DEPARTMENT OF MANAGEMENT

Oxytocin and cooperative behavior in social dilemmas: The moderating role of explicit incentives, social cues and individual differences

Carolyn H. Declerck, Christophe Boone & Toko Kiyonari

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University of Antwerp, City Campus, Prinsstraat 13, B-2000 Antwerp, Belgium
Research Administration – room B.213
phone: (32) 3 220 40 32
fax: (32) 3 220 47 99
e-mail: joeri.nys@ua.ac.be

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Carolyn H. Declerck, Christophe Boone & Toko Kiyonari

Universiteit Antwerpen
Departement Management,
Faculteit TEW
Prinsstraat 13, B-2000, Antwerpen

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Correspondent voor dit artikel: Carolyn H. Declerck,
carolyn.declerck@ua.ac.be

Universiteit Antwerpen

Abstract

The neuropeptide Oxytocin (OT), implicated in mammalian social behavior, may affect cooperation through its anxiolytic and affiliative properties. The current study experimentally investigates how OT interacts with three well-studied determinants of cooperative behavior in social dilemmas: extrinsic incentives, social cues, and individual differences. Participants received OT or a placebo following a double blind procedure and played two economic games with randomly determined partners: a Coordination Game (with strong extrinsic incentives to cooperate (CG)) and a Prisoner's Dilemma (with weak extrinsic incentives (PD)). Social cues were present when participants had the chance to meet their partners in advance, and absent when the interactions were anonymous. A first prediction, that OT enhances cooperation when social cues are present, was confirmed by the data. This appeared to be more pronounced when participants played a CG. In contrast, in a PD we predicted that OT's influence on cooperation would depend on the subject's intrinsic willingness to cooperate, as assessed by means of his/her Social Value Orientation and Machiavellianism. The data indicate that for prosocials, OT and social cues appear to be substitutes, with either one being sufficient to overcome fear of betrayal and elicit cooperation. For proselfs, OT and social cues appear to be complements: their concurrence is essential to overcome greediness in situations with weak cooperative incentives. Machiavellists cooperated very little overall, and the combination of OT and social cues, in contrast to proselfs, actually reduced machiavellists' willingness to cooperate.

Introduction

Understanding the origins of cooperation under uncertainty is a major research objective in both the social and biological sciences. Proximate psychological mechanisms leading to mutual cooperation seem to fall into three separate categories. First, behavioral economists have emphasized the importance of motivational determinants on the willingness to cooperate. Indeed, much experimental evidence in both laboratory and field settings indicate that cooperation increases when extrinsic incentives are incorporated into the decision-making matrix, so that the cooperative decision in itself becomes rewarding (1). Second, evolutionary psychologists have repeatedly shown that subtle social cues affect cooperation when they trigger heuristics that have been shaped by natural selection to help people solve problems related to social exchange (2, 3). Such cues are thought to be informative with regards to the profitability of cooperation in several ways, including kin relationships (4), possible reputational benefits (5), or trust (6). The latter is particularly important in shaping one's expectations regarding the cooperative behavior of others involved in the exchange. Finally, the influence of personality and preferences on cooperative behavior is well documented. Some people are intrinsically motivated to cooperate and will naturally do so as long as they trust that their cooperative acts will be reciprocated, while others need to be prompted into cooperation by extrinsic incentives (7, 8).

In addition to these psychological determinants, the biological processes of cooperation are also receiving more attention, including the identification of neural correlates (9), as well as accompanying neurochemicals (10). Among, the latter, it would be interesting to investigate the effects of oxytocin because of its well-documented role in social affiliation. Oxytocin (OT) is an evolutionary conserved nanopeptide hormone which facilitates reproduction in all mammalian taxa. Among humans, this consists of peripherally stimulating uterine contractions during labor, and milk ejection during lactation. In the central nervous system, OT acts as a neuromodulator with receptor sites located primarily in the limbic system of males and females alike (11).

As is the case for social bonding, cooperation between people may result from a combined effect of several properties of OT. One of the most consisting findings is OT's strong anxiolytic effect, reducing social fear through inhibiting amygdala activation (12). Consistent with this are the reports that nasal OT administration is associated with a decline in salivary cortisol (13, 14) and an increase in trust (15). The latter study also documents the importance of the social context in which OT operates. In laboratory economic games, investors who had received a dose of nasal OT were willing to transfer more money into the account of a trustee who had the choice of sharing the profits, compared to investors who received a placebo. However, no such risk-bearing behavior was observed when the return on investment was randomly determined without human interaction. In a similar experiment, people who received a large trust signal in an investment game (those who received a large sum of money) tended to have higher plasma levels of OT and also tended to reciprocate trust more compared to those who received little or no money. Again, no differences in OT plasma levels were observed for those participants who received a similar but randomly determined sum of money without social interaction (16).

Other properties of OT that may play a role in establishing cooperation include enhanced social cognition and social motivation. Nasal OT administration has been shown to increase the accuracy of people's perceptual judgments of others' emotions and intentions (17), improve recognition memory (18), and stimulate eye contact (19). In children diagnosed with autism spectrum, plasma OT administration tends to improve social information processing and increase the number of self-initiated social interactions (20). OT receptor sites are numerous in the ventral tegmental area (VTA) and nucleus accumbens where OT is believed to stimulate dopamine (DA) release, hence modulating activity in the mesolimbic DA reward system (21).Therefore, it has been suggested that OT can positively enhance prosocial motivation by linking it to the capacity to experience reward from social interaction (22, 23).

The purpose of the current study is to investigate if and in which circumstances OT helps people to establish mutual cooperation in uncertain situations. Cooperation is a complex behavior which requires the simultaneous fulfillment of being (intrinsically or extrinsically) willing to cooperate, and trusting that the other(s) will cooperate as well (24). Therefore, we suggest that OT might play an integrative role in developing cooperative motivation and/or trust. However, to fully understand how mutual cooperation can emerge in the face of uncertainty, a comprehensive view is necessary that integrates the impact of different psychological determinants (such as incentives, social cues and personality) together with their biological underpinnings. Unfortunately, prior studies have mainly investigated these drivers of cooperation in isolation. While such studies might be revealing in and of itself, it ignores the fact that human decision-making is modulated by many influences at the same time in subtle ways (6, 25, 26). Similarly, knowledge of the concomitant neural processes may help to understand how these influences are coordinated in the brain leading people to decide to cooperate.

To further our understanding of the complex process of cooperation we decided to set up an experiment to investigate how incentives, social cues, personality, and OT interact to affect cooperation in social dilemmas. Specifically, we compared the behavior of 259 subjects that played a dyadic one shot Prisoner’s Dilemma (weak extrinsic cooperative incentives (PD)) and a Coordination game (strong extrinsic cooperative incentives (CG)). The decision matrices for these games as used in the present experiment are shown in Figure 1A and Figure 1B, respectively. The CG is also known in the literature as the Stag Hunt game, the Trust dilemma or the Assurance game. Both games have extensively been used to study social cooperation (see (24, 27, 28) for examples). The major difference between both games is that there is an incentive to defect in a PD when one expects the other party to cooperate. In a CG, in contrast, the best strategy is to cooperate when one trusts the other party to do so. As a result, the PD generates a strong conflict between individual rationality and collective outcomes, whereas the CG balances personal risk and mutual benefit (28). Note that the PD is easily transformed to a CG by simply lowering the pay-off from defection in the PD to or below the level of the pay-off resulting from mutual cooperation. Social cues were manipulated by allowing participants to have minimal contact with their potential partners prior to decision making (compared to anonymous interaction). Half of the subject received nasal doses of OT, whereas the other half a placebo. The intrinsic motivation to cooperate was inferred by means of two fundamental personality traits, i.e., Social Value Orientation (SVO) and Machiavellianism. SVO refers to stable individual differences with respect to self- versus other regarding preferences. This trait reflects how people evaluate interdependent outcomes for self and others, distinguishing so-called prosocials and proselfs. Although both SVO (proself orientation) and Machiavellianism are proxies for “greediness,” the two constructs differ in their degree of social competence. Machiavellists are, in addition to being greedy, known for their lack of trust and trustworthiness (29), and are typically shunned as social partners (30). With their detached and opportunistic stance towards values and social norms, they are prototypes of “*Homo economicus*,” taking advantage of other people’ s trust (29).

Figure 1A-B

Pay-off matrices for the Prisoner’s Dilemma (1A) and the Coordination Game (1B).

Figure 1A

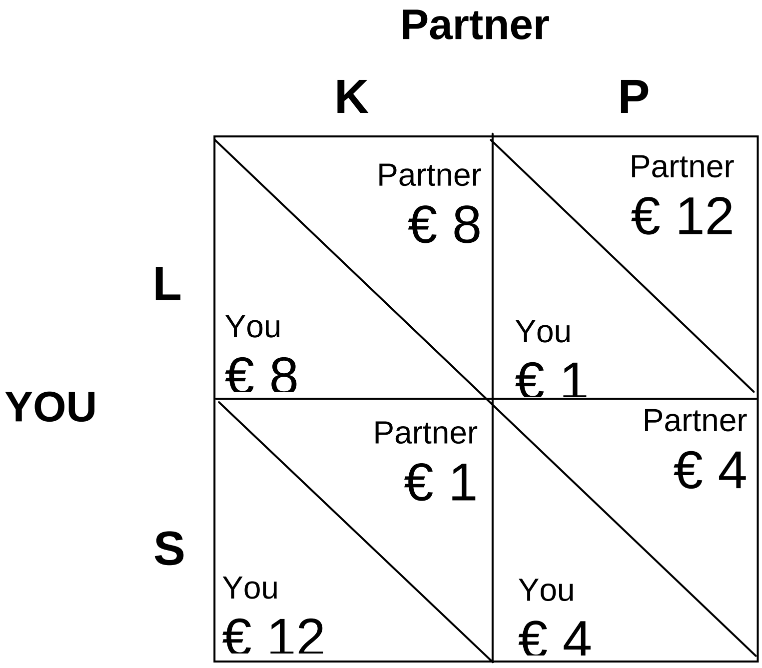
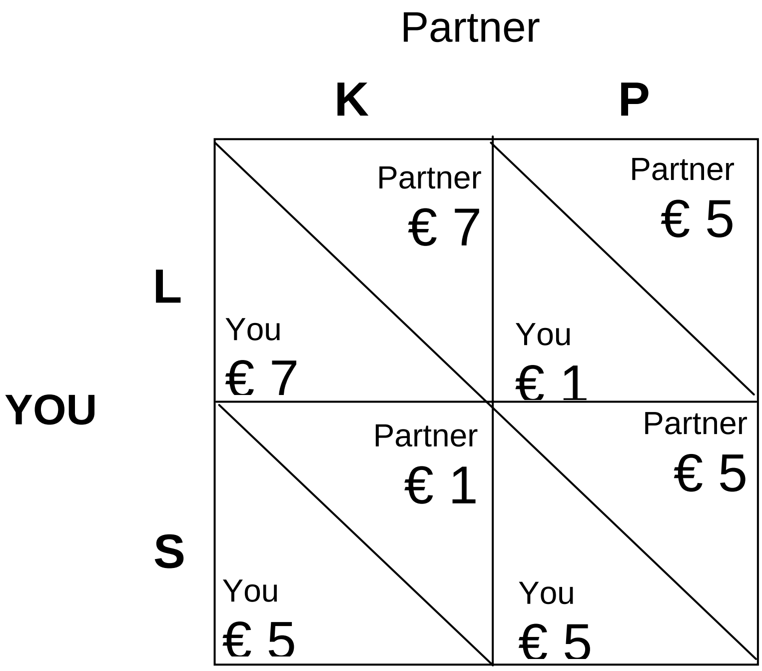


Figure 1B



Predictions

In the present paper we focus on developing and testing predictions with respect to how the combined effect of OT and social cues interact with extrinsic incentives and personality. Considering the importance of a social context with respect to OT (15, 16), our baseline prediction is that OT will increase cooperation (choosing option L in Figure 1A and 1B) when social cues are present. In anonymous interactions, OT will not affect behavior as the absence of a salient social context reduces its functionality. In addition, we predict that this combined effect will be more pronounced in the CG compared to the PD game. In the former, cooperation is the best strategy even for self-interested people as there is no incentive to defect when the other party cooperates. Due to strong cooperative incentives the willingness to cooperate is high and minimal trust suffices to trigger mutual cooperation. As OT is expected to enhance trust in social interactions it will subjectively reduce the uncertainty of the interaction. Specifically, we expect that OT (when social cues are present) will help people to form positive expectations of the cooperative behavior of others by positively responding to social cues that are concurrently present.

Our second prediction is that OT's effect (when social cues are present) on cooperation in mixed motive situations (PD) will depend on personality. Mixed motive games have a dominant strategy which is to defect: whatever alter does, "greedy" people can always increase their pay-off by choosing option S in Figure 1A. Anticipating that a possibly egoistic alter may be tempted to defect, "cooperative" people may also choose to defect for fear of being betrayed. So, in the absence of strong extrinsic cooperative incentives (as in CG), motives of fear and greed are triggered simultaneously, so that enhanced trust (possibly generated by OT) may not always lead to cooperation. In such cases, we predict different outcomes depending on one's intrinsic willingness to cooperate, i.e. on whether one is a "greedy" or "cooperative" person.

Two alternative predictions can be proposed. If the combined effect of OT and social cues mainly increases a person's social motivation, especially "greedy" people, who are not intrinsically socially motivated, will be spurred to cooperate. In contrast, if the combined effect of OT and social cues mainly reduces the fear of betrayal, especially "cooperative" people will boost their cooperation rates. This is expected because cooperative people, who are already intrinsically willing to cooperate, may still be sensitive to the anxiolytic effect of OT.

Results

Visual inspection of the results presented in Figure 2 seems to confirm that OT appears to enhance cooperation, but only when social cues (here in the form of minimal Prior contact) are present. (Cooperation is actually decreased when the interaction occurs completely anonymous). These effects are more pronounced in the CG.

Figure 2A-B

Percent cooperation in the Prisoner's Dilemma (2A) and the Coordination game (2B).

Figure 2A

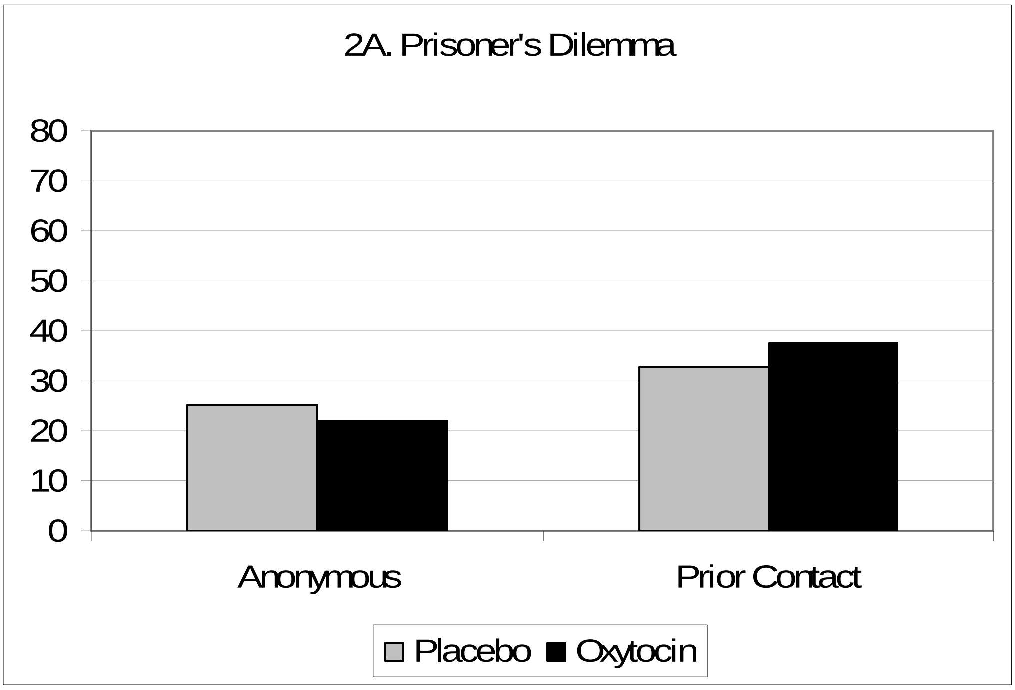
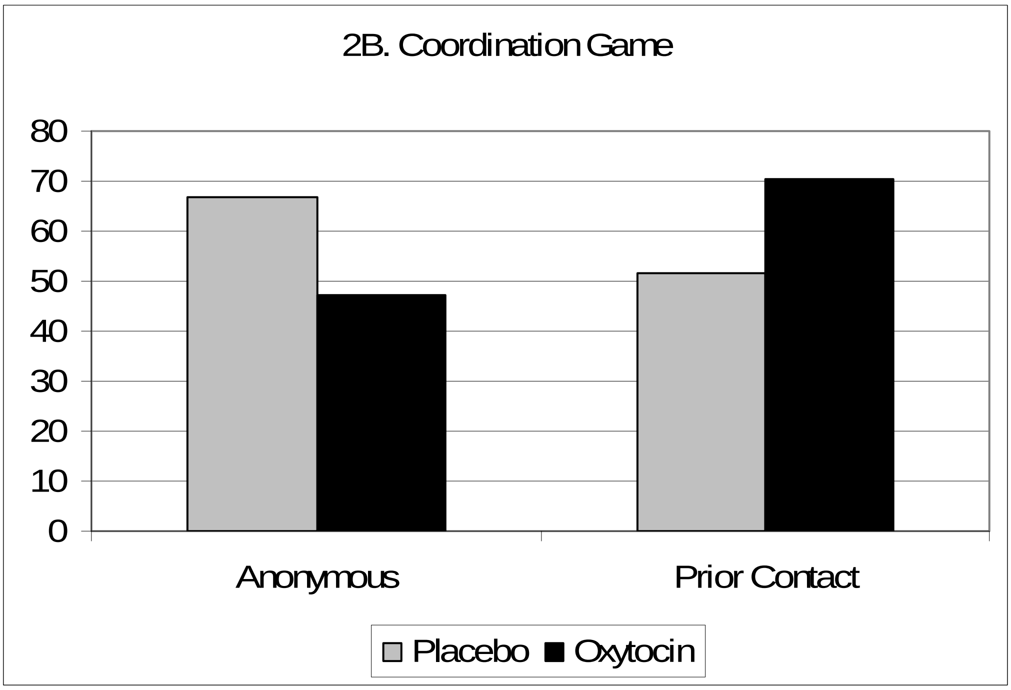


Figure 2B



To statistically validate these observations, we analyzed the data in panel form treating each individual decision as a unit, so the total number of observations is 518 (259 subjects * 2 decisions). Cooperative (non-cooperative) decisions are coded as 1 (zero). We performed logistic regression using Liang and Zeger's (31) method of generalized estimating equations

(GEE), which generalizes quasi-likelihood estimation to the panel data context and represents a very flexible way to deal with autocorrelation resulting from clustered data. GEE is a common statistical analysis in social as well as medical research (see the study by Coates & Herbert (32) for an example of GEE applied to a recent neuroeconomic study similar to ours). Because the two decisions of each individual are not necessarily independent, we also report robust standard errors of the estimates using the sandwich estimators (33, 34). Note that we control for possible order effects in presenting the games (PD played first equals 1, zero otherwise), gender (male equals 1) and the subject's age. The regression results are shown in Table 1. Models II and III statistically confirm our baseline expectations. The former reveals that OT spurs cooperation when social cues are present (see the positive coefficient of PC * OT). The significant three-way interaction in Model III shows that this is especially the case in the CG (positive coefficient of PC*OT *Incentives).

Table 1

*Results of GEE logistic regression models of Prior contact (PC), Oxytocin (OT), and Incentives (Coordination Game versus Prisoner's Dilemma) on cooperative decisions. Sex, Age, and the order in which the two games were played are added as control variables. Robust standard errors are reported in parentheses. n= 518. *P <0.05; ** P<0.01, ***P<0.001, two-tailed.*

	Model I	Model II	Model III
Sex	.07 (.056)	09 (.21)	.09 (.21)
Age	.08 (.21)	.08 (.06)	.08 (.06)
Order	-.13 (.21)	-.12 (.21)	-.12 (.22)
PC	.30 (.22)	-.02 (.34)	.32 (.39)
OT	-.05 (.21)	-.6 (.37)	-.22 (.41)

Incentives	**1.2***(.16)**	**1.4 ***(.29)**	**1.8***(.36)**
PC*OT		**1.1** (.43)**	-1.0 (.47)
PC*Incentives		-.38 (.32)	.38 (.55)
OT*Incentives		.008 (.32)	-.64 (.46)
PC*OT*Incentives			**1.2* (.64)**
Constant	-2.6*	-2.4* (1.1)	-2.6* (1.1)
Wald Chi2	66.8	67.6	71.0

To test our second prediction - personality moderates the combined effect of OT and social cues in a situation with weak (PD) but not with strong (CG) cooperative incentives - we performed ordinary binary logistic regressions separately for the CG and the PD (n = 258). These regression results are shown in Table II.

Table 2

*Results of ordinary logistic regression models of Prior contact (PC), Oxytocin (OT), Social Value Orientation (Number of Prosocial choices), and Machiavellianism (HiMach versus LowMach) on cooperative decisions. PD = Prisoner's Dilemma; CG = Coordination Game. Sex, Age, and the order in which the two games were played are added as control variables. Robust standard errors are reported in parentheses. n= 258. *P<0.05; **P<0.01, ***P<.001, two-tailed.*

	Model IV	Model V	Model VII	Model VIII	Model IX	Model X
	PD	**CG**	**PD**		**CG**	
Sex	- .065 (.32)	.32 (.27)	.010 (.33)	-.10 (.32)	.35 (.28)	.38 (.28)
Age	.14 * (.060)	.0059 (.054)	.14* (.060)	.16* (.061)	-.0039 (.056)	-.00082 (.056)
OrderGames	-.020 (.30)	-.23 (.26)	.079 (.31)	-.083 (.31)	-.20 (.27)	-.27 (.27)

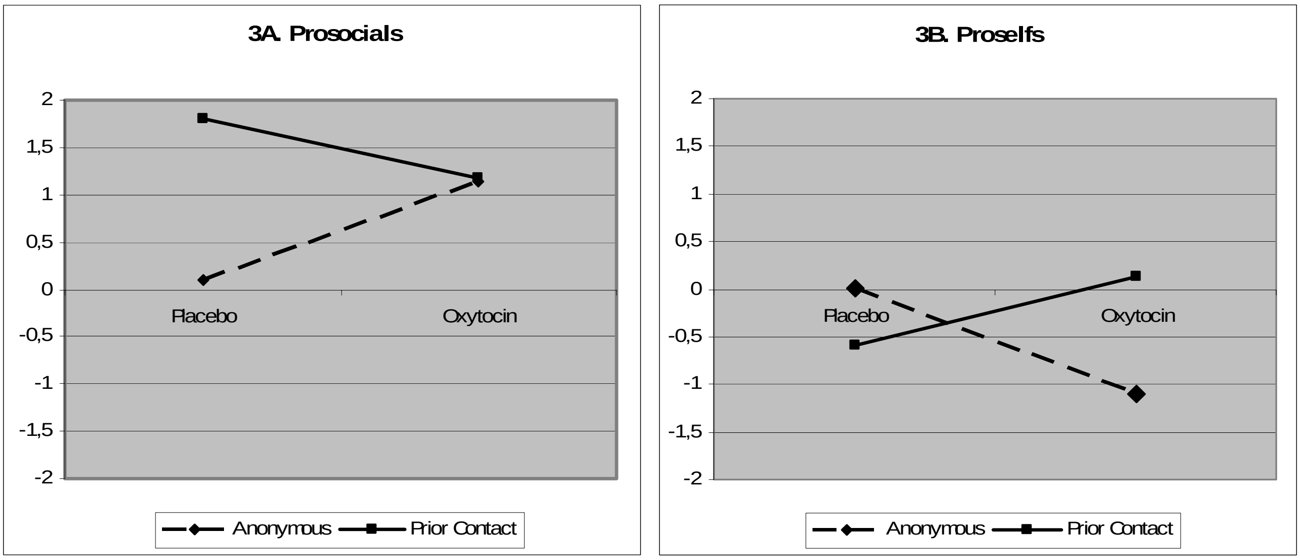
PC	.61* (.31)	.20 (.26)	-.89 (.73)	-1.8 (3.7)	-1.0 (.55)	-2.1 (2.8)
OT	.047 (.30)	.010 (.26)	-1.4 (.77)	-7.7* (3.7)	-.86 (.53)	-5.4 (3.0)
NrProsocial	.18 *** (.041)	.087* (.036)	.012 (.082)	.19*** (.043)	.033 (.073)	.079* (.037)
HiMach	-.041 ** (.015)	.006 (.011)	-.047** (.015)	-.070* (.031)	.0049 (.012)	-.018 (.022)
PC*OT			2.3* (1.0)	10* (5.4)	1.9* (.76)	3.9 (4.6)
PC*NrProsocial			2.9* (.12)		.11 (.10)	
PC*HiMach				.027 (.040)	.	.016 (.030)
OT*NrProsocial			2.7* (.12)		.014 (.10)	
OT*HiMach				.084* (.041)		.049 (.032)
PC*OT*NrProsocial			-.44** (.17)		-.070 (.15)	
PC*OT*HiMach				-.111* (.058)		-.024 (.048)
Constant	-1.0 (1.8)	-.78 (1.6)	.39 (1.9)	1.3 (3.1)	.12 (1.7)	2.0 (2.5)
Pseudo R2	0.14	.026	.17	.16	.057	.060

A first finding is that the effect of our independent variables Prior contact, SVO, and Machiavellianism on cooperation is much larger in the PD than in the CG (compare Models IV and V). Strong extrinsic cooperative incentives *per se* reduce the impact of social cues and individual differences. As expected, the hypothesized three-way interactions between OT, Prior Contact, and the two personality traits are significant in the PD (see Model VII for SVO (coefficient of PC*OT *NrProsocial) and Model VIII for Machiavellianism (coefficient of PC*OT*HiMach)), but not in the CG (see coefficients of same variables in Models IX and X).

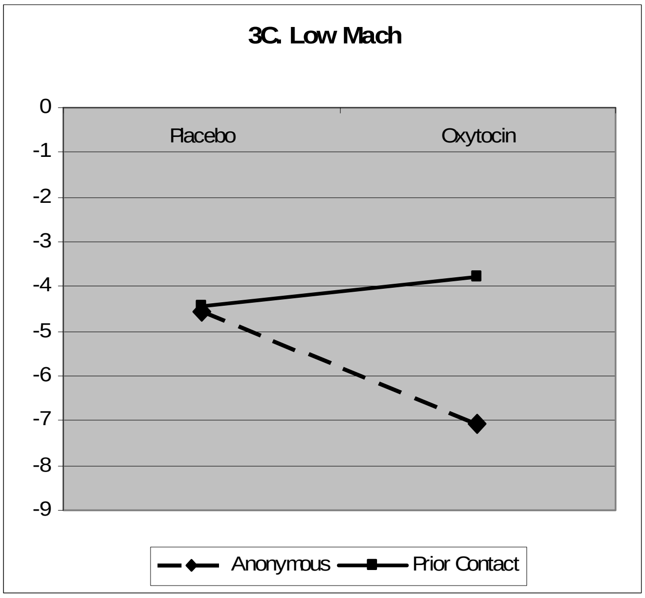
We visualize these two significant three-way interactions by drawing the combined effect of PC and OT (based on the estimates of Models VII and VIII) for prosocials versus proselfs, and for high versus low Machiavellianism, respectively. These were calculated as the sum of the relevant terms in the regression equation, substituting the personality variable in the equation with the extreme values measured by the scales (35).* Figures 3A and 3B show how prosocials cooperate more with OT in the anonymous condition, while proselfs cooperate more with OT in the Prior contact condition. Figures 3C and 3D indicate that these results are different for the Machiavellianism personality construct. Baseline cooperation of high Machiavellianism is already very low, and is reduced even further by the combination of OT and Prior contact.

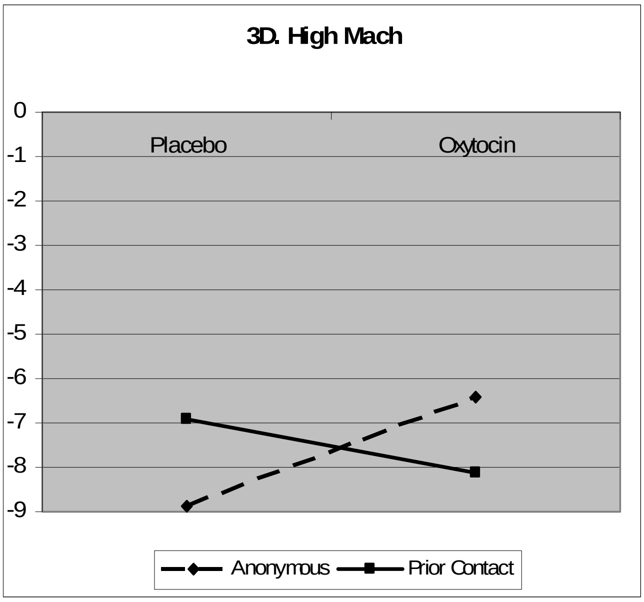
Figure 3A-D

Effect of Oxytocin on the likelihood of cooperation in the Prisoner's Dilemma in the Anonymous and Prior contact condition comparing Prosocials versus Proselfs (3A and 3B), and Low versus High Machiavellianism (3C and 3D). Y-axis represents the predicted logit calculated by means of the regression estimates reported in Models VII and VIII of Table 2.



* For prosocials this equals to 9 prosocial choices, for proselfs 0. We used these values because they represent the modal SVO choices (23 % and 39 %, respectively). Likewise, we used the extreme values for high and low Machiavellianism. As a robustness check, we repeated the calculation using the mean Machiavellianism score +/- one standard deviation, and found the resulting graphs to be very similar.





Discussion and conclusion

A major conclusion that can be drawn from this experiment is that OT and social cues are critically intertwined when it comes to cooperative behavior, and that they have different effects in situations with or without extrinsic cooperative incentives. When strong incentives are present (as in a CG), people are willing to cooperate when they trust others will do so as well. Trust is apparently enhanced by the combination of OT and social information. These findings are compatible with OT's reported role in trust-building, and are consistent with our expectations.

The findings in the PD (where strong incentives are absent and motives of fear and greed are present) are much more complicated than expected. Although the effects of OT and social cues did appear to delicately depend on personality, the findings were opposite for SVO compared to Machiavellianism. For prosocials, OT and social cues seem to act as "substitutes," with each having independent positive effects on cooperative behavior. Thus, either social contact or OT sufficed to spur cooperation among prosocials. People that are intrinsically motivated to cooperate do not need much additional cues to cooperate. Surprisingly, when they are both present, cooperation was actually not enhanced. We speculate that OT's anxiolytic effect reduces the fear of being exploited among prosocials especially in anonymous situations. For intrinsically cooperative people OT might allow approach behavior and the initiation of social interaction, even with an anonymous partner. This would be a first step towards meeting new people with whom it may be possible to create new cooperative bonds.

Among proselfs, the effects of OT and social cues appeared to complement each other in affecting cooperative behavior. This is consistent with our initial prediction that only the combined effect of OT and social cues helps proselfs to reach goal transformation and become motivated towards more prosocial behavior. Proselfs are believed to have selfish goals but otherwise display normal social interaction. Machiavellists share these goals, as indicated by the modest correlation between Machiavellianism scores and number of proself decisions ($r = 0.14$; $P = 0.025$, $n = 258$). But because of their additional belief that the end justifies the means, also in social interaction, Machiavellianism could be indicative of "anti-sociality." This might explain the intriguing result that the very same combination of factors actually reduced machiavellists' willingness to cooperate. Apparently, machiavellists defect more when affiliation is triggered in a social context in which mixed motives are present. Presumably, their manipulative nature tempts them to exploit alters even more in the presence of induced trust.

In conclusion, our results show that OT has an important role in shaping cooperation, in interaction with incentives, social cues and personality. The pattern of findings is consistent with the different functions that have been associated with OT in prior research, including its role in reducing anxiety and increasing social motivation. However, several unresolved questions remain for future research. More research is needed to pinpoint the potentially different underlying putative mechanisms of how OT operates for different people in different circumstances. First, it would, for instance, be interesting to investigate why and how OT boosts social motivation among proselfs in mixed motive games, and to test if this is accomplished through OT modulation of the mesolimbic DA reward system (23). Second, it needs to be explained why the very same factors make machiavellists even more greedy. What seems to be particularly interesting is that the effects of OT and social cues on cooperation depend on the intrinsic, stable motives people have. This makes us wonder if biological processes related to OT's role in trait affiliation might also account for fundamental differences between prosocials ("cooperative" people), proselfs ("greedy" people) and machiavellists ("greedy and manipulative" people).

Methods

The experiment was conducted at the University of Antwerp during the spring of 2008. Participants (n = 259, with 119 males, 140 females) were recruited via webmail and signed up for one of 8 sessions (with a minimum of 30 and a maximum of 36 participants per session). They were informed that they participated in a study investigating the effect of a hormone on decision-making. Full anonymity was guaranteed at all times, and monetary incentives were emphasized. All procedures were approved by the University of Antwerp Ethics Advisory Commission.

Participants gathered in one large classroom where they filled out a consent form and a personality questionnaire. Social Value Orientation (SVO) was assessed by means of the decomposed measure (36) in which either a prosocial or a proself choice has to be indicated for nine consecutive decision outcomes. We use the number of prosocial choices as an indicator of a subject's prosocial orientation. A review of current research results (37) reveals adequate validity and reliability of this measure. Machiavellianism was assessed using a translated version of Christie and Geis' Mach IV questionnaire consisting of 20 items. A high score implies a machiavellistic orientation. Cronbach alpha for our sample questionnaire equals 0.747. Validity and reliability for the Dutch version of this test are discussed elsewhere (38).

Following the questionnaire, participants were split in 4 groups (about 8 per group) and guided to another classroom for the actual experiment. Using a double blind procedure, each participant received a nasal spray containing either OT (4 IU per puff) or a placebo. One puff was administered in each nostril, and this procedure was repeated three times in 5 minute intervals (24 IU oxytocin total). To allow sufficient time for OT to diffuse through the brain-blood barrier, participants waited for an additional 30 minutes after the last puff (39). During this entire time, participants did not converse with each other.

The presence or absence of social cues was manipulated as follows: half of the participants (n = 128) were called one by one out of the experimental room to meet in a smaller group of 8 inside a cozy little conference room. Here they were asked to introduce themselves, state their favorite hobby, and shake hands.

The instructions of the subsequent games stated that each participant would be matched with a partner in one of the other rooms, and that they were to make decisions for which they could earn real money. For each decision, they would be matched with a different partner and they would never find out who this was. The outcome of the decision would depend on their decision as well as on the decision of their partner. In the Prior Contact condition, the instructions stated that they would be matched with one of the people they just met and who is sitting in a different room. Note that this Prior Contact manipulation does not allow exact identification of the partner, which prevents possible retaliation or reputation effects. To ensure that all participants adequately understood the monetary pay-offs of the games, the game instructions also included 8 confirmation questions that subjects had to answer correctly before continuing with the actual experiment. The actual decisions were made with paper and pencil in answer booklets. Each subject played the two games consecutively with pay-offs as in Figures 1A and1B. In 4 out of the 8 sessions (counterbalanced), the PD was played first. In the other 4, the order was reversed. At the end of the experiment, all participants were paid in truth the actual amount they earned.

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