3).

DISCUSSION

The current study evaluated the effects of a single dose of intranasally administered OT on performing a cooperative task, utilizing a novel model of cooperation that relies on interpersonal coordination and synchronization of motor actions. OT was found to improve cooperative, but not individual, performance.

The data on accurate performance of the task following the administration of a PL indicate that the participants performed better alone than as a couple. This effect is in line with previous reports demonstrating that acting together requires additional demands, which are harder to overcome than when acting alone (Knoblich & Jordan, 2003). Yet, the administration of OT improved performance in the task to the level of individual performance, suggesting that OT improves the coordination of behaviors.

Cooperative social interactions involve interpersonal coordination and synchronization of behaviors to achieve a common goal (Nöe, 2006; Brosnan & de Waal, 2002). The couple condition in this study models coordinated action-based cooperation, as the two participants are required to coordinate and synchronize their key pressing in the "Etch-a-Sketch" tracing task in a dynamic manner that varies according to the target shape. Throughout the task, the pairs used different strategies of division of labor, as in horizontal and vertical lines, and conjoint actions for diagonal lines, to accomplish the task. Both strategies and the switching between them required paying attention to the partner's actions and coordinating one's own actions with them. The current data suggest that the oxytocinergic system may play a key role in promoting the behavioral coordination and synchronization that underlie cooperation.

In naturalistic settings, Feldman, Weller, Zagoory-Sharon, and Levine (2007) showed that plasma OT during pregnancy and postpartum predicted maternal bonding behaviors, including gaze, vocalizations, positive affect, and affectionate touch. Similarly, Gordon, Zagoory-Sharon, Leckman, and Feldman (2010) reported that paternal OT levels correlated with the degree of stimulatory parenting behaviors, such as tactile stimulation. Feldman, Gordon, and Zagoory-Sharon (2010) also found that parental and infant OT levels were interconnected and were related, in turn, to greater affect synchrony and infant social engagement.

The current data also correspond with previous reports regarding oxytocinergic functions and cooperation in different "game theory" tasks that involve reciprocal cooperation, trustworthiness, and betrayal aversion (for a review, see De Dreu, 2012). Roberts and Sherratt (1998) suggested that cooperation evolves according to increasing confidence in the relationship between the cooperators. Zak and colleagues (2004, 2005) demonstrated that OT levels are increased after receiving a social signal of trust and that higher OT levels are associated with trustworthy behaviors. Furthermore, intranasal OT administration was found to elevate trust and affected the willingness to take social risks arising from interpersonal interactions (Kosfeld et al., 2005), while also improving "mind-reading" ability (Domes et al., 2007). Continuously mounting evidence heavily supports the hypothesis that OT plays a key role in cooperation, but the mechanisms remains unclear. Whereas Rilling and colleagues (2012) suggest that OT increases the activity in the reward system, De Dreu (2012) found that the effects of OT on cooperation were mediated by "betrayal aversion."

Yet, the performance in the currently used model of cooperation does not rely on taking "economic risks," trusting one's partner, or fearing defection and betrayal. Thus, the results of this study demonstrate for the first time a key role of the OT system in a form of "motor cooperation" as performing the task as a couple is based on interpersonal coordination and synchrony of motor actions. As opposed to previous paradigms of cooperation, in this study, we modeled motor coordinated cooperation as the two participants were required to coordinate and synchronize their key pressing. Although OT improved performance in the coordination-dependent "couple" condition, it did not improve performance in the ALONE condition, further excluding the possibility that OT improves basic motor abilities. It is suggested that the oxytocinergic system may improve cooperation by promoting coordination and synchronization of motor actions and increasing attention to others, regardless of emotional states. Indeed, a single dose of intranasally administered OT was reported to increase negative emotions of both envy and gloating in a manner that corresponded with relative gains and losses during a fake monetary game of chance (Shamay-Tsoory et al., 2009). These findings were suggested to indicate that the oxytocinergic system does not promote positive pro-social emotions, but rather social salience, that is, attention to others in different social contexts (Shamay-Tsoory, 2010). This "social salience" hypothesis was further supported by studies demonstrating that a single dose of intranasally administered OT facilitated the accurate perception of "competition" among men, but "kinship" among women (Fischer-Shofty et al., 2010). It is therefore possible that OT increases the salience of social agents in a manner that enables social synchrony.

Furthermore, the effects of OT reported here were dependent upon the subject's tendency to cooperate as assessed by the SVO. We selected the SVO paradigm since it addresses related, yet distinct, aspects of cooperative behavior than the one required for cooperative performance of the "Etch-a-Sketch" task. Whereas the cooperative "Etch-a-Sketch" task involved interpersonal coordination of motor actions, the SVO assesses broad motivational orientation to either prosocial (maximizing joint outcomes), individualistic (maximizing personal outcomes), or competitive (maximizing the difference between individual and "other" outcome). Interestingly, it has been reported that the OT receptor gene is associated with differential monetary allocations in the SVO (Israel et al., 2009). Thus, the SVO classification served in the current study to both validate the cooperative "Etch-a-Sketch" task and to examine whether the administration of OT had a differential effect on participants with different social predispositions.

Indeed, we show that, in the PL condition, the participants classified as competitive and those classified as individualistic performed significantly worse in the COUPLE as compared with the ALONE condition, confirming that the competitive and individualistic individuals (also classified as proself) are better at performing alone as compared with performing in pairs. Moreover, the participants classified as cooperative did not perform worse in the COUPLE as compared with the ALONE condition.

Interestingly, the administration of OT improved only the performance of the competitive participants and not the performance of the cooperative and individualistic participants. These findings are compatible with a recent study showing that the administration of OT enhanced social-cognitive performance only in individuals who are less socially competent (Bartz et al., 2010). Although the number of participants in the competitive group is small, the improvement in the "proself" participants may indicate that OT may improve the ability to cooperate particularly in individuals with impaired ability to cooperate.

It is of note that despite the prevailing use of intranasal administration of OT, few studies have examined the relationship between the intranasal administration of OT and the endogenous oxytocinergic system. Furthermore, there is no consensus regarding a correlation between OT levels in plasma and the brain (Winslow, Noble, Lyons, Sterk, & Insel, 2003; Wotjak et al., 1998; Neumann, Ludwig, Engelmann, Dittmann, & Landgraf, 1993; Amico, Challinor, & Cameron, 1990). Yet, the consistency of behavioral changes observed following the administration of OT has been suggested to indicate that the exogenous administration of OT simulates an extreme adaptation of the naturally occurring neural condition (Fischer-Shofty et al., 2010). Moreover, the intranasal administration of OT has been found to elevate plasma levels (Domes et al., 2010) and affect salivary cortisol levels in a similar manner to that of endogenous OT released during suckling (Heinrichs et al., 2003). Other studies (e.g., Domes et al., 2007, 2010; Labuschagne et al., 2010; Baumgartner et al., 2008; Kirsch et al., 2005) have reported that the administration of OT decreases amygdaloid functioning, further supporting the effects of OT treatment and social behavior. Thus, the current study findings may suggest that the exogenous administration of OT simulated an extreme adaptation of the naturally occurring coordinated behaviors.

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REFERENCES

Amico, J. A., Challinor, S. M., & Cameron, J. L. (1990). Pattern of oxytocin concentrations in the plasma and cerebrospinal fluid of lactating rhesus monkeys (macca mulatto): Evidence for functionally independent oxytocinergic pathways in primates. *The Journal of Clinical Endocrinology & Metabolism, 71,* 1531–1535.

Bartz, J. A., Zaki, J., Bolger, N., Hollander, E., Ludwig, N. N., Kolvezon, A., et al. (2010). Oxytocin selectively improves empathic accuracy. *Psychological Science, 21,* 1426–1428.

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,* 639–650.

Beecher, M. D., Campbell, S. E., & Nordby, J. C. (2000). Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour, 59,* 29–37.

Bernieri, F. J. (1988). Coordinated movement and rapport in teacher-student interactions. *Journal of Nonverbal Behavior, 12,* 120–138.

Bernieri, F. J., & Rosenthal, R. (1991). Interpersonal coordination: Behavior matching and interactional synchrony. In R. S. Feldman & B. Rimé (Eds.), *Fundamentals of nonverbal behavior* (pp. 401–432). Paris: Editions de la Maison des Sciences de l'Homme.

Bielsky, I. F., & Young, L. J. (2004). Oxytocin, vasopressin, and social recognition in mammals. *Peptides, 25,* 1565–1574.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the taï national park. *American Journal of Physical Anthropology, 78,* 547–573.

Brosnan, S. F., & Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism. *Human Nature, 13,* 129–152.

Carter, C. S., Grippo, A. J., Pournajafi-Nazarloo, H., Ruscio, M. G., & Porges, S. W. (2008). Oxytocin, vasopressin and sociality. *Progress in Brain Research, 170,* 331–336.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology, 76,* 893–910.

Choleris, E., Gustafsson, J. A., Korach, K. S., Myglia, L. J., Ptaff, D. W., & Ogawa, S. (2003). An estrogen-dependent four-gene micronet regulating social recognition: A study with oxytocin and estrogen receptor-α and -β knockout mice. *Proceeedings of the National Academy of Sciences, 100,* 6192–6197.

de Boer, A., van Buel, E. M., & Ter Horst, G. J. (2012). Love is more than just a kiss: A neurobiological perspective on love and affection. *Neuroscience, 201,* 114–124.

De Dreu, C. K. (2012). Oxytocin modulates the link between adult attachment and cooperation through reduced betrayal aversion. *Psychoneuroendocrinology, 37,* 871–880.

de Kwaadsteniet, E. W., van Dijk, E., Wit, A., & de Cremer, D. (2006). Social dilemmas as strong versus weak situations: Social value orientations and tacit coordination under resource size uncertainty. *Journal of Experimental Social Psychology, 42,* 509–516.

Dluzen, D. E., Muraoka, S., Engelmann, M., Ebner, K., & Landgraf, R. (2000). Oxytocin induces preservation of social recognition in male rats by activating alpha-adrenoceptors of the olfactory bulb. *European Journal of Neuroscience, 12,* 760–766.

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

Domes, G., Lischke, A., Berger, C., Grossman, A., Hauenstein, K., Heinrichs, M., et al. (2010). Effects of intranasal oxytocin on emotional face processing in women. *Psychoneuroendocrinology, 35,* 83–93.

Eisenberger, R., Kuhlman, D. M., & Cotterell, N. (1992). Effects of social values, effort training, and goal structure on task persistence. *Journal of Research in Personality, 26,* 258–272.

Feldman, R. (2012). Oxytocin and social affiliation in humans. *Hormones and Behavior, 61,* 380–391.

Feldman, R., Gordon, I., & Zagoory-Sharon, O. (2010). The cross-generation transmission of oxytocin in humans. *Hormones and Behavior, 58,* 669–676.

Feldman, R., Magori-Cohen, R., Galili, G., Singer, M., & Louzoun, Y. (2011). Mother and infant coordinate heart rhythms through episodes of interaction synchrony. *Infant Behavior & Development, 34,* 569–577.

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,* 965–970.

Ferguson, J. N., Young, L. J., Hearn, E. F., Matzuk, M. M., Insel, T. R., & Winslow, J. T. (2000). Social amnesia in mice lacking the oxytocin gene. *Nature Genetics, 25,* 284–288.

Fischer-Shofty, M., Shamay-Tsoory, S. G., Harari, H., & Levkovitz, Y. (2010). The effect of intranasal administration of oxytocin on fear recognition. *Neuropsychologia, 48,* 179–184.

Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences, U.S.A., 105,* 8557–8562.

Gordon, I., Zagoory-Sharon, O., Leckman, J. F., & Feldman, R. (2010). Oxytocin and the development of parenting in humans. *Biological Psychiatry, 68,* 377–382.

Guastella, A. J., Mitchell, P. B., & Dadds, M. R. (2008). Oxytocin increases gaze to the eye region of human faces. *Biological Psychiatry, 63,* 3–5.
Hall, M. L., & Peters, A. (2008). Coordination between the sexes for territorial defence in a duetting fairy-wren. *Animal Behaviour, 76,* 65–73.
Harmon, A., Huhman, K., Moore, T., & Albers, H. (2002). Oxytocin inhibits aggression in female Syrian hamsters. *Journal of Neuroendocrinology, 14,* 963–969.
Hart, B. L., & Hart, L. A. (1992). Reciprocal allogrooming in impala. *Animal Behavior, 44,* 1073–1083.
Heinrichs, M., Baumgartner, T., Kirscbaum, C., & Ehlert, U. (2003). Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biological Psychiatry, 54,* 1389–1398.
Heinsohn, R., & Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. *Science, 269,* 1260–1262.
Hurlemann, R., Patin, A., Onur, O. A., Cohen, M. X., Baumgartner, T., Metzler, S., et al. (2010). Oxytocin enhances amygdala-dependent, socially reinforced learning and emotional empathy in humans. *The Journal of Neuroscience, 30,* 4999–5007.
Israel, S., Lerer, E., Shalev, I., Uzefovsky, F., Riebold, M., Laiba, E., et al. (2009). The oxytocin receptor (OXTR) contributes to prosocial fund allocations in the dictator game and the social value orientations task. *PLoS One, 4,* e5535.
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,* 11489–11493.
Kliegl, R., Wei, P., Dambacher, M., Yan, M., & Zhou, X. (2010). Experimental effects and individual differences in linear mixed models: Estimating the relationship between spatial, object, and attraction effects in visual attention. *Frontiers in Psychology, 1,* 238.
Knoblich, G., & Jordan, J. S. (2003). Action coordination in groups and individuals: Learning anticipatory control. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 29,* 1006–1016.
Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature, 435,* 673–676.
Kruuk, H. (1972). The spotted hyena: A study of predation and social behavior. Chicago, IL: University of Chicago Press.
Labuschagne, I., Phan, K. L., Wood, A., Angstadt, M., Chua, P., Heinrichs, M., et al. (2010). Oxytocin attenuates amygdala reactivity to fear in generalized social anxiety disorder. *Neuropsychopharmacology, 35,* 2403–2413.
LaFrance, M. (1979). Nonverbal synchrony and rapport: Analysis by the cross-lag panel technique. *Social Psychology Quarterly, 42,* 66–70.
Lim, M. M., & Young, L. J. (2006). Neuropeptidergic regulation of affiliative behavior and social bonding in animals. *Hormones and Behavior, 50,* 506–517.
Lubin, B. (1965). Depression Adjective Check Lists: Manual (2nd ed.). San Diego, CA: Educational and Industrial Testing Service.
Lubin, B., & Riesenmy, K. R. (1996). Further study of the diagnostic and screening efficiency of the ST-Depression Adjective Check Lists. *Journal of Clinical Psychology, 52,* 26–31.
Maynard Smith, J. (1978). The evolution of sex. Cambridge: Cambridge University Press.
Messick, D. M., & McClintock, C. G. (1968). Motivational bases of choice in experimental games. *Journal of Experimental Social Psychology, 4,* 1–25.
Neumann, I., Ludwig, M., Engelmann, M., Pittman, Q. J., & Landgraf, R. (1993). Simultaneous microdialysis in blood and brain: Oxytocin and vasopressin release in response to central and peripheral osmotic stimulation and suckling in the rat. *Neuroendocrinology, 58,* 637–645.
Noë, R. (2006). Cooperation experiments: Coordination through communication versus acting apart together. *Animal Behaviour, 71,* 1–18.
Norscia, I., & Palagi, E. (2011). Yawn contagion and empathy in Homo sapiens. *PLoS One, 6,* e28472.
Noy, L., Dekel, E., & Alon, U. (2011). The mirror game as a paradigm for studying the dynamics of two people improvising motion together. *Proceedings of the National Academy of Sciences, U.S.A., 108,* 20947–20952.
Parks, C. D. (1994). The predictive ability of social values in resource dilemmas and public good games. *Personality and Social Psychology Bulletin, 20,* 431–438.
Petrovic, P., Kalisch, R., Singer, T., & Dolan, R. J. (2008). Oxytocin attenuates affective evaluations of conditioned faces and amygdala activity. *The Journal of Neuroscience, 28,* 6607–6615.
Platow, M. J. (1994). An evaluation of the social desirability of prosocial self–other allocation choices. *The Journal of Social Psychology, 134,* 61–68.
Popik, P., & van Ree, J. M. (1991). Oxytocin but not vasopressin facilitates social recognition following injection into the medial preoptic area of the rat brain. *European Neuropsychopharmacology, 1,* 555–560.
Richardson, M. J., Marsh, K. L., & Baron, R. M. (2007). Judging and actualizing intrapersonal and interpersonal affordances. *Journal of Experimental Psychology: Human Perception and Performance, 33,* 845–859.
Richardson, M. J., Marsh, K. L., Isenhower, R. W., Goodman, J. R. L., & Schmidt, R. C. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. *Human Movement Science, 26,* 867–891.
Rilling, J. K., DeMarco, A. C., Hackett, P. D., Thompson, R., Ditzen, B., Patel, R., et al. (2012). Effects of intranasal oxytocin and vasopressin on cooperative behavior and associated brain activity in men. *Psychoneuroendocrinology, 37,* 447–461.
Roberts, G., & Sherratt, T. N. (1998). Development of cooperative relationships through increasing investment. *Nature, 394,* 175–179.
Scheel, D., & Packer, C. (1991). Group hunting behaviour of lions: A search for cooperation. *Animal Behaviour, 41,* 697–709.
Schneiderman, I., Zagoory-Sharon, O., Leckman, J. F., & Feldman, R. (2012). Oxytocin during the initial stages of romantic attachment: Relations to couples' interactive reciprocity. *Psychoneuroendocrinology, 37,* 1277–1285.
Schuster, R. H. (1976). Lekking behavior in kafue lechwe. *Science, 192,* 1240–1242.
Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences, 10,* 70–76.
Serpell, J. (1981). Duets, greetings and triumph ceremonies: Analogous displays in the parrot genus trichoglossus. *Zeitschrift Für Tierpsychologie, 55,* 268–283.
Shamay-Tsoory, S. G. (2010). Oxytocin, social salience, and social approach. *Biological Psychiatry,* 67, e35.
Shamay-Tsoory, S. G., Fischer, M., Dvash, J., Harari, H., Perach-Bloom, N., & Levkovitz, Y. (2009). Intranasal administration of oxytocin increases envy and schadenfreude (gloating). *Biological Psychiatry, 66,* 864–870.
Siller, M., & Sigman, M. (2002). The behaviors of parents of children with autism predict the subsequent development of their children's communication. *Journal of Autism and Developmental Disorders, 32,* 77–89.

Sober, E., & Wilson, S. D. (1998). Multilevel selection and the return of group-level functionalism. *Behavioral and Brain Sciences, 21,* 305–306.

Spoon, T. R., Millam, J. R., & Owings, D. H. (2006). The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, nymphicus hollandicus. *Animal Behaviour, 71,* 315–326.

Tognoli, E., Lagarde, J., DeGuzman, G. C., & Kelso, J. A. S. (2007). The phi complex as a neuromarker of human social coordination. *Proceedings of the National Academy of Sciences, U.S.A., 104,* 8190–8195.

Van Lange, P. A. M., & Kuhlman, D. M. (1994). Social value orientations and impressions of partner's honesty and intelligence: A test of the might versus morality effect. *Journal of Personality and Social Psychology, 67,* 126–141.

Van Lange, P. A. M., & Liebrand, W. B. (1991). Social value orientation and intelligence: A test of the Goal Prescribes Rationality Principle. *European Journal of Social Psychology, 21,* 273–292.

Winslow, J. T., Noble, P. L., Lyons, C. K., Sterk, S. M., & Insel, T. R. (2003). Rearing effects on cerebrospinal fluid oxytocin concentration and social buffering in rhesus monkeys. *Neuropsychopharmacology, 28,* 910–918.

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,* 855–861.

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.

Zak, P. J., Kurzban, R., & Matzner, W. T. (2004). The neurobiology of trust. *Annals of the New York Academy of Sciences, 1032,* 224–227.

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