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Intranasal oxytocin, testosterone reactivity, and human competitiveness

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ABSTRACT

Competitiveness is an essential feature of human social interactions. Despite an extensive body of research on the underlying psychological and cultural factors regulating competitive behavior, the role of biological factors remains poorly understood. Extant research has focused primarily on sex hormones, with equivocal findings. Here, we examined if intranasal administration of the neuropeptide oxytocin (OT) – a key regulator of human social behavior and cognition – interacts with changes in endogenous testosterone (T) levels in regulating the willingness to engage in competition. In a double-blind placebo-control design, 204 subjects (102 females) self-administrated OT or placebo and were assessed for their willingness to compete via an extensively-validated economic laboratory competition paradigm, in which, before completing a set of incentivized arithmetic tasks, subjects are asked to decide what percentage of their payoffs will be based on tournament paying-scheme. Salivary T concentrations ($n = 197$) were measured throughout the task to assess endogenous reactivity. Under both OT and placebo, T-reactivity during competition was not associated with competitiveness in females. However, in males, the association between T-reactivity and competitiveness was OT-dependent. That is, males under placebo demonstrated a positive correlation between T-reactivity and the willingness to engage in competition, while no association was observed in males receiving OT. The interaction between OT, T-reactivity, and sex on competitive preferences remained significant even after controlling for potential mediators such as performance, self-confidence, and risk-aversion, suggesting that this three-way interaction effect was specific to competitive motivation rather than to other generalized processes. These findings deepen our understanding of the biological processes underlying human preferences for competition and extend the evidence base for the interplay between hormones in affecting human social behavior.

1. Introduction

Human social relations can frequently be described as contests in which competing agents have the opportunity to expend scarce resources – such as effort, money, or time – in order to affect the probabilities of winning prizes (Darwin, 1871; Dechenaux et al., 2015). Winning a competition, of course, may carry considerable benefits (e.g., territory, prestige, wealth), however, losing may have considerable drawbacks; these include both the forgone resources invested in the competition, as well as the consequences of losing (e.g., physical harm, loss in status). Thus, as part of their social interactions, individuals often face a decision whether to compete or not.

The last decade has seen the blossoming of an active program of research examining differences in competitive preferences under controlled laboratory conditions. In the classic "willingness to compete" paradigm (Niederle and Vesterlund, 2007), participants are asked to choose how they will be paid for performing a task. Under a piece-rate payment, participants are paid for each correct solution, and their earnings under this scheme are solely a function of their own performance. Alternatively, under a tournament-style payment, participants are paid a larger sum, but only if their performance is better relative to all other participants in their group. Thus, by selecting a tournament payment, participants demonstrate a willingness to engage in competition. Moreover, including additional assessments of self-confidence, risk aversion, and performance; enables researchers to disentangle the motivation to compete from other factors contributing to competitive

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engagement.

This paradigm has been widely used in the economics literature to test the hypothesis that the well-established and cross-cultural gap between males and females in wages and social position[1] may be due, not only to structural factors such as gender-bias or to differences in skills, but also due to a difference in the willingness to engage in (or shy away from) competitive environments. Indeed, research has demonstrated that sex-differences in competitive preferences can be manipulated by targeting key processes that socialize males and females differently to competitive environments (Booth et al., 2019; Niederle and Vesterlund, 2011; Zhong et al., 2018; Zhong and Fu, 2019).

Despite gains in understanding the contextual and psychological factors affecting human competitiveness, the contribution of biological factors remains poorly understood. This is a crucial next step for advancing a more integrated perspective of the processes which give rise to sex differences in human psychology and behavior (Eagly and Wood, 2013). Research in social neuroendocrinology demonstrates the essential effects of hormones in regulating emotions, cognition, and behavior (McCall and Singer, 2012). Traditionally, research into the biological foundations of competitive behaviors has focused on gonadal hormones (Booth et al., 2006; Carré and Archer, 2018; Eisenegger et al., 2011; Mazur and Booth, 1998).

Laboratory studies find that while baseline testosterone (T) levels do not show a consistent association with competitive preferences (Apicella et al., 2011; Zhong et al., 2018), rather it is changes in T levels that serve as a better indicator (Carré and McCormick, 2008; Mehta and Josephs, 2006; Zhong and Fu, 2019; Zilioli and Watson, 2014). Consistent with these findings, predominant theories characterizing the social neuroendocrinology of status, notably the *challenge hypothesis* and the *biosocial model of status*, place rises in T levels as indicators of competitive engagement. While conceptually similar, the two theories make disparate predictions regarding the contexts under which T levels should rise. The challenge hypothesis proposes that T increases whenever social status is being challenged (Archer, 2006; Wingfield et al., 1990). In contrast, the biosocial model of status proposes that T increases or decreases depending on whether social status is gained or lost (Mazur, 1985). Such effects seem most prominent in males. A meta-analysis by Geniole et al. (2017) examining the 'Biosocial Model of Status', analyzed the results of 33 lab experiments. T-reactivity was associated with competition outcome in males, but not for females. A similar pattern was found in a recent study by Casto et al. (2020), in which, T reactivity during competition was associated with performance in males, but not for females.

Given that competition is inherently social, it can be reasoned that, besides testosterone, the neuropeptide hormone oxytocin (OT) – a key regulator of social approach and motivation – may also play a role in regulating competitive preferences. In the brain, oxytocin exerts varied effects on social cognition and behavior, either by its action as a neurotransmitter (Meyer-Lindenberg et al., 2011)) via projections from the hypothalamus to limbic sites, or as a neurohormone via diffusion through the intracellular space to local or distant targets (Meyer-Lindenberg et al., 2011).

Despite an extensive body of research demonstrating that OT regulates social behavior and cognition, it has not yet been implicated in regulating competitive preferences. OT has been theorized to modulate the motivation component of social approach and withdrawal behaviors via its connection to dopaminergic neurons in the nucleus accumbens (Gordon et al., 2011). This represents a shift from earlier findings which characterized OT effects as largely prosocial, based on findings that intranasal OT increases interpersonal trust and generosity, and facilitates empathy and affiliation (MacDonald and MacDonald, 2010).

The vast majority of experiments examining the effects of intranasal OT have been conducted on males; however, recent studies suggest that the manner by which OT regulates social motivation differs between males and females. For example, OT has been shown to facilitate sex-specific strategies for interacting with the social environment, including differential sensitivity to social cues of threat or affiliation (Fischer-Shofty et al., 2013; Gao et al., 2016; Rilling et al., 2014; Scheele et al., 2014; Xu et al., 2020). In mice exposed to a social stressor, OT administration increases social interactions in males, but leads to greater withdrawal in females (Steinman et al., 2016). These findings of sex-specific effects of OT on social behavior and motivation, parallel the finding of sex differences in OT receptor expression (Zingg and Laporte, 2003), sexually dimorphic effects of intranasal OT on amygdala (Gao et al., 2016) and putamen reactivity (Feng et al., 2015), and the role of gonadal hormones estradiol and testosterone in regulating OT expression in the brain (Johnson et al., 1991).

Amidst ongoing interest in understanding the factors driving differences in competitive preferences between males and females, here we test for interacting roles between (exogenous) OT and (endogenous) T on competitive preferences. Despite the prominent roles of T and OT in modulating social behavior (Crespi, 2016), few studies have examined their possible interaction in humans. Animal models raise the intriguing possibility that OT social effects may be contingent on T levels (Winslow and Insel, 1991). In one of the few studies in humans examine these hormones together, high endogenous T levels were associated with less attentional processing of infant's faces. This effect was canceled after intranasal OT administration (Holtfrerich et al., 2016). In this exploratory study, we aimed to test if the association between T-reactivity and competitive behavior is moderated by exogenous administration of OT. Given previous research showing sex differences in response to intranasal OT and in T-reactivity, we were also interested in examining if their effects on the willingness to engage in competition are sex-dependent.

2. Methods

2.1. Subjects

Two hundred and four subjects (102 F) participated in a double-blind, placebo-controlled, between-subject design experiment. Subjects were recruited in groups of eight or twelve, with an even number of males and females in each of the 18 total sessions. The sample size was determined using G*power 3.1.9.2 with f^2 of 0.055, which is within the range that is suggested to be sufficient for detecting an effect in experiments using intranasally applied OT (Holtfrerich et al., 2016, 2018; Walum et al., 2016). Seven subjects (3F) were excluded from the main analysis due to missing or unreliable saliva samples (see Saliva Samples and T Assays Section 2.3. for details), leaving 197 subjects (99F) for further analysis.

Subjects were recruited across multiple campus sites to capture a broad assortment of undergraduate majors across the social science, humanities, life and physical sciences. Subjects were <35 years old, had no history of psychiatric or endocrine illness, smoked less than 15 cigarettes a day, and were not taking any prescription medications that might interact with OT. For females, exclusion criteria also included current pregnancy or breastfeeding. Subjects were instructed to refrain from smoking, eating, or drinking (except water) for 2 h before the experiment, and from physical activity, alcohol, and caffeine consumption for 24 h before the experiment. Subjects received 100 New Israeli Shekels (NIS; ~ 25$) or equivalent course credit for completing the study, and an additional fee (ranging from 0 to 58 NIS) based on their performance and decisions. The study was approved by the Helsinki Committee of the local university hospital.

[1] According to the Economic Participation and Opportunity sub-index of the Global Gender Gap Index 2020 report (Global Gender Gap Report 2020, 2020), a gender gap in wages, management positions, etc., exists in all the 153 countries that are included in the report.

2.2. Mood assessment

To test if OT had any general effects on subjective state, subjects filled a visual analog scale (VAS) questionnaire directly before intranasal administration, and again at the conclusion of the experiment. The 8-items assessed were: working capacity, tiredness, anxiety, anger, conversation, closeness, concentration, and sadness. Each item was scaled from 1 ("not at all") to 10 ("very much"). As was expected, the differences between the first and the second VAS scores were not affected by OT (*t*-tests for change scores; all p's > 0.05).

2.3. Saliva samples and T assays

Saliva samples were collected at four time-points during each session, but for this study, only the first three-samples were analyzed (since the fourth sample was taken after participants completed another unrelated experiment; see Procedure Section 2.7. and Fig. 1). T levels were measured from saliva by passive drool. Subjects were asked to spit into a small polystyrene tube. Saliva samples were frozen immediately following collection and stored at −80 °C. At the end of the collection period, samples were assayed in our laboratory using competitive enzyme immunoassays for T (Salimetrics EIA, product number: 1-2402). Sample and standard reactions were run in duplicate, and the sample concentrations used in the analyses are the averages of the duplicates. Interassay coefficients of variation were 12.35% for low pools and 6.65% for high pools. The intrassay coefficient of variation was 5.76%. Samples for whom the coefficient of variation exceeded 15% between duplicates, indicating unreliable assay results, were excluded from analyses (overall eight samples; Time-1 – four samples, Time-2 – one sample, Time-3 – three samples). The intrassay coefficient of variation for the remaining samples was 4.81%. In addition, T concentrations could not be obtained for 14 samples due to insufficient saliva provided during the collection periods (Time-1 – six samples, Time-2 – four samples, Time-3 – four samples).

2.4. Drug administration

Subjects self-administered either 24 IU of OT (three puffs of 4 IU in each nostril; Syntocinon spray; Novartis, Basel, Switzerland) or a placebo under an experimenter's supervision. The placebo included all the Syntocinon ingredients except for the active hormone. The administration of OT or placebo was randomized within sex to ensure an equal number of males and females in every condition. Both the experimenter and the subjects were blind to the drug condition, and subjects could not differentiate between OT and placebo (Fisher's exact test, $p = 0.551$). The experimental paradigm started approximately 30 m after hormone administration, of which, subjects could read National Geographic magazines for the first 25 m. In the remaining 5 m, the second saliva sample was collected.

2.5. Competitive preferences paradigm

Subjects were assigned to a four-person group, and were not informed who are the other three subjects in their foursome (group composition remained constant throughout the experiment). Next, subjects completed a standardized set of arithmetic tasks (adding five 2-digit numbers), which differed only in the mechanism by which subjects were paid for the number of problems they solved. In the first 3-rounds, subjects tried to solve as many problems as they could during 4 m per round. Subjects were allowed to use a pencil and paper for calculations, but not a calculator. Upon submitting an answer to the designated box, subjects were informed if it was correct, a counter of solved-problems was updated, and the next problem was shown. During each task, a countdown timer was shown on the screen.

The payment-schemes were as follows:

Round-1 (Piece-Rate Payment-Scheme): in this round, each subject received one NIS for every problem solved, regardless of how many problems the other subjects in the foursome solved.

Round-2 (Tournament Payment-Scheme): in this round, the subject, in each foursome, who solved the most problems received four NIS for every solution, while the remaining three subjects received nothing. In case of a tie, each one of the winners received one NIS per solved-problem.

Round-3 (Payment-Scheme Choice): in this round, before performing the task, subjects decided which payment-scheme composition will be applied to their performance. That is, each subject chose, by a slider scale, how to allocate a 100-point endowment between the piece-rate and the tournament payment-schemes.[2] For each point subjects allocated to the piece-rate scheme, they received 0.01 NIS for every solved-problem. For each point subjects allocated to the tournament-scheme, they received 0.04 NIS for every solved-problem, but only if the number of problems they solved was greater than the number of problems that each of the three other subjects solved in Round-2 (tournament).[3] Otherwise, no payment was given for points that were allocated to the tournament-scheme. In case of a tie, subjects received 0.01 NIS per solved-problem for each point they allocated to the tournament-scheme. Subjects' point-allocation did not affect the earnings of others, nor did it depend on how the other subjects allocated their points.

Round-4 (Past Performance): subjects were reminded of their performance in Round-1, and were asked to decide (retroactively) which payment-scheme composition would be applied to it. For each point subjects allocated to the piece-rate scheme, they received 0.01 NIS for every problem they solved in Round-1. For each point subjects allocated to the tournament-scheme, they received 0.04 NIS for every problem they solved in Round-1, but only if the number of problems they solved in Round-1 was greater than the number of problems that each of the three other subjects solved at Round-1. Otherwise, no payment was given for points that were allocated to the tournament-scheme. In case of a tie, for each point that was allocated to the tournament-scheme, subjects received 0.01 NIS for every solved-problem. As in Round-3, subjects' point-allocation did not affect the earnings of others, nor did it depend on how the other subjects allocated their points.

Because, as opposed to Round-3, points allocated to tournament-scheme in Round-4 do not require subjects to actually engage in a competition, but rather are based on their previous performance, point allocation in this round acts as an important control for other general or unmeasured factors associated with the tournament, such as performance anxiety.

Subjects' Payment: Before Round-1, subjects were informed that their total payment would be set according to their earnings in one of four rounds which would be randomly chosen at the end of the experiment. This payment procedure ensured that decisions in a given round are not affected by the outcomes of other rounds (wealth effect).

To limit the effect of the first round's outcomes on subjects' point-allocations in subsequent rounds, subjects were not informed regarding their performance relative to other subjects until the very end of the experimental session.

2.6. Performance, self-confidence, and risk-preferences

Performance was operationalized as the number of solved-problems in Round-1 and Round-2, since only in these rounds, payment schemes were identical across all subjects. To assess subjects' confidence in their

[2] This linear choice measure (Saccardo et al., 2018) was preferred over the more commonly used dichotomous choice between competition or piece-rate in order to maximize statistical power.

[3] To ensure that subjects' point-allocations in Round-3 were not biased by their expectations regarding the chosen compositions of the other subjects in their foursome, subjects' performance in this round was compared to the performance of the three other subjects in Round-2.

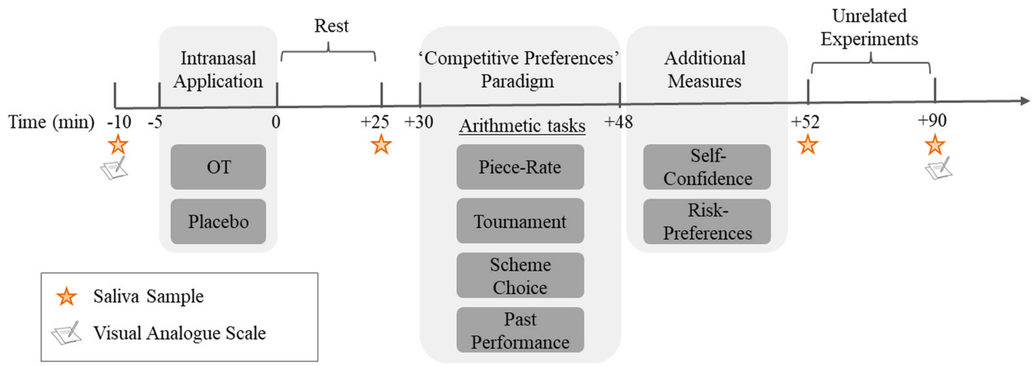

Fig. 1. Experiment timeline.

performance at the arithmetic tasks, following the four rounds, subjects were asked to guess their rank (from first to fourth) in Round-1 and Round-2. Each successful guess awarded subjects with one NIS. Subjects' risk-preferences were measured by a price list design (Zhong et al., 2018). Subjects were asked to make 10 choices between two alternatives. For every choice, option A was winning 10 NIS with a 50% chance or 0 NIS with a 50% chance, and option B was winning, with complete certainty, an increasing amount of NIS, starting with 2.5 NIS, in the first choice, increasing by 0.5 NIS on every choice, up to 7 NIS in the last choice. A later switching point (from option A to option B) indicates a greater risk-preference. One randomly chosen subject in every experimental session received payment based on one of his or her choices.

2.7. Procedure

To control for diurnal rhythms in circulating OT and T levels, all experimental sessions were scheduled for 14:00, in keeping with the recommended guidelines for OT administration studies (Guastella et al., 2013). After signing a written consent form, subjects were seated in front of computers at cubicles, the first saliva sample (Time-1) was collected, and subjects completed the mood assessment measure. Then, subjects self-administered either OT or a placebo. Twenty-five minutes after the administration, the second saliva sample (Time-2) was collected. Approximately 30 m after hormone administration, the subjects completed the competitive preferences paradigm, and the self-confidence and risk-preference measures, which were followed by the collection of the third saliva sample (Time-3). After two additional unrelated experiments, subjects completed the second mood assessment measure and a demographic questionnaire, and the fourth saliva sample (Time-4) was collected. At the end of the session, subjects were directed to another room and received payment privately (see Fig. 1 for the experiment's timeline). Subjects were instructed not to communicate with each other throughout the session.

2.8. Statistical analyses

We conducted logit and linear regression analyses with treatment (placebo/ OT), T baseline levels and reactivity, and sex (female/male) as between-subjects variables. The willingness to engage in competition was assessed by applying a general linear model with a logit link function and the binomial distribution on the proportion of points allocated to tournament in Round-3 (ranging between 0 and 1). To account for potential heterogeneity between experimental sessions, standard errors were clustered by session (using the Huber-white sandwich with d.f. correction).

To account for known sex differences in T levels (baseline levels in our sample; Males: $M = 150.87$, $SE = 5.57$, *Females:* $M = 50.96$, $SE = 2.00$, *t-test on logarithmized values* $(192) = -21.12$, $p < .001$, *Cohen's* $d = -3.03$), values at Time-1– Time-3 were standardized for each sex separately *(to* $M = 0$ and $SD = 1$). Outliers were winsorized to ±3 SDs.

T-reactivity was assessed by regressing T levels (standardized and winsorized by sex) onto T levels (standardized and winsorized by sex) at an earlier time-point and saving the unstandardized residuals (Welker et al., 2017). For example, T-reactivity from Time-2 (pre-competition) to Time-3 (post-competition) was assessed by the unstandardized residuals of regressing T levels at Time-3 onto T levels at Time-2. Since the residuals represent changes in T levels that are not explained by T levels at the earlier time-point, this reactivity assessment is statistically independent of T levels at the earlier point. For all analyses, assessing T-reactivity as the absolute change in T levels did not affect the significance of the results.

3. Results

3.1. Do T-reactivity, OT, and sex interact to affect the willingness to engage in competition?

Our main variable of interest – the willingness to compete – consists of the proportion of points subjects chose to allocate to tournament-scheme in Round-3. We find that the interaction between OT, T-reactivity from pre-competition (Time-2) to post-competition (Time-3), and sex, significantly predicted tournament point-allocation ($p = 0.036$; see Table 1 Model 3, Fig. 2, and Fig. S1). In females, T-reactivity did not predict tournament point-allocation, neither under placebo (b = 0.20, SE = 0.40, p = 0.620, Odds Ratios (OR) = 1.22, Pseudo $R^2 = 0.0015$), nor under OT (b = 0.03, SE = 0.31, p = 0.915, OR = 1.03, Pseudo $R^2 < 0.001$). However, in males, T-reactivity was a significant predictor of points allocated to the tournament under placebo (b = 1.33, SE = 0.32, p < 0.001, OR = 3.79, Pseudo $R^2 = 0.042$), but not under OT (b = −0.03, SE = 0.35, p = 0.930, OR = 0.97, Pseudo $R^2 < 0.001$). None of these variables were by themselves significant predictors of the proportion of points allocated to the tournament (all p's > 0.05; see Table 1 Model 1). Relatedly, baseline T levels were also not a significant predictor of the willingness to compete (b = 0.08, SE = 0.04, p = 0.052, OR = 1.09, Pseudo $R^2 = 0.005$), nor did baseline T levels interact with OT, sex, or the OT × sex interaction to predict the willingness to compete (all p's > 0.05, OR's range = [0.82, 0.98], Pseudo R^2 = [0.003, 0.010]).

To examine the specificity of the three-way interaction (OT × T-reactivity × sex) on competitive motivation, we tested if these interactive effects could be accounted for indirectly, via their effect on performance, self-confidence or risk-preferences. While performance ($b = 0.14$, $SE = 0.03$, $p < 0.001$, OR = 1.15, Pseudo $R^2 = 0.028$) and confidence ($b = 0.66$, $SE = 0.09$, $p < 0.001$, OR = 1.93, Pseudo $R^2 = 0.045$) were strongly predictive of points allocated to the tournament-scheme in Round-3, risk was only marginally so ($b = 0.20$, $SE = 0.10$, $p = 0.063$, OR = 1.22, Pseudo $R^2 = 0.007$). Nevertheless, the OT × T-reactivity × sex interaction was still a significant predictor of points allocated to the tournament-scheme even after controlling for performance, confidence and risk-preferences ($p = 0.010$; see Table 1 Models

Table 1
Regression analysis on the proportion of tournament point-allocation in Round-3.

Model	(1)	(2)	(3)	(4)	(5)	(6)	(7)
OT	0.08	–0.20	–0.20	–0.16	–0.26	–0.19	–0.17
	(0.19)	(0.20)	(0.20)	(0.20)	(0.19)	(0.20)	(0.21)
	[1.09]	[0.82]	[0.82]	[0.85]	[0.77]	[0.83]	[0.84]
Male dummy	0.29	–0.03	–0.08	–0.13	–0.32	–0.29	–0.26
	(0.19)	(0.21)	(0.22)	(0.20)	(0.22)	(0.25)	(0.25)
	[1.33]	[0.97]	[0.93]	[0.88]	[0.73]	[0.75]	[0.77]
T-Reactivity	0.23	0.48	0.20	0.20	0.13	–0.03	--0.04
	(0.20)	(0.33)	(0.40)	(0.36)	(0.29)	(0.27)	(0.26)
	[1.26]	[1.62]	[1.22]	[1.22]	[1.14]	[0.97]	[0.96]
OT × Male		0.60*	0.63*	0.66**	0.78**	0.73*	0.66*
		(0.27)	(0.27)	(0.25)	(0.26)	(0.30)	(0.26)
		[1.82]	[1.87]	[1.94]	[2.19]	[2.07]	[1.93]
OT × T-Reactivity		–0.69*	–0.17	–0.08	–0.05	–0.01	–0.10
		(0.33)	(0.51)	(0.45)	(0.42)	(0.43)	(0.40)
		[0.50]	[0.85]	[0.93]	[0.95]	[0.99]	[0.90]
Male × T-Reactivity		0.37	1.13*	1.13**	1.18**	1.38**	1.17*
		(0.44)	(0.48)	(0.40)	(0.38)	(0.45)	(0.46)
		[1.45]	[3.11]	[3.11]	[3.26]	[3.96]	[3.21]
OT × Male × T-Reactivity			–1.20*	–1.30*	–1.24*	–1.29*	–1.03*
			(0.57)	(0.54)	(0.52)	(0.50)	(0.47)
			[0.30]	[0.27]	[0.29]	[0.27]	[0.36]
Performance				0.14***	0.05*	0.06•	0.05•
				(0.03)	(0.02)	(0.03)	(0.03)
				[1.15]	[1.05]	[1.06]	[1.06]
Confidence					0.56***	0.63***	0.47**
					(0.11)	(0.14)	(0.13)
					[1.75]	[1.88]	[1.59]
Risk-preference						0.14	0.09
						(0.09)	(0.09)
						[1.15]	[1.10]
Points' allocation at Round-4							0.96***
							(0.26)
							[2.62]
Constant	–0.61***	–0.48**	–0.47**	–1.36***	–2.12***	–2.39***	–2.27***
	(0.14)	(0.14)	(0.14)	(0.22)	(0.24)	(0.33)	(0.33)
	[0.54]	[0.62]	[0.62]	[0.26]	[0.12]	[0.09]	[0.10]
Pseudo R^2	0.006	0.015	0.018	0.041	0.060	0.076	0.089
Observations	197	197	197	197	197	181	181

Notes: Factors contributing to the proportion of points that were allocated to the tournament in Round-3, were assessed via a general linear model with a logit link function and the binomial distribution. Male dummy = 1 if subject is male, 0 otherwise. Values in each cell represent log odds ratios. Parentheses contain robust standard errors, clustered by session. Odds ratios are reported in brackets.

a – Sixteen subjects were excluded from analysis in models 6 and 7 due to inconsistent decisions in the risk-preference measure.

• Significant at 10%.
* Significant at 5%.
** Significant at 1%.
*** Significant at 0.1%.

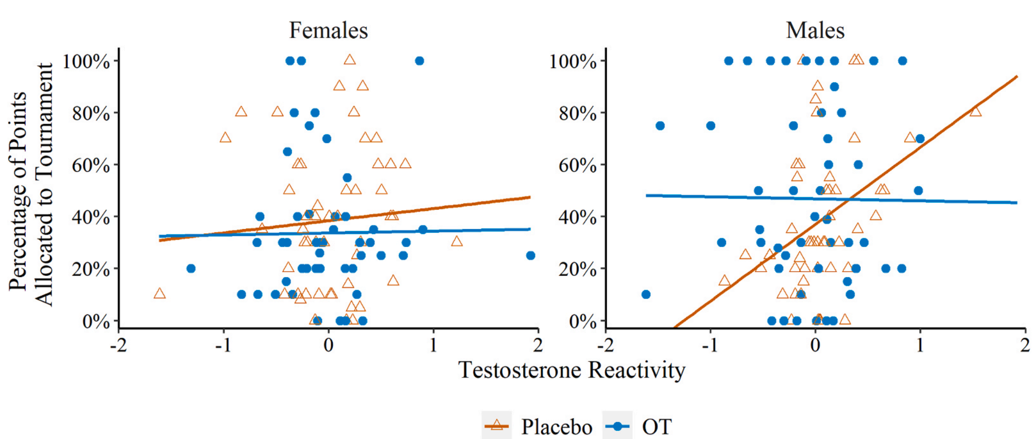

Fig. 2. Scatterplots by sex of the relationship between testosterone (T) reactivity during competition, oxytocin (OT), and the proportion of points subjects allocated to the tournament-scheme in Round-3. T-reactivity is based on residuals of predicting T levels (standardized by sex) at Time-3 (post-competition) by T levels (standardized by sex) at Time-2 (pre-competition).

4–6).

In Round-4, subjects allocated points retrospectively based on their performance in Round-1, but do not actually engage in a competition. While tournament point-allocation in Round-4 is significantly correlated with tournament point-allocation in Round-3 ($r(202) = 0.41$, $p < 0.001$), importantly, the three-way interaction of OT × T-reactivity × sex did not predict tournament point-allocation in Round-4, when competitive performance is absent ($b = -0.96$, $SE = 0.73$, $p = 0.188$, OR = 0.38, Pseudo $R^2 = 0.014$). Notably, even after controlling for the combined effects of performance, self-confidence, risk, and points allocated in Round-4, the OT × T-reactivity × sex interaction still predicted tournament point-allocation in Round-3 ($p = 0.029$; see Table 1 Model 7). Additional analyses showed that this finding was robust to additional controls for female menstrual cycle-phase and contraceptive use (see Supplemental Material for additional analysis).

3.2. Is T-reactivity dependent on OT administration and sex?

To examine if T-reactivity was by itself dependent on OT administration, we regressed T-reactivity on OT, sex, and the OT × sex interaction. T-reactivity was not affected by OT administration (Time-1 to Time-2: $b \approx 0.00$, $SE = 0.08$, $p = 0.953$, $\beta = 0.01$, $R^2 < 0.001$; Time-1 to Time-3: $b = -0.08$, $SE = 0.09$, $p = 0.416$, $\beta = -0.13$, $R^2 = 0.004$; Time-2 to Time-3: $b = -0.07$, $SE = 0.07$, $p = 0.307$, $\beta = -0.14$, $R^2 = 0.005$), sex (Time-1 to Time-2: $b = -0.03$, $SE = 0.08$, $p = 0.753$, $\beta = -0.05$, $R^2 < 0.001$; Time-1 to Time-3: $b = -0.03$, $SE = 0.09$, $p = 0.704$, $\beta = -0.06$, $R^2 < 0.001$; Time-2 to Time-3: $b = 0.01$, $SE = 0.05$, $p = 0.906$, $\beta = 0.01$, $R^2 < 0.001$), or by the OT × sex interaction (Time-1 to Time-2: $b \approx 0.00$, $SE = 0.12$, $p = 0.986$, $\beta \approx 0.00$, $R^2 < 0.001$; Time-1 to Time-3: $b = -0.10$, $SE = 0.16$, $p = 0.544$, $\beta = -0.16$, $R^2 = 0.0065$; Time-2 to Time-3: $b = -0.08$, $SE = 0.12$, $p = 0.532$, $\beta = -0.16$, $R^2 = 0.007$), suggesting that OT administration itself did not alter T levels over the course of the study.

3.3. Do T-reactivity, OT, and sex interact to affect how 'rationally' participants allocate points to the tournament?

Allocating points to the tournament is only worthwhile if a player has a chance of winning. While performance in the arithmetic task varied considerably between subjects, we next asked the question, if for a given level of performance, does the OT × T-reactivity × sex interaction affect the degree to which subjects optimize their points allocated to the tournament? Put differently, does the OT × T-reactivity × sex interaction affect the amount by which subjects maximize their total monetary return? We calculated the odds, for each subject, that the number of their solved-problems exceeded the number of solved-problems in the preceding round of three other randomly chosen subjects. Thus, for any given performance, we could estimate the probability of winning the tournament, and what the optimal proportion allocated to the tournament should be. Next, we calculated the gap between the actual proportion of points that subjects allocated to the tournament to the proportion that would maximize their expected total return. This allowed us to assess the total 'money on the table' left by each subject.

For a given number of solved-problems in Round-3, the 'Money on the table' (MOT) for subject i was defined by:

$$MOTi = \begin{cases} Ai - Pi^3 & if \quad Pi^3 < Ai \\ 0 & if \quad Pi^3 = Ai \\ \left(Pi^3 - Ai\right) \times 3 & if \quad Pi^3 < Ai \end{cases}$$

where Pi denotes the percentile rank of subject-i's number of solved-problems in Round-3 within the distribution of number of solved-problems in Round-2 among all subjects in the study, and Ai denotes the actual allocation of this subject. We regressed this 'money on the table' variable on treatment, T-reactivity, and sex. Whereas the OT × T-reactivity × sex interaction did not predict the amount of money subjects left on the table ($b = -6.83$, $SE = 26.61$, $p = 0.800$, $\beta = -0.06$, $R^2 = 0.062$), the OT × T-reactivity did ($b = -33.60$, $SE = 11.28$, $p = 0.008$, $\beta = -0.29$, $R^2 = 0.051$; see Fig. 3). That is, while under placebo, T-reactivity was not related to the optimization of tournament point-allocation, given performance ($r(96) = 0.07$, $p = 0.489$), under OT, T-reactivity positively correlated with the level that subjects optimized their point-allocation ($r(97) = -0.22$, $p = 0.025$; Difference between OT to placebo correlations = 0.30, Fishers Z-test = 2.07, $p = 0.039$, Cohen's d = 0.29). Neither OT × sex ($b = 7.05$, $SE = 14.38$, $p = 0.630$, $\beta = 0.13$, $R^2 = 0.034$), nor the T reactivity × sex ($b = -15.99$, $SE = 12.26$, $p = 0.210$, $\beta = -0.14$, $R^2 = 0.027$) interactions were significant predictors of the amount of money subjects left on the table.

4. Discussion

In an era of increasingly selective educational programs, vigorous races for career promotion, and a scarcity of high-paying jobs, opportunities for success come disproportionately to those who embrace competition. Despite intense interest in understanding the factors giving rise to individual differences in competitiveness, knowledge regarding biological mechanisms has been surprisingly elusive. Here, we show that the combination of OT administration and T-reactivity in response to a competition affecting competitive-preferences in a sex-dependent manner. In males receiving placebo, a greater rise in endogenous T levels was associated with a greater willingness to compete; however, under OT, this association was absent. In contrast, for females, T-reactivity during competition was not related to the willingness to engage in competition, both under placebo and under OT.

Previous research has shown that endogenous T concentration levels play a role in modulating behaviors and preferences that are at the core of competition, including performance (Casto et al., 2020), risk-preferences (Apicella et al., 2014), and self-confidence (Eisenegger et al., 2017). In addition, several studies have shown a relationship between T-reactivity and competition (Trumble et al., 2012; van der Meij et al., 2012). Here, we demonstrate that in males under placebo, T-reactivity was associated, specifically, with the willingness to engage in a competition when controlling for potential confounds such as subjects' performance, risk-attitude, or self-confidence.

In terms of existing theory, the 'Biosocial Model of Status' could not be tested in our study, since subjects were not informed regarding the competition outcome till the very end of each session. However, our results in males under the placebo condition are consistent with the 'Challenge Hypothesis' which posits the T levels increase in response to social challenges, such as competition, regardless of the outcome of the competition (Archer, 2006; Wingfield et al., 1990). As opposed to males, females under placebo in our study showed no association between T-reactivity to competitiveness. This finding is consistent with previous studies showing T-reactivity during competitive tasks for males, but not for females (Casto and Prasad, 2017; Geniole et al., 2017). It has been argued that sex differences in the association between T-reactivity and behavior may reflect sex differences in the level of social engagement with the task (Geniole et al., 2017). However, males and females in our study showed similar performance in the number of problems solved (females in our study solved an average of 6.42 ($SD = 2.42$) of problems per task; males solved an average of 6.92 ($S.D. = 3.28$) problems per task; $t(202) = -1.25, p = 0.214$), so sex differences in the level of social engagement with the task does not seem to be a suitable explanation for our findings here. Research applying T administration exogenously indicates that T effects on competition may be person and context dependent. For example, in females, exogenous T increased the willingness to compete again following a victory in high-dominant females, but decreased it after a defeat regardless of dominance level (Mehta et al., 2015). T administration also increased status seeking behavior in males, but particularly for those with low social status (Losecaat

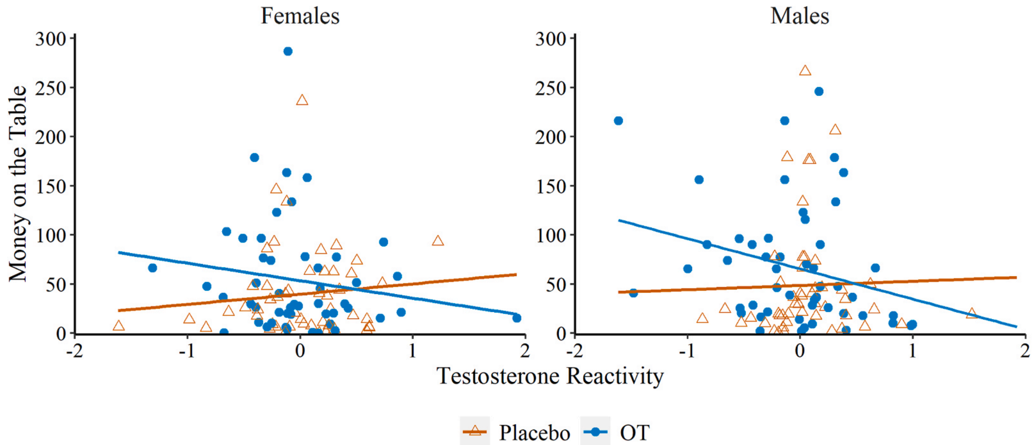

Fig. 3. Scatterplot of the association between testosterone (T) reactivity and the amount of money subjects left on the table in Round-3. T-reactivity is based on residuals of predicting T levels (standardized by sex) at Time-3 (post-competition) by T levels (standardized by sex) at Time-2 (pre-competition).

Vermeer et al., 2020). These findings are consistent with the notion that T facilitates competitive motivation when there is an opportunity for higher status.

Under OT, there was no association between T-reactivity to competitiveness in both sexes. Aromatization of T to estradiol in several brain regions has been shown to upregulate the expression of the OT receptor (Johnson et al., 1989) and increase OT binding affinity (Johnson et al., 1991). However, given that the time course of such effects is typically over the course of several hours, this seems unlikely to be an explanation here. Rather, our findings suggest that at least in males, while OT did not directly affect levels of salivary T or competitiveness, it canceled out effects of T-reactivity on competitiveness which were observed under placebo. In females, the lack of association between T reactivity and competitiveness was evident also under placebo. One possibility for this sex dependent finding may be that naturally occurring differences in endogenous OT levels may act to cancel out T-related effects on competitiveness, while speculative, this is consistent with the finding of higher OT levels in plasma for females (Engel et al., 2019). These findings are also consistent with the broader notion of opposing roles of OT and T in modulating human social behavior (Crespi, 2016; Procyshyn et al., 2020). Our finding that under OT there was a decreased correlation between T-reactivity and money on the table suggests that OT reduced the saliency of T-reactivity as a driver of competitive performance. Interestingly, reduced attention to interoceptive signaling has been postulated as one mechanism by which OT may modulate social cognition (Yao et al., 2018).

Under placebo, males and females did not show differences in the proportion of points invested in the tournament. This is in contrast to the majority of previous studies examining sex differences in competitive preferences which show that males more readily engage in competition – even in instances when it is disadvantageous, and females are more likely to shy away – even when they would gain from competing (Balafoutas and Sutter, 2012; Niederle and Vesterlund, 2007; Saccardo et al., 2018; Zhong et al., 2018). However, several cases have also been reported in which females compete at equal rates as males, highlighting the importance of socio-cultural factors in mitigating or exacerbating these differences (Dariel et al., 2017; De Paola et al., 2015; Khachatryan et al., 2015). While perhaps surprising, the lack of sex-differences could be explained by socio-cultural factors such as gender equality. Our study was conducted in Israel on a sample of Israeli students. The vast majority of studies that reported sex-differences in competitive preferences were conducted in countries with greater gender equality than Israel, according to the global gender gap index (Global Gender Gap Report 2020, 2020). In contrast, studies that were conducted in countries with lower gender equality than Israel (e.g., Armenia, Italy, and United Arab Emirates), did not observe sex-differences in competitive preferences (Booth et al., 2019; Dariel et al., 2017; De Paola et al., 2015; Khachatryan et al., 2015). This pattern is consistent with previous research showing that differences in economic preferences between males and females tend to be greater in countries where the gender gap in wages is smaller (Falk and Hermle, 2018), and further highlights the role of social and cultural factors in contributing to sex differences in competitiveness (Zhong and Fu, 2019). Indeed, the nascent field of cultural neuroscience aims to characterize how differences in beliefs, expectations, and values, may be embodied into biological systems (Kitayama et al., 2019; Kitayama and Salvador, 2017). Because culture is such critical lens for interpreting the social environment, factors which regulate the processing and salience of the social environment (such as OT) may show disparate effects, depending on their cultural milieu.

More broadly, our findings support the proposition that rather than having a uniform effect on behavior, OT interacts with T in affecting competitiveness in a sex-specific manner (Holtfrerich et al., 2016, 2018). These findings deepen our understanding of the neuroendocrine processes underlying human preferences for competition, suggest a new path for the interaction between OT and T on human social behavior, and extend the evidence base for sex-dependent effects of OT on this behavior.

Author contributions

B.R. Cherki, E. Winter, and S. Israel designed the experiment; D. Mankuta gave medical support; B.R. Cherki ran the experimental sessions; and B.R. Cherki and S. Israel analyzed the data and wrote the paper. All authors approved the final version of the manuscript for submission.

Declaration of conflicting interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.psyneuen.2021.105352.

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