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Preliminary data on increased reactivity towards children in distress after testosterone administration in women: A matter of protection?

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ABSTRACT

Emotional reactivity to others' distress is a vital prerequisite for a caring response. Testosterone, in contrast, is mostly associated with protection of personal dominance and decreased responsiveness to others' needs. However, experimental work also indicates that rising testosterone levels in response to infant distress can potentially facilitate protection. We assessed the impact of testosterone administration on participants' emotional reactivity to infants in distress, measuring their facial responses on the corrugator supercilii forehead muscle ('frowning') and the zygomaticus major ('smiling') as an index of emotional responses towards children. Moreover, we probed whether the effect of testosterone is moderated by participants' self-reported nurturance and protective tendencies. Our preliminary results showed that testosterone not only increased emotional reactivity to empathy eliciting images of children, but that this increase was strongest in participants with strong protective tendencies. Our administration study is the first to link testosterone to infant protection.

1. Introduction

Young children are dependent on a warm, responsive, and protective environment for survival and healthy development (Bowlby, 1983). Emotional reactivity is a key aspect in providing this environment, since it allows parents to quickly recognize their children's needs and respond to them accordingly (Joosen, Mesman, Bakermans-Kranenburg, & van IJzendoorn, 2012; Leerkes, 2010; Morris, Cui, & Steinberg, 2013). In contrast, a failure to engage in emotional interaction with the child causes distress for all parties involved and disrupts social interactions in the long run (Weinberg, Olson, Beeghly, & Tronick, 2006). Accumulating evidence indicates an important role of the endocrine system in underpinning this emotional reactivity (Bos, 2017).

In this regard, testosterone (T), which is traditionally associated with dominance and emotional reactivity, as well as decreases in emotional sensitivity (Bos, Panksepp, Bluthe, & Honk, 2012; Montoya, Terburg, Bos, & van Honk, 2012), is often overlooked or even considered to hamper care-taking behaviors (Wingfield, Hegner, Dufty, & Ball, 1990). The recurring finding that overall T levels decrease in the context of caring relationships seems to support the notion of T as antagonistic to caregiving among both sexes (Grebe, Sarafin, Strenth, & Zilioli, 2019; Meijer, van IJzendoorn, & Bakermans-Kranenburg, 2019; Roney & Gettler, 2015). However, compelling findings imply that increases in T may in fact contribute to the immediate response to a child's signals of distress, potentially facilitating protection or motivation to act (Bos, Hermans, Montoya, Ramsey, & van Honk, 2010; Bos, 2017; van Anders, Tolman, & Volling, 2012). Yet, there is little causal evidence on the immediate effect of T in situations demanding caregiving responses. The current study aims to delineate these effects of T on childcare by testing if administration of T in a group of healthy young women increases emotional reactivity towards images of children in distressing situations.

Behavioral evidence of T's significance for own survival and support of social status has been well documented over the last two decades, and shows that T enhances the saliency of stimuli mirroring social threats and dominance challenges among both sexes (Bos et al., 2012; Eisenegger, Haushofer, & Fehr, 2011). Furthermore, T increases the

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likelihood of responding to such stimuli with reactive aggression by reducing fear and facilitating approach-related or impulsive behavior (Geniole, Bird et al., 2019; Geniole, Procyshyn et al., 2019; Hermans, Putman, Baas, Koppeschaar, & van Honk, 2006). T is therefore suggested to play an important role in protecting the individual from (status-related) threats (Eisenegger et al., 2011). Parenthood on the other hand, has been associated with a decrease in endogenous T concentrations, especially during caring contexts (Bos, 2017). In fathers, decreases in T concentrations are found to be proportionate to the time invested in childcare (Gettler, McDade, Feranil, & Kuzawa, 2011) and positively predict nurturing responses as well as father-infant synchrony (Gordon, Pratt, Bergunde, Zagoory-Sharon, & Feldman, 2017; Rilling & Mascaro, 2017). Following the challenge hypothesis, lower T concentrations are suggested to be an adaptive biological mechanism to facilitate sensitive caregiving (Gettler et al., 2011; Wingfield et al., 1990). Consistent with this, recent studies propose a role for T as mediator in the trade-off between the pursuit of social dominance and the sensitive care of offspring, with a decrease in T inducing a behavioral shift from competition towards increased parental reactivity and attentiveness (Gettler, 2014). Although women generally have lower levels of T compared to men, the function of variability in T is assumed to be comparable between both men and women. In fact, most of the T administration studies investigating effects on social behavior have been performed on women. Furthermore, parental status is also known to reduce T levels among women (Kuzawa, Gettler, Huang, & McDade, 2010).

Interestingly, a number of studies have actually found that endogenous T concentrations of male participants rise during acute situations of infant distress (Fleming, Corter, Stallings, & Steiner, 2002; Storey, Noseworthy, Delahunty, Halfyard, & McKay, 2011; van Anders et al., 2012). Moreover, administration of T enhanced neural responses to infant cries among women, and this was accompanied by a less aversive experience (Bos et al., 2010). Considering that higher endogenous T concentrations among women also increased the overall reward value of infant faces (Hahn, DeBruine, Fisher, & Jones, 2015), increases in T that are induced by infant distress may enhance the motivation to take protective action (Bos, 2017; Rilling & Mascaro, 2017). This suggestion aligns with the Steroid/Peptide Theory of Social Bonds (van Anders, Goldey, & Kuo, 2011), which describes the relevance of T - together with vasopressin - for protective aggression in parental behavior. In fact, in male ursine monkeys, T levels were positively associated with offspring protection (Teichroeb & Sicotte, 2008). These findings imply that while T is generally associated with self-defense mechanisms, these tendencies may extend to the protection of one's next of kin. In this protective context, the typical threat approaching effects of T can be considered adaptive.

However, there is almost no empirical work on humans that links T responses to protective tendencies. An exception to this is a recent study in which fathers' basal T levels were found to be related to neural activation and behavioral responses to videos depicting children in threatening situations (Lotz et al., 2020), though the findings were inconclusive. Apart from our own study and that by Lotz et al., most research on parenting does not differentiate protective tendencies from other forms of care. This is the case, even though Hofer et al. (2017) recently revealed that protective and nurturing motives independently predicted individual differences in parental care motivation, as well as a number of behavioral outcomes. Where protection "reflects a motivational inclination to protect young children from imminent harm", nurturance reflects "an approach-oriented response toward children and a motivational inclination to treat children in a supportive and nurturing manner" (Hofer, Buckels, White, Beall, & Schaller, 2017). The previous lack of differentiation between these motivational tendencies and a focus on nurturing aspects of care, might have led to an underestimation of T's role in parenting.

In this study, we experimentally probed the effect of T on emotional reactivity towards children's distress in a group of young nulliparous women. Moreover, we related this effect to participants' inclinations towards nurturance or protection. To this end, we assessed participants' sensitivity to infants in distress in comparison to neutral social scenes by measuring their subjective evaluations and electromyographic (EMG) response on the corrugator supercilii forehead muscle ('frowning'), as well as the zygomaticus major ('smiling'). Frowning, a facial response predominantly associated with negative affect, as assessed by EMG, has been shown to capture a range of social responses including empathic distress and perspective taking (Lamm, Porges, Cacioppo, & Decety, 2008) for instance towards disadvantaged children (Bos, Jap-Tjong, Spencer, & Hofman, 2016), but also emotional reactivity to unfairness, moral transgression, or threatening stimuli (Kraaijenvanger, Hofman, & Bos, 2017; Seibt, Muhlberger, Likowski, & Weyers, 2015).

The stimuli used consisted of a set of pictures, which were previously validated by our lab as depicting children in either very negative or neutral situations. To relate the response to either nurturance or protection, we then included participants' self-reported scores on the nurturance and protection subscales according to Hofer et al. (2017) and tested whether these interacted with the effect of T. We included young nulliparous women under the assumption that in humans, as an alloparental species, the mechanism we investigate will be comparable in both parents and non-parents, and that effects are more likely to depend on caregiving motivation instead of parental status. Nonetheless, this assumption needs to be tested in future studies. Beyond taking into account trait differences in parental tendencies, we also analyzed the effect of participants' digit ratio (2D:4D). The digit ratio is considered to relate to participants' prenatal exposure to T or estradiol and to affect their sensitivity to T administration (Breedlove, 2010). Although the validity of the digit ratio as a proxy for prenatal T is highly disputed (Leslie, 2019), studies from our own lab that used the same T administration protocol as currently employed, have demonstrated that it predicts variation in the effect T has on cognitive empathic ability (van Honk et al., 2011), cooperation (van Honk, Montoya, Bos, van Vugt, & Terburg, 2012) and moral decision-making (Montoya et al., 2013).

To summarize, in contrast to an overall down-regulating effect of T on empathic responses, we predicted that when confronted with children in distress, T in conjunction with protective tendencies might result in stronger affective responses. Accordingly, we hypothesized an increase of corrugator response with T (H1) that is also associated with participants' nurturance (H2) and protection (H3) scores. Specifically, we expected both nurturance and protective tendencies to be positively associated with corrugator activation towards infants in distress. However, we expected T to interact only with participants' protective tendencies, such that the relation between T and corrugator activation is especially pronounced in participants with high protective tendencies (H4). Since previous studies on the zygomaticus response to negatively valenced pictures have shown either no response or deactivation (Kraaijenvanger et al., 2017; Seibt et al., 2015), we expected a similar irresponsive pattern in this study. However, we included the zygomaticus to probe the emotion-specificity of our effect. For the subjective responses on compassion, we expected to find a similar relation between T and caregiving tendencies as predicted for the corrugator, although previous T administration studies have often reported dissociations between implicit physiological responses and subjective evaluations (Bos et al., 2012).

2. Methods

2.1. Participants

Twenty-two healthy nulliparous Caucasian women with normal or corrected to normal vision (age = 21.7, SD = 3.5) were recruited via email advertisement to participate in the study. All participants were students and were screened for the exclusion criteria of smoking, use of hormonal contraceptives and history of medical, psychiatric or endocrine illness. The Human Research Ethics Committee (HREC) of the

University of Cape Town approved the study in accordance with the latest declaration of Helsinki. Only women were included since the pharmacokinetic validation of our administration protocol has only been performed for women and ethical approval does not cover men.

We initially aimed for a sample size of 40 participants, based on power calculations that included results from previous studies conducted in our lab using comparable outcome measures. These studies used EMG in within-subject experimental designs with context manipulations, which resulted in large effect sizes with 26 subjects (Hofman, Bos, Schutter, & van Honk, 2012) and 40 subjects (Bos, Hofman et al., 2016). G*power was used to calculate the required sample size (α of 0.05 and a power of .80), employing an ANOVA with 4 within-groups measures (emotion condition (2) X drug condition (2)). However, due to organizational circumstances unrelated to the research execution itself, we were forced to stop inclusion.

2.2. Study design and administration procedure

The study followed a randomized, double-blind, placebo-controlled, within-subjects design and was conducted on two separate session days, with at least one free day between sessions. All participants were invited to the lab during the follicular phase of their menstrual cycle (1–12 days after the start of the menstruation), since endogenous sex steroids are typically low during that time (Montoya & Bos, 2017). In line with previous T administrations studies, participants then sublingually took samples consisting of 5 mg cyclodextirine and 0.5 mg T (respectively 0 mg T in the placebo condition) and waited for four hours until the beginning of the first task (Bos et al., 2012).

2.3. Task and stimuli

While much previous research focuses on participants' response to infant crying (Witteman et al., 2019), we chose visual stimuli that are not in themselves considered aversive – as is often the case with infant crying sounds. Thus, responses to the stimuli should reflect emotional reactions towards the emotion of the children depicted. The stimuli consisted of ecologically valid pictures depicting children in negative or neutral contexts. Pictures defined as negative displayed children in socially distressing scenes, e.g. surrounded by destroyed buildings. Neutral stimuli depicted emotionally neutral scenes, e.g. a child with a neutral expression playing with toys. To validate stimuli for their suitability to measure emotional reactivity with facial EMG, we conducted a pilot study measuring participants' responses to this set of negative and neutral stimuli as well as a number of positive images (to be used in another study). Responses from 41 female participants (M age = 21.54, SD = 2.15) confirmed that corrugator supercilii activity differed significantly between conditions, ($F(1, 7) = 22.52, p < 0.001, \eta 2 = .36$) and was most pronounced in response to negative images. Meanwhile, a main effect of condition on activity of the zygomaticus major ($F(2, 7) = 4.486, p = .014, \eta 2 = .01$) was driven mostly by responses to positive conditions.

Twenty-four stimuli in each condition were shown for a duration of 2 s at the center of the screen and preceded by a 1 s fixation cross. After each stimulus was presented, participants reported how negative they thought the photo was (1 not at all to 7 very negative), how distressing they experienced viewing the picture (1 not at all to 7 very distressing) and how much compassion they felt for the child (1 no compassion to 7 much compassion). No time limit was set for responses and responses were followed by a black screen with a duration of 1 s. Thus, intertrial durations varied according to the reaction time of participants. The same stimuli were used in both drug sessions.

2.4. Self-Reported questionnaires

Participants completed the validated parental care and tenderness questionnaire (PCAT: Buckels et al., 2015) to assess individual differences in activation of the parental care motivational system. Based on Hofer et al. (2017), 10 items from the PCAT were used and aggregated into two separate subscales referred to as "nurturance" and "protection" scores. Cronbach's alpha for the reported subscales is 0.87 and 0.75 respectively. In the context of another study, the participants also completed the interpersonal reactivity index (IRI) (Davis, 1983) and the Behavioral inhibition/activation scale (BIS/BAS) (Carver & White, 1994).

2.5. Digit ratio

Participants' right hands were scanned to assess their digit ratio (2D:4D), i.e. the relation of finger length from the ventral proximal crease to the tip of the finger regarding the second and fourth digit. Finger length was assessed from the image scan by two different raters, using the Adobe Photoshop measurement tool (inter-rater correlation: 0.93). The average value across these two raters was used as the final measure of 2D:4D (Breedlove, 2010). Due to an error, the digit ratio of one participant was not assessed and is treated as a "missing value" in the data analysis.

2.6. EMG data collection and processing

Bipolar electrode montages over the left corrugator supercilii and left zygomaticus major were used to measure frowning and smiling responses respectively, to both sets of stimuli (Fridlund & Cacioppo, 1986). As ground electrodes, we used active common mode sense (CMS) and passive driven right leg (DRL) electrodes placed on the midline of the forehead right before the hairline. EMG signals were sampled at 2048 Hz using a Biosemi ActiveTwo amplifier and stored for offline analysis. Raw data were then 30−500 Hz band pass filtered at a rolloff of 24 db and a notch filter of 50 Hz. We segmented data for each trial into -1000 – 2000 ms epochs time-locked to stimulus onset. The data were then rectified and baseline corrected by subtracting the averaged EMG activity 1000 ms before stimulus onset from the post stimulus activity. Finally, EMG signals were averaged into 250 ms intervals, resulting in a total of 8 time bins. EMG data from trials with an averaged post-stimulus activity ± 3 SD from the mean within subjects were considered as artifacts and rejected from analyses. There was no significant difference between the number of excluded trials for placebo vs. T treatment. Data processing was performed using Brain Vision Analyser 2.0.

2.7. Statistical analyses

Analyses were carried out in "R" Version 3.4.1. (Team, 2013) and related "R" packages in their most recent version, using the checkpoint function set to 3 October 2018, to ensure reproducibility. Data were analyzed using linear mixed effects analysis with the help of the lme and lmer packages in R and significant omnibus tests, using type 3 anovas (Kuznetsova, Brockhoff, & Christensen, 2015).

2.7.1. Subjective rating data

To assess the effect of T on subjective evaluation of the stimuli, we ran three separate models, using participants' ratings of the emotions they experienced (negativity, distress, compassion) as the dependent variable and emotionality of the picture, drug and session (first or second visit, irrespective of drug) as independent variables. Since the effect of T on participants' response to emotional content might differ depending on whether they saw the pictures for the first or the second time, we also included a three-way interaction between these variables (emotion x drug x session). To account for heterogeneity between subjects, random slopes and intercepts were added for emotion as well as drug in all three models. In the last model describing participants' compassion, the random intercept had to be dropped in order to achieve conversion (Barr, Levy, Scheepers, & Tily, 2013).

2.7.2. EMG data

EMG data were analyzed for each muscle separately. Since we were interested in the effect of T in response to emotional content (compared to social scenes in general), and to not overcomplicate the potential models and interactions, EMG response to neutral stimuli was subtracted from the response to negative stimuli. T-tests confirmed that participants' averaged Δ muscle activity over time was significantly different from zero for both ZYG and COR (COR: $M = 0.6$, $t(20) = 2.38$, $p = 0.03$, ZYG: M=-0.16, $t(20)$=-2.58, $p = 0.02$), with COR responses enhanced in response to negative stimuli and ZYG responses stronger in response to neutral stimuli. Therefore, Δ muscle activity over time was used as the dependent variable in further analyses and indicated reactivity to emotional content. In the interest of keeping the structure of the mixed model maximal, random slopes and intercepts were added for all repeated effects, i.e. time and drug (Barr et al., 2013). No interaction term was included in the random slope, since there would have only been one value per participant per cell. For visualization purposes, both ZYG and COR activity in response to both conditions *and* Δ muscle activity are plotted in all figures (Fig. 2–6).

Based on our hypotheses, we modeled EMG data in three steps. First, to assess an overall effect of the administration, we tested the effect of T for each muscle separately on Δ muscle activity. As independent variables, we included administered drug, time (scaled) and session. Interactions of all three variables were tested (three-way interaction drug x time x session), since drug effects may vary depending on whether participants completed the task for the first or second time at the time of drug administration.

Second, to test the hypothesis that the effect of T is supported by an individual's protective rather than nurturing tendencies, we ran a third model consisting of the base model as well as participants' self-reported nurturance and protection scores, which we derived from the PCAT (Hofer et al., 2017). Interactions of these scores were tested with time and administered drug.

Third, following previous results from our lab, we included digit ratio as a potential moderator of the effect of T, and an interaction between T, digit ratio and time, in the base model. Post hoc analysis was conducted using lsmeans (Lenth, 2016). We report 95 % confidence intervals and Tukey corrected p-values.

3. Results

3.1. Subjective ratings of the stimuli

Main effects of emotion in all three models showed that in response to the emotional pictures, participants experienced significantly more negativity ($F_{(1|18)} = 838.68$, $p < 0.0001$), distress ($F_{(1|18)} = 337.34$, $p < 0.0001$), and compassion ($F_{(1|18)} = 168.12$, $p < 0.0001$), confirming the validity of the stimuli (see Fig. 1). Regarding compassion, the model further revealed an interaction between emotion and session ($F_{(1|36)} = 6.2186$, $p = 0.01737$) and a marginal three-way interaction between drug, session and emotion ($F_{(1|18)} = 3.2338$, $p = 0.08893$).

Post hoc analyses revealed that participants felt slightly more compassion towards all stimuli during the first session irrespective of the individual order of administration (es = 0.2, SE = 0.1, $t_{(35)} = 2.04$ $p < 0.05$), but less towards neutral pictures compared to negative ones (es=3.18, SE=0.27, $t_{(20)} = 13.16$ $p < 0.0001$). There was no effect of any of the other variables on ratings.

3.2. EMG measures

3.2.1. Corrugator

3.2.1.1. Base model 1. Model comparison confirmed that the base model fits the data better than the null model consisting only of session, time and the random slopes accounting for inter-subject variation of time courses (AIC 971.07 vs. 846.89, BIC 1001.98 vs. 904.85,

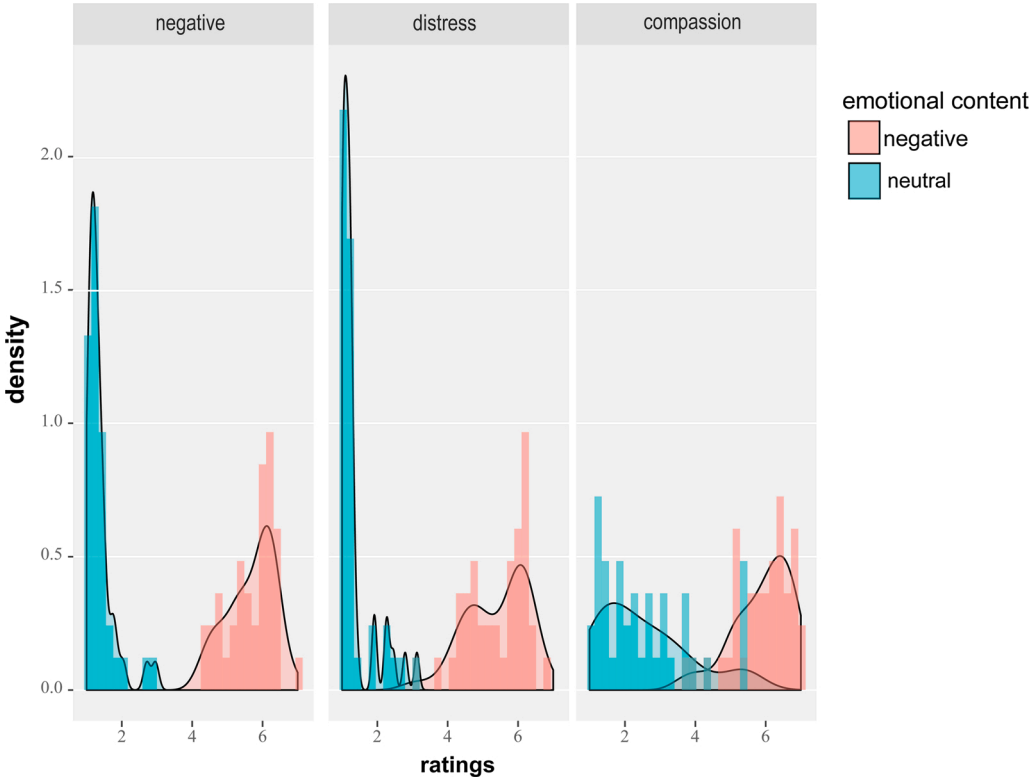

Fig. 1. Histogram of participant's stimulus ratings. Panels are divided by the question asked to the participant. Blue bars indicate ratings of neutral and red bars ratings of negative pictures, black lines depict smoothed data using the "geom_density" function. (For interpretation of the references to colour in this Figure legend, the reader is referred to the web version of this article).

$p < 0.0001$). Moreover, the model revealed a significant main effect of time ($F_{(1|20)} = 7.5380$, $p = 0.01247$) as well as an interaction between time and drug ($F_{(1|284)} = 4.0289$, $p = 0.04568$, see Fig. 2).

Post hoc analyses showed that the reactivity to emotional content increased over time in both the T and placebo conditions (P: es = 0.46, SE = 0.2, 95 % CI [0.06, 0.87], $t(21) = 2.361$, $p = 0.0278$; T: es=0.6, SE=0.2, 95 % CI [0.19, 1], $t(21) = 3.049$, $p = 0.0061$). However, this increase was significantly greater after T administration (es=-0.13, SE=0.07, $t(284)$=-2.01, $p = 0.0457$).

To further validate that the corrugator responses reflect affective motivational responses related to empathy and valence, three models were run in which the subjective ratings were regressed onto the slopes of the corrugator response. For all these models, the subjective ratings were significantly related to corrugator responses: negativity ($F_{(1|217)} = 13.14$, $p < 0.001$), distress ($F_{(1|217)} = 11.62$, $p < 0.001$), compassion ($F_{(1|277)} = 35.76$, $p < 0.001$).

3.2.1.2. Model 2 including participants' nurturance and protection scores. A model including participants' self-reported nurturance and protection ratings fits the data significantly better than the base model (AIC 971.07 vs 845.47, BIC 904.85 vs. 934.33, p = 0.03). This model revealed a main effect of nurturance ($F(1|18) = 5.2321$, $p = 0.034497$) (see Fig. 3), a two-way interaction between drug and time ($F(1|282) = 4.6431$, $p = 0.032025$) as well as between session and time (F(1|282)=6.5291, $p = 0.011137$) and a three-way interaction between drug, time and protection scores (F(1|282)=7.3217, $p = 0.007228$) (see Fig. 4). Finally, there were trends for an effect of session ($F(1|18) = 3.2548$, $p = 0.087977$), as well as an interaction between time and nurturance (F(1|18)=3.6059, $p = 0.073726$).

Post hoc tests showed that emotional reactivity increased overall with nurturance (es = 0.61, SE = 0.27). In addition, this model revealed that the effect of increased emotional reactivity over time after T administration compared to placebo, was driven by participants with self-reported protection scores at the mean level or higher (P vs. T at mean protection scores: es=-0.14, se = 0.066, t(282)=-2.155, $p = 0.032$; mean protection scores + 1 SD es=-0.34, se=0.1, t(282)=-3.386, $p = 0.0008$, mean protection scores -1 SD es=0.055, se=0.1, t(288)=0.571, $p = 0.5682$). The interaction between session and time seems to be caused by a slightly stronger activation increase during the first session (es=0.1, SE=0.04).

3.2.1.3. Model 3, including digit ratio. Model comparisons using likelihood ratios confirmed that the second model, including digit ratio (AIC:780.20, BIC: 852.72) fit the data better than the null model ($p < 0.0001$) as well as the base model ($p < 0.0001$).

Model 3 confirmed a main effect of time ($F_{(1|18)} = 5.9729$, $p = 0.025054$) and a significant interaction between drug and time ($F_{(1|270)} = 7.5431$, p 0.006429). In addition, it demonstrated a significant three-way interaction between drug, time and digit ratio ($F_{(1|270)} = 25.3457$, $p < 0.0001$, see Fig. 5). There was a marginal interaction between drug and digit ratio ($F_{(1|18)} = 3.41$, $p = 0.081280$, see Fig. 5).

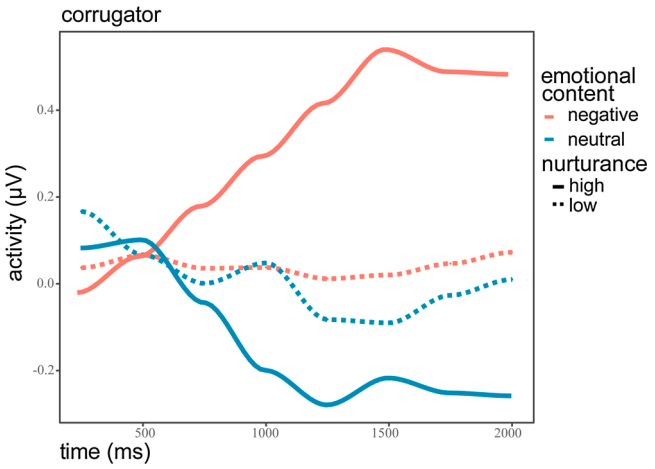

Fig. 3. Effect of nurturance: COR response over time, aggregated across drug condition. For visualization purposes, participants were split into a low-nurturance and high-nurturance group using median split. Left panel reflects COR activity over time in low-nurturance group and right panel reflects activity in high nurturance group.

Post hoc analyses revealed that T increased emotional reactivity over time compared to placebo, primarily observed in participants with a digit ratio at or below the mean (P vs. T at mean digit ratio: es=-0.51, se = 0.09, t(270)=-5.528, $p < 0.0001$; mean digit ratio + 1 SD es=-0.18, se=0.05, t(270)=-2.746, $p = 0.0064$, es=0.15, se=0.09, t(270)=1.638, $p = 0.1250$).

3.2.1.4. Exploratory correlation analysis between protection scores and digit ratio. Since both digit ratio and protection scores significantly interacted with T, we checked for a correlation between the two variables. However, they were not found to be significantly related (t(19)=-0.14, cor=-0.03, $p = 0.894$)

3.2.2. Zygomaticus

3.2.2.1. Base model 1. The base model fits the data significantly better than the null model including only time and session ($p > 0.001$). However, the resulting model showed only a main effect of time (F(1|20) = 6, p = 0.02) and a marginal interaction between time and session. There was no effect of drug or time X drug interaction (Fig. 6).

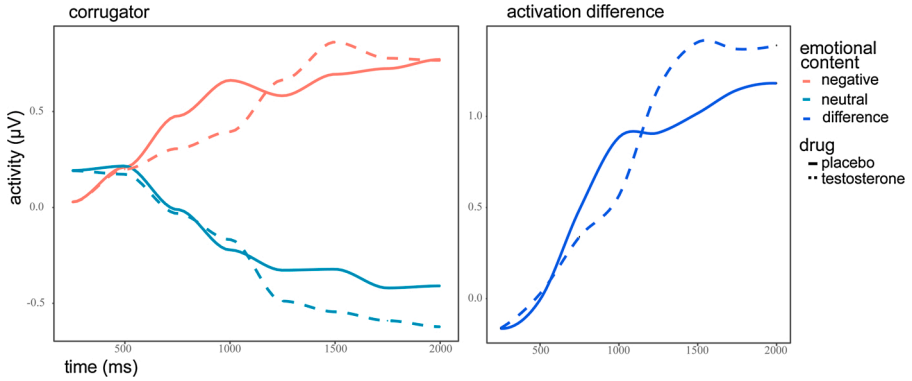

Fig. 2. Corrugator (COR) activity over time. Left panel: COR activity separated by emotional condition and drug for visualization purposes. Right panel: Δ COR activity used for analyses (negative - neutral). Dotted line = T.

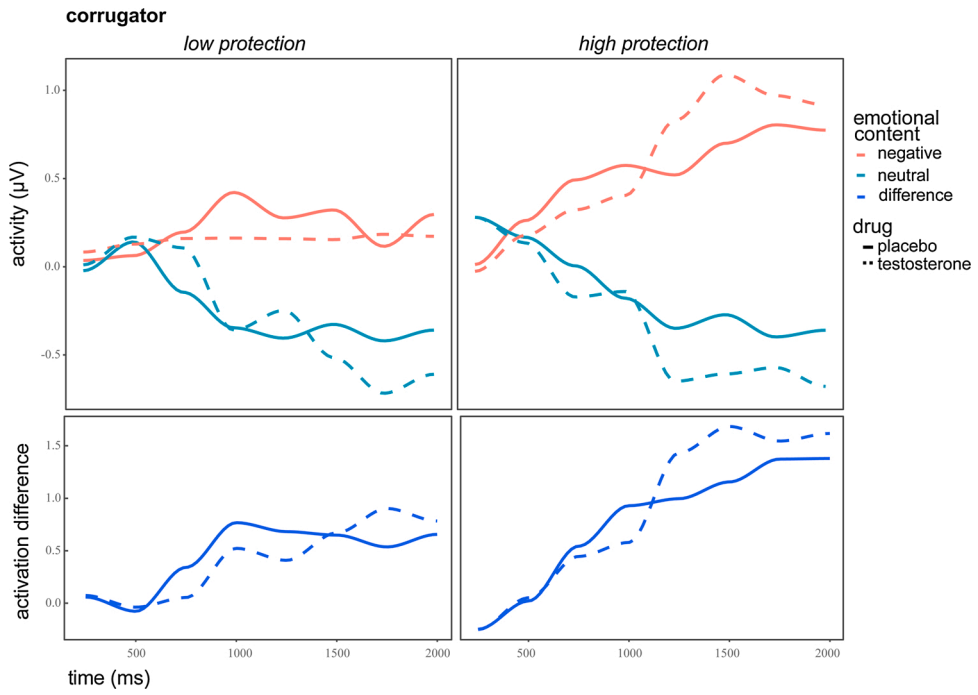

Fig. 4. Interaction between drug, protection and time. COR response over time, protection scores divided by median split (left: low protection scores, right: high protection scores). Upper panel: values plotted by emotion x drug (red = negative), for visualization purposes. Lower panel: difference scores (negative- neutral) used for analysis. Dotted line = T. (For interpretation of the references to colour in this Figure legend, the reader is referred to the web version of this article).

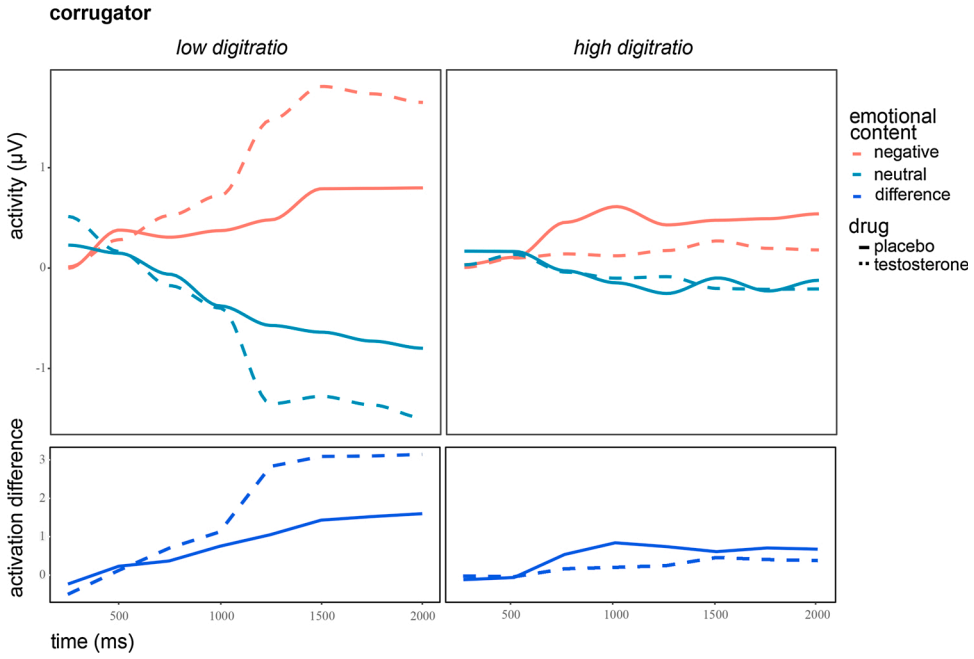

Fig. 5. Interaction between drug, digitratio and time. Digit ratio divided by median split (left: low digit ratio, right: high digit ratio), Left panel: Original values plotted by emotion x drug (red = negative) for visualization purposes. Right panel: Corrugator response over time plotted as difference scores (negative-neutral) used for analysis, for corrugator (above) and zygomaticus (below). Dotted line- = T. (For interpretation of the references to colour in this Figure legend, the reader is referred to the web version of this article).

3.2.2.2. Model 2 & 3, including participants' protection and nurturance scores or their digit ratio. Since there was no effect of drug in the base model, we did not further investigate interactions with nurturance and protection scores or digit ratio.

4. Discussion

This study aimed to test if T increases emotional reactivity to children in distress and whether this effect is driven by protective motivation. The results confirm our hypothesis that T increases participants' emotional reactivity, as measured using COR responses (H1). Hence, we show that T increases emotional reactivity not only to social threat cues (Bos et al., 2012; Eisenegger et al., 2011) and infant crying (Bos et al., 2010), but also to non-aversive visual cues of children in distress. In addition, increased reactivity was positively predicted by participants' individual nurturing tendencies (H2), which supports our interpretation that the facial responsiveness reflected empathic motives. There was no main effect of protective tendencies on COR responses (contrary to H3), but subjective evaluations of the stimuli did predict COR responses. Further, as hypothesized, we found that protective tendencies increased

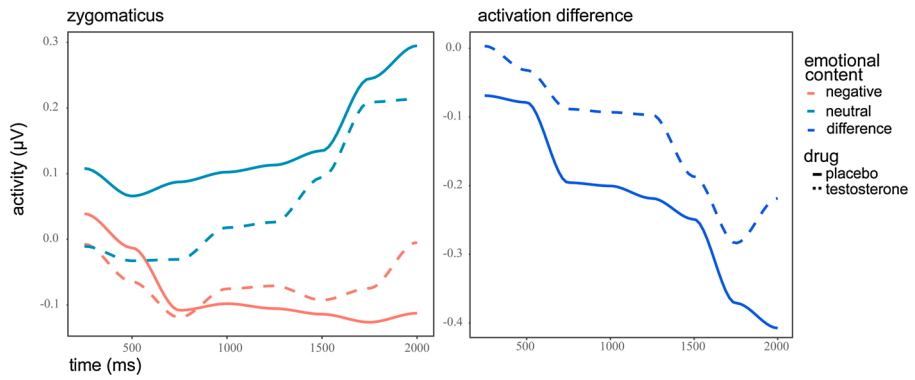

Fig. 6. Zygomaticus Response: Zygomaticus response over time. Left panel: Values plotted by emotion x drug, Lower panel: difference scores (negative- neutral). Dotted line = T.

emotional reactivity in interaction with T (H4). That is to say, the effect of T on the corrugator was driven by participants who reported strong protective tendencies in the PCAT.

Increased activation of the corrugator as observed in the current study is in line with our previous finding that corrugator responses may indeed reflect an empathic response to children's circumstances (Bos, Hofman et al., 2016). This emotional reactivity might capture a number of sentiments ranging from empathic responses (Lamm et al., 2008; Westbury & Neumann, 2008) to moral outrage or aggression (Kraaijenvanger et al., 2017; Seibt et al., 2015), all of which reflect a stronger emotional engagement with the children's situation. Since we find no effects on the subjective evaluations, we cannot be sure what the emotional response in our participants reflects, and whether it is the same for all participants. However, the inclusion of the parental motivation questionnaire, together with previous findings on facial responses towards children, provides for some directionality in the interpretations of our findings. It is important to note that an increase in corrugator activation over time after T administration in response to pictures of children in a negative context was observed as compared to a decrease in corrugator activation in response to pictures of children in a neutral situation. These neutral scenes nonetheless depict children, who are universally perceived as non-threatening and rewarding (Hahn et al., 2015). This shows that the possible 'prosocial' effect of T might also partly be driven by reduced negative affective responses towards children in a non-threatening environment. In contrast to the corrugator response, there was no effect of T on the zygomaticus muscle but only a main effect of time which manifested in a stronger smiling response towards the neutral versus the negative stimuli.

First, since nurturance relies strongly on empathic responses (Panksepp & Panksepp, 2013) and has frequently been related to empathic behaviors and sentiments (Batson, Lishner, Cook, & Sawyer, 2005; Lishner, Oceja, Stocks, & Zaspel, 2008), it is likely that the main effect of nurturance in our study also reflects empathy. Second, the effect of T is in line with previous studies showing that participants given T responded to infant distress with more activation of the anterior insula; an area frequently observed in relation to empathy as well as to infant threat (Bos et al., 2010; Mascaro, Hackett, Gouzoules, Lori, & Rilling, 2014; van 't Veer, Thijssen, Witteman, van IJzendoorn, & Bakermans-Kranenburg, 2019). Together, these findings suggest that T might facilitate active coping when confronted with children's distress by increasing emotional reactivity and the willingness to take action. This is in line with the finding that increased neural responses to infant crying after T administration are accompanied by decreased aversion to these sounds (Bos et al., 2010). Increased vigilance towards threat cues as observed in the current study might help this reactive response. Intriguingly, T administration does not increase neural reactivity in response to adults' pain (Heany, Terburg, Stein, van Honk, & Bos, 2020), and even decreases automatic imitation of facial expressions (Hermans, Putman, & van Honk, 2006), emphasizing the importance of target vulnerability and potentially a protective situation. Consistent with this view, we find the T induced increase in emotional reactivity to be strongest in participants who self-report high degrees of protective tendencies in relation to childcare, directly linking T's effect to offspring protection. The fact that people with high protective tendencies are most affected by T fits with the more general view of T as a hormone that lowers the threshold for reactive behavioral responses and facilitates action tendencies (Bos et al., 2012; Kaldewaij, Koch, Volman, Toni, & Roelofs, 2016). T thus aids the execution of a behavioral repertoire, rather than initiating it. In this light, a protective role of T has been proposed by more recent accounts on the role of T in parenting (Bos, 2017; Rilling & Mascaro, 2017). However, ours is the first administration study to show that T is related to protection motives towards children.

In addition, the interaction of T and the digit ratio in our study indicates that the response to T in distressing situations is shaped by participant's hormonal predispositions, which may reflect prenatal exposure to estrogen or T (Breedlove, 2010). Our results are in line with previous findings showing that T affects emotional reactivity more strongly in participants with a low digit ratio (van Honk et al., 2011) and that its effect leads to a reluctance to harm others in moral dilemma paradigms, possibly also indicating more sensitivity to distress (Montoya et al., 2013). Early T exposure might increase sensitivity to T, resulting in stronger emotional reactivity in these participants. While we found no interaction between digit ratio and protection scores, it would be interesting to assess this link in a larger number of women and men, especially since a recent study failed to find the association reported by van Honk et al. (2011) in a large sample of males (Nadler et al., 2019).

From a broader perspective, T's interaction with protection but not nurturance further supports Hofer et al.'s observation that protection is indeed a parenting dimension in its own right (Hofer et al., 2017; Schaller, 2018), which might build on a distinguished endocrine response. From an evolutionary perspective, mammals that rely on parental protection for survival might have built on the fight or flight response to include the safety of kin. That is to say, mechanisms that first served the protection of the self, such as the T induced increase in emotional threat reactivity and approach, might have evolved to serve protective aspects of caregiving, resulting in a release of T also in response to potential infant threat. Intriguingly, these protective responses might also recruit the neuropeptide oxytocin (OXT), which is responsive to stressful situations and is seen as an important component underlying sensitive caregiving and nurturance (Bos, 2017; Feldman, 2017). However, previous administration studies addressing the function of OXT and T have often observed opposite effects on components of social-emotional behavior, such as trust and cognitive empathy (Bos et al., 2012). To what extent OXT and T act in concert during stressful interactions with infants that require protective responses is a critical

question for future studies. A possibility is that depending on situational demands, OXT and T can have either agonistic or antagonistic effects, both augmenting protective responses during threatening situations, but having different effects in relatively safe situations that require nurturing responses. In the context of imminent threat, nurturing and soothing responses may actually be maladaptive (for a different perspective see: Taylor et al., 2000). However, sensitive responding to a child's needs remain critical for the long-term well-being of children (Morris et al., 2013). Thus, T's facilitation of emotionally reactive responses to a child in distress needs to be accompanied by sufficient nurturing in the aftermath of the threat. Given the different functions of nurturing and protective responses to distress, such differences in psychophysiological responses may adaptively comply with the specific demands of the situations. In order to sooth the child, a nurturing response should increase sensitivity to the child's signals. In contrast, protection in interaction with T might facilitate fast and active response to environmental threat and potentially even enable an aggressive response directed toward a potential offender. A recent study by Procyshyn, Watson, and Crespi (2020) showed increased oxytocin and decreased testosterone levels among individuals in response to a video of a gravely ill child, although the testosterone decrease was not observed for more empathic individuals. Unfortunately, this study did not investigate the extent to which the video elicited protective and nurturing tendencies. Nevertheless, these physiological and behavioral differences towards children emphasize the important role of endocrine components in flexible switching between nurturing and protective states, which is a critical aspect of the behavioral repertoire of human caregiving.

Despite its novelty, it is important to consider the current findings as preliminary. Even when taking into account the statistical strength of the within-subjects design, our current sample size is relatively small and consists of only women. Given the current emphasis on larger samples in T administration studies with respect to replicability and the moderating roles of personal factors (Carré & Robinson, 2020), our study warrants replication. Studies including both sexes as well as parents and non-parents will allow for investigating such moderating roles of personal factors. Another important limitation of the current findings is that no effects on subjective evaluations of the stimuli were observed. It might be that subjective evaluation is not a sensitive enough measure to capture the effects of T, as subjective responding is more prone to social desirability. Also, T acts mostly on neural circuits involved in emotional responding that are not always accessible to cognitive deliberation (Bos et al., 2012). A replication with a larger sample could also give more insight into whether T actually affects subjective responses on the current task. Nonetheless, physiological effects of T during social-emotional tasks unaccompanied by subjective effects have been reported more often in the literature (Bos et al., 2012; Bos, Hofman et al., 2016).

In sum, our study confirms that T not only increases emotional reactivity to threat signals related to the self, but can actually increase responsiveness to others' distress and that this response is driven by protective tendencies. It thus provides a more nuanced perspective on the role of T in human caregiving.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declaration of Competing Interest

The authors report no competing interests. The authors alone are responsible for the content and writing of the paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.biopsycho.2021.108176.

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