Testosterone, oxytocin, and the development of human parental care

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ABSTRACT

The steroid testosterone (T) and neuropeptide oxytocin (OT) have each been implicated in the development of parental care in humans and animals, yet very little research addressed the interaction between these hormones at the transition to parenthood in mothers and fathers. One hundred and sixty mothers and fathers (80 couples) were visited 1 and 6 months after the birth of their first child, plasma OT and T were assayed at each time-point, and interactions between each parent and the infant were observed and micro-coded for two key parental behaviors; affectionate touch and parent-infant synchrony. T showed gender-specific effects. While paternal T was individually stable across the first six months of parenting and predicted lower father-infant synchrony, maternal T was neither stable nor predictive of maternal behavior. An interaction of OT and T showed that T has complex modulatory effects on the relations of OT and parenting. Slope analysis revealed that among fathers, only when T was high (+1SD), negative associations emerged between OT and father affectionate touch. In contrast, among mothers, the context of high T was related to a positive association between OT and maternal touch. Our findings, the first to test the interaction of OT and T in relation to observed maternal behavior, underscore the need for much further research on the complex bidirectional effects of steroid and neuropeptide systems on human mothering and fathering.

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1. Introduction

The neuropeptide oxytocin (OT) and the steroid hormone testosterone (T) each play a role in supporting psycho-physiological changes essential for the establishment of parental care across mammalian species (Gordon and Feldman, 2015; Feldman, 2012, 2015; Saltzman and Ziegler, 2014; Ziegler and Snowdon, 2000). Yet, despite their significant involvement, surprisingly little research addressed their combined contribution to the development of human mothering and fathering. In the current study, we followed first-time parents from birth to six months and assessed plasma OT and T in mothers and fathers in relation to observed parent-infant interactions at 1 and 6 months. We sought to examine baseline levels and individual stability of each hormone in mothers and fathers, their associations with prototypical patterns of maternal and paternal caregiving, and whether T moderates the known effects of OT on the emergence of parenting behavior. To our knowledge, only one study to date has tested T levels in human mothers in relation to observed maternal behavior (Cho et al., 2015a, 2015b) and this study assessed a high-risk cohort of very low birth weight infants. Therefore, our study is the first to explore T in healthy mothers and infants.

OT has long been recognized as a "maternal hormone", implicated in birth and breastfeeding (Carter, 1998), and elevated levels of plasma OT during pregnancy and the postpartum have been shown to predict maternal attachment, engagement, and mother-child synchrony (Levine et al., 2007; Feldman, 2012). OT is also significant for fathering. For instance, functioning of the OT system is shaped by care-giving experience in male rodents in bi-parental species (Kenkel et al., 2014; Lambert et al., 2011). Similarly, in non-human primates, male's hormonal changes in OT prior to birth are associated with greater paternal responsiveness (for review see Storey and Ziegler, 2015) and contact with pregnant or lactating female and exposure to infant cues can influence levels of OT in males (for a review on these effects in mammalian and avian species see: Ziegler, 2000). In human fathers, OT administration increases physiological and behavioral markers of social engagement that support paternal-infant bonding (Weisman et al., 2012). Moreover, OT has been linked with the unique behavioral repertoire characteristic of maternal and paternal care in humans (Gordon et al., 2010a); in mothers, OT is associated with more affectionate touch and social gaze during interactions whereas in fathers, OT is related to increased positive arousal and stimulation (Feldman et al., 2010a, 2010b).

Functioning of the OT system that supports bond formation, including its central and peripheral branches, is closely related with activity of the gonadal steroid hormones of the HPG-axis: T and estradiol (E) (Choleris et al., 2008; Gordon et al., 2011; Viau, 2002). Steroids exist in both sexes and figure prominently in the regulation of sexual and social

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behavior, partly through their interaction with OT (Pedersen, 1997; Schumacher et al., 1990). A study examining pup sensitization in sexually naïve mice revealed that gonadectomy in males increased the number of OT neurons in the paraventricular nucleus of the hypothalamus. In the same study, T implants were shown to impair pup sensitization and reduce the number of OT neurons in both sexes (Okabe et al., 2013). The authors suggest that these parallel effects of T on OT and behavior may point to an inhibitory effect of T on parental behavior via the OT neural system. Furthermore, aromatization of T to E, which increases central E levels, functions to increase OT receptor binding (Johnson et al., 1991; Tribollet et al., 1990). Across mammalian species, central OT has been linked with bond formation, including parent-infant and pair bonding (Insel, 1990, Numan and Young, 2016). In humans, peripheral OT measured in plasma and saliva have been associated with the expression of maternal and paternal caregiving behavior at the early stages of parenting (Feldman et al., 2010a, 2010b, Gordon et al., 2011). It is thus possible that T may function as one modulator of OT secretion and of the manifestation of OT receptors in crucial brain regions that regulate the expression of parental behavior in mammals (Sladek et al., 2000).

Generally, a decline in T in males is thought to support the emergence of involved fathering. In bi-parental primates, fathers exposed to scents of their infants displayed a significant drop in T compared to non-parent males (Prudom et al., 2008). In human fathers, a decline in T during the transition to parenthood (Berg and Wynne-Edwards, 2001; Perini et al., 2012) was related to positive paternal behavior (Fleming et al., 2002). Men with lower T levels displayed higher sympathy and motivation to respond to the infant when listening to their infant's cry as compared to men with higher T (Fleming et al., 2002). It has been suggested that T fluctuations in males during the transition to parenthood support the trade-off between mating and parenting (Gettler et al., 2011a, 2011b, 2013; Ziegler, 2000a, b), such that for example, in cotton-top tamarins, fathers' T levels can actually increase during the postpartum if females show readiness to mate (Ziegler, 2000a). In human fathers, the decline in T after childbirth is associated with the amount of childcare (Gettler et al., 2011a, 2011b). However, in contrast to the extant research on T in fathers, very few studies tested T levels in human mothers. Administration of T to nulliparous women increased neural responsiveness to infant cries (Bos et al., 2010), and women's T levels were positively associated with self-reported infant facial cuteness (Hahn et al., 2015). Increases in T have been observed in pregnant women (Edelstein et al., 2015; Fleming et al., 1997) and mothers' T levels correlated with infants' physical and socio-emotional health and lower depressive symptoms (Cho et al., 2015a, 2015b, Cho et al., 2012, Cho et al., 2008). Overall, these studies suggest that T may play diverse roles in mothering compared to fathering in humans.

Despite the fact that the involvement of OT and T in parenting has been extensively investigated in humans and animals, little research examined how OT and T interact to predict human parental behaviors and the few existing studies yielded mixed results. In Tsimane tribes, men returning home after hunting exhibited parallel increases in OT and T levels which were positively related to the duration of the hunt. The researchers interpreted these results in the context of father-son interactions occurring during the hunting period (Jaeggi et al., 2015). Another study tested salivary T in fathers following OT administration and found that the increase in T following OT administration was related to the amount of paternal behavior, including social gaze, stimulatory touch, and vocal synchrony (Weisman et al., 2014). These findings point to a complex relationship between these two hormones in predicting paternal behaviors.

According to the "bio-behavioral synchrony" model (Feldman, 2012, 2015, 2016; Gordon and Feldman, 2015), the coordination of parent's and infant's social behavior during moments of social contact provides a template for the development of human social competencies and is underpinned by physiological support systems, including hormones, brain networks, and autonomic functioning. The bio-behavioral model postulates that the increase in parental OT during the postpartum, stimulates the expression of the human-specific parental repertoire in the gaze, affect, vocal, and touch modalities, similar to that observed in other

mammals (Champagne, 2008). Yet, synchronous interactions undergo substantial development during the first months of life, when parental behaviors move from the touch-based interactions characterizing the newborn period to social exchanges that involve the coordination of parent and infant's non-verbal signals at six months (Feldman, 2007, 2016). Such synchronous parent-infant interactions have been found to be supported by the parent and infant's OT secretion (Feldman et al., 2010a, 2010b, 2011), though no study to date has examined the possibility that the inter-relationship of OT and T also plays a role in their expression.

In the current study, we examined how circulating levels of OT and T in new mothers and fathers across the first six months of parenthood shape parental behavior at 6 months. We focused on two key human parental behavior; affectionate touch and parent-infant synchrony. Affectionate touch describes moments when parents touch their infants affectionately (e.g. kiss, caress, light pokes) and for no practical purpose (e.g., moving, wiping infant's face). Parental touch emerges immediately after birth and is considered a basic mammalian parenting behavior that continues throughout infancy (Feldman, 2007, 2016). Parental affectionate touch is related to parents' OT (Feldman et al., 2012) and is enhanced by OT administration at 5 months (Weisman et al., 2012). Parental touch appears in a more "maternal" form, when moments of affectionate touch are integrated with maternal social gaze at the infant, and a more "paternal" form, when affectionate touch is combined with increased positive arousal and stimulation (Feldman et al., 2010a, 2010b; Gordon et al., 2010a, 2010b). We predicted that OT and T to correlate with these two types of touch in parent-specific ways. Parent-infant synchrony is a human-specific mode of interaction and emerges in the third month of life. Parent-infant synchrony (Feldman, 2007) in both mother and father has been associated with higher levels of OT (Feldman et al., 2011), and lower paternal T (Weisman et al., 2014).

The following hypotheses were proposed. First, we predicted that OT and T will show individual stability in mothers and fathers. Second, we predicted to find associations between OT and T for mothers and fathers. Third, higher OT and lower T will be associated with the parent-specific form of touch and parent-infant synchrony. Finally, it was hypothesized that T will moderate the previously found associations between OT and parent-infant synchrony (Feldman et al., 2011). Due to the fact that no prior research exists on the topic, we expect this moderation to be uniquely expressed in mothers and fathers, but the direction of the interaction between OT and T in predicting parent-infant synchrony remains a research question.

2. Method

2.1. Participants

As part of a larger project examining longitudinal bio-behavioral correlates of the transition to parenthood, 160 mothers and fathers (80 couples) and their firstborn infant participated in this study (37 girls and 43 boys). Families were visited at home during the evening hours (4-8 PM; t_1: mean = 18:29, SD = 1:16, t_2 = 18:18, SD = 1:22) at approximately 1 month (mean days between birth and home-visit = 51.69, SD = 14.65, Range = 71) and again at 6 months (mean days between birth and home-visit = 175.27, SD = 31.65, Range = 174). Fathers' mean age was 29.281 (SD = 4.2) and mothers' mean age was 27.72 years (SD = 3.52). All parents were well educated (mean education years in fathers = 15.3, SD = 2.47; and in mothers = 16.25, SD = 2.11) and of medium-high socio-economic status.

2.2. Procedure

Initially, the experimenter explained the study and its procedures to the parents and they signed an informed consent to participate. Mothers and fathers first completed self-report measures assessing a range of demographic and health variables (e.g., weight, height, smoking). Next, a registered nurse sampled blood from each parent for later assessment of OT and T. Following, each parent was videotaped

for 5 min interacting with their child in a free-play interaction. Mothers and fathers were each observed separately with their infant. The co-parent was not present in the room when the recording took place. To allow for an ecologically valid observation of parent-infant social play, parents were instructed to play together with the infant for 5 min as they normally do. The study's procedure was approved by the university's institutional review board to assure ethical conduct in studies with human subjects. Each family received ~$70 (in local currency) for their participation at the end of each visit.

2.2.1. Parent-infant dyadic free play interactions

Interactions from the second home visit were micro-coded by trained graduate students in psychology on a computerized system (Noldus; The Vaggengingen, Netherlands), consistent with previous research on parent–infant interactions at this age (Feldman and Eidelman, 2007; Feldman et al., 2004, 2007, 2010a, 2010b). Five non-verbal categories of parenting behavior were coded. Each category included a set of mutually exclusive codes (an "uncodable" code was added to each category to address moments when codes could not be determined). Categories and codes were as follows: *Parent Gaze* – to infant, to object or aspects of the environment, gaze aversion (moments when gaze is not directed to partner, infant, or objects). *Parent Vocalization* – Motherese type of vocalization, regular speech, talk directed to another person in the room (such as the experimenter), no talk. *Parent Affect* - positive, neutral, withdrawn, negative; *Parent-Infant Proximity* – Infant in parent's hands or on parent's lap, infant is positioned within the parent's arms' reach, infant is far and out of parent's arms' reach. *Parent Touch* - affectionate touch (e.g., kissing, stroking, hugging), touch of infant extremities, functional touch, proprioceptive touch (i.e., changing infant position in space), touch with an object, stimulatory touch, none. For each behavior, we measured the proportion of time out of the entire interaction this behavior occurred.

Two behavioral composites were assessed: *Parent Affectionate Touch* and *Parent-Infant Synchrony*. Consistent with prior research, parental behavioral composited were constructed by summing up discrete behavioral building blocks that were coded microanalytically, in order to create a meaningful behavioral state that includes aspects of parental gaze, touch affect and vocalizations. In line with previous studies, *Parent Affectionate Touch* was computed in a "maternal form" (sum proportion of time mother displayed the following behaviors: 1. touched the infant 2. gazed at the infant's face; i.e. *Affectionate Touch*) and the "paternal form" (sum proportions of time father displayed the following behaviors: 1. touched the infant 2. displayed positive affect 3. vocalized to the infant; i.e. *Stimulatory Affectionate Touch*). *Parent-Infant Synchrony*, was computed, by considering times in which the parent displayed affectionate parenting while the infant was signaling a willingness to engage socially via eye gaze direction. Specifically, consistent with prior research (Feldman and Eidelman, 2007; Apter-Levi et al., 2014) as a conditional probability assessing the proportion of time parent engaged in social gaze, affectionate touch, and "motherese" vocalization while the infant looked at the parent and expressed positive affect. For the current study only these behavioral measures from the second home visit were predicted by hormonal markers.

2.2.2. Hormonal collection and analysis

Testosterone – blood was drawn from antecubital veins into a 5 mL EDTA vacutainer tube. Plasma samples were kept ice-chilled for up to two hours before being centrifuged at 4 °C at $1000 \times g$ for 15 min. Supernatants were collected and stored at −70 °C until assayed. We should note that this kit measures the total blood levels of testosterone.

To determine T concentrations plasma samples were defrosted to room temperature, immediately before analysis. Determination of T was done by Chemiluminescent Immunoassay (CLIA) technology, measured by Advia-Centaure auto-analyzer, Siemens Healthcare. The instrument measured relative light units, and the concentration of T was then calculated by using a 4-parameter logistic curve fit. All samples were measured by reagents Kit of the same lot. The relevant intra-

assay coefficient was 14.2%. Inter-assay coefficient is not reported as all measurements were run on the same day and in a single kit to reduce variability and increase the validity of the assessment.

Oxytocin - blood was drawn from antecubital veins into a 9 mL chilled vacutainer tube containing lithium heparin that was supplemented with 400 KIU of Trasylol (Trasylol -Bayer, Germany) per 1 mL blood. Blood samples were kept ice-chilled for up to 2 h before being centrifuged at 4 °C at 1000g for 15 min. Supernatants were collected and stored at −80 °C until assayed. Determination of OT was performed using a commercial OT ELISA kit (Assay Design, MI, USA) consistent with previous research (Carter et al., 2007; Feldman et al., 2007; Levine et al., 2007; Gordon et al., 2008). Measurements were performed in duplicates and the concentrations of samples were calculated by using MatLab-7 according to relevant standard curves. The intra-assay and inter-assay co-efficient are <12.4% and 14.5% respectively.

We were able to assay biological and behavioral measurements from 145 parents (72 fathers; 73 mothers) during the first postpartum month and from 106 parents at six months (49 fathers; 57 mothers). Of these, two mothers were excluded from the sample since their OT levels at time 1 was >5 SD from the mean.

2.3. Statistical analysis

Results were analyzed using the IBM SPSS statistics software. As a preliminary step, T and OT distributions in mothers and fathers were examined. T and OT distributions were sufficiently close to normal and values were not log-transformed. Following, extreme cases were examined and data from 2 families in which maternal OT was above 5 SD from group mean were excluded from the sample. We first explored differences in T and OT levels between mothers and fathers, and between hormone levels in t_1 compared to t_2. This was done using a repeated measures ANOVA, with time as a within subject variable and parents' gender as a between subject variable. Following, we examined the correlation between all study variables via Pearson's correlations.

Prior to examining our main hypothesis on the moderating role of T on the relations between OT and parental behavior, the role of breastfeeding on OT and behavior in mothers was evaluated. Finally, four hierarchal multiple regression analyses were conducted, to predict the two types of parental behavior from time2 in fathers and in mothers. In each model, OT and T levels were added in the first step, and the interaction between OT and T was added in the second step. In order to examine the significant interactions, post-hoc analysis was conducted via the PROCESS computational tool (Preacher et al., 2007). This tool generates the conditional effect of T (i.e., "simple slope") on OT, displaying the slope of OT in predicting parental behavior when T levels are at mean level or at 1SD above and below the mean. This analysis enables a post-hoc examination of the moderation effect of T on the correlation between OT and parental behavior (Preacher et al., 2007).

3. Results

3.1. T and OT in mothers and fathers at 1 and 6 months

3.1.1. Testosterone

In order to examine the means and SDs of T levels for mothers and fathers at the two times of data collection, a repeated measures ANOVA was conducted including time as a within subject variable and gender of the parent as a between subject variable. As can be seen in Fig. 1, there was a significant effect for time ($F(1,40) = 4.62$, p = 0.038, eta^2 = 0.10) such that T levels were higher in t_2 than in t_1. Additionally, there was a strong effect for gender of the parents ($F(1,40) = 436.72$, p < 0.001, eta^2 = 0.92), with fathers showing higher levels of T than mothers . Finally, a significant time by gender interaction emmerged ($F(1,40) = 4.56$, p = 0.039, eta^2 = 0.10), so that fathers showed a bigger change between t_1 and t_2 ($t(45) = -1.46$, p = 0.15), than mothers ($t(54) = -0.66$, p = 0.51).
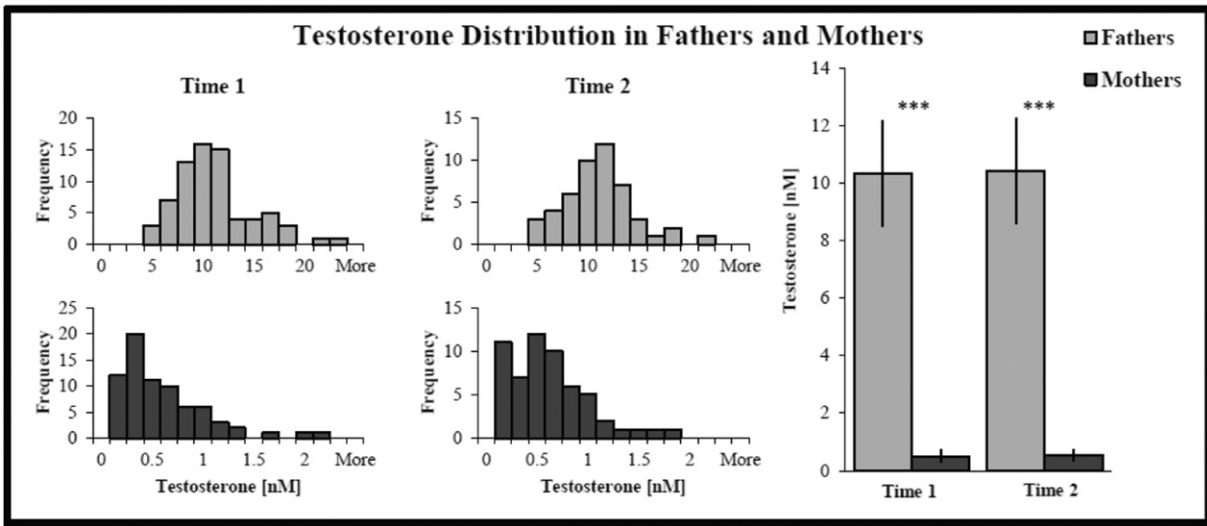
Fig. 1. The distributions of testosterone in mothers and fathers in the 1st and 6th postpartum month.

For the entire sample, T levels were highly correlated across time (*Pearson's* $r(46) = 0.92$, p < 0.001). However, when assessing each gender separately, mothers' T levels were not correlated across time (*Pearson's* $r(55) = -0.09$, p = 0.52) whereas fathers T levels were individually stable (*Pearson's* $r(46) = 0.58$, p < 0.001). Fathers' and mothers' T levels were not correlated among couples at either time point (t_1: *Pearson's* $r(67) = -0.05$, p = 0.71; t_2: *Pearson's* $r(47) = -0.10$, p = 0.47).

3.1.2. Oxytocin

Oxytocin distribution in new mothers and fathers has already been reported elsewhere (Gordon et al., 2010a, 2010b), and thus we will only give a short review of the values found in the current study. In order to examine the means and SDs of OT levels for mothers and fathers at the two times of data collection, a repeated measures ANOVA was conducted including time as a within subject variable and gender of the parent as a between subject variable. As predicted there was no significant effect for gender (F(1,47) = 3.46, p = 0.07, eta² = 0.07). Nor was there a significant effect for time (F(1,47) = 1.76, p = 19, eta² = 0.04), nor for the interaction between time and gender (F(1,47) = 1.24, p = 0.27, eta² = 0.03).

Consistent with previous findings (Feldman et al., 2013; Schneiderman et al., 2012), for the entire sample, OT levels were highly correlated across time (*Pearson's* $r(48) = 0.85$, p < 0.001). When assessing each gender separately, both mothers OT levels (*Pearson's* $r(57) = 0.80$, p < 0.001) and fathers' OT levels (*Pearson's* $r(51) = 0.88$, p < 0.001) were found to be individually stable across time. Fathers' and mothers' OT levels were significantly correlated among couples at both time points (t_1: *Pearson's* $r(70) = 0.30$, p = 0.011; t_2: *Pearson's* $r(48) = 0.28$, p = 0.045).

No associations were found between OT and T in either fathers or mothers or overall.

Table 1
t-Tests examining differences between mothers' and fathers' interaction behaviors.

	Mothers		Fathers		
	Mean	SD	Mean	SD	Df
Parent-infant synchrony	70.7	60.78	43.93	52.32	46
Parent affectionate touch	44.2	31.88	26.11	26.87	43
Parent stimulatory affectionate touch	139.81	46.35	127.03	63.36	55

+ - p < 0.1, * - p < 0.05, ** - p < 0.01, *** - p < 0.001.

3.2. Parenting behavior and hormone-behavior correlations

Results for the behavioral measures at the two time-points are presented in Table 1. As can be seen, mothers showed greater proportions of *Parent-Infant Synchrony* and *Affectionate Touch* compared to fathers. In contrast to our expectation, no difference was found in *Stimulatory Affectionate Touch*.

Pearson correlations between hormones and behavior were computed for fathers (Table 2A) and mothers (Table 2B) separately. As can be seen in Table 2A, fathers' T at t_1 was negatively correlated with *Parent-Infant Synchrony* and *Parent Affectionate Touch*, and fathers' T at t_2 was negatively correlated with *Stimulatory Affectionate Touch*. Fathers OT at both time points was not significantly correlated with the interaction behaviors. In mothers, (Table 2B) OT at both times was correlated with *Parent-Infant Synchrony* and *Parent Affectionate Touch*, and T at both time-points was not significantly correlated with any interaction behavior.

3.3. Breastfeeding

At t_1 84% of the mothers were breastfeeding and 16% were not, and at t_2 74% of the mothers were breastfeeding and 26% were not. The mean time between breastfeeding and blood draw at t_1 was 1:40 h (SD = 0:55 h), and 3:31 h at t_2 (SD = 4:15 h). The interval of time from breastfeeding to blood sampling did not significantly correlate with maternal hormones or behaviors in either t_1 or t_2. Yet, since we could not isolate whether this non-significant finding is due to sample size, we entered this factor as a covariate to the following analyses in order to control for subject variability in it. As can be seen in the following sections and in Table 3, breastfeeding interval did not have a significant contribution to explaining variability in maternal behaviors.

3.4. The interaction of T and OT in predicting parental behavior

Prior to conducting the regression analyses we examined time of measurement as a possible covariate of the hormonal data. We did not find any significant correlation between time of blood draw and the hormonal levels both in mothers (t_1; T: r(72) = −0.04, OT: r(70)=0.01, t_2; T: r(48)=0.03, OT: r(39)=−0.03) and in fathers (t_1; T: r(71) = −0.14, OT: r(69)=0.09, t_2; T: r(45)=−0.09, OT: r(31)=−0.05). Moreover, as can be seen, the correlation values were extremely low, as such, we did not enter them as covariates to the following regression analyses.

For each gender, we created two multiple regression models, one predicting *Parent Affectionate Touch*, the second predicting *Parent-Infant*

Table 2
Correlation matrixes between study variables in fathers (A) and mothers (B).

	2	3	4	5	6	7
A.						
1. Oxytocin time 1	0.88***	−0.05	0.02	0.14	0.15	0.10
2. Oxytocin time 2		0.08	−0.01	0.07	0.07	0.02
3. Testosterone time 1			0.58***	−0.30*	−0.27*	−0.07
4. Testosterone time 2				−0.07	−0.02	-0.35*
5. Father-infant synchrony					0.89***	−0.02
6. Father affectionate touch						0.06
7. Father stimulatory affectionate touch						
B.						
1. Oxytocin time 1	0.80***	0.01	0.10	0.25*	0.19+	−0.26*
2. Oxytocin time 2		−0.06	0.02	0.33*	0.31*	−0.10
3. Testosterone time 1			−0.09	0.02	−0.03	0.15
4. Testosterone time 2				0.12	−0.03	0.14
5. Mother-infant synchrony					0.82***	0.07
6. Mother affectionate touch						0.06
7. Mother stimulatory affectionate touch						

+ $p < 0.1$.
* $p < 0.05$.
*** $p < 0.001$.

Synchrony. We used parents' hormonal measurements from the first and second time points. Results are presented in Table 3.

In mothers, *Parent Affectionate Touch* was best predicted by hormones from t_1 ($R^2 = 0.192$, $F(3,42) = 3.32$, $p < 0.05$) with a significant interaction effect between OT and T (see Table 3). Simple slope analysis revealed that mothers' OT became more significant in predicting *Parent Affectionate Touch* as their T levels increased. When mothers' T levels were low (−1SD) or at a mean level, no significant correlation was found between mothers' OT and *Affectionate Touch* (at −1 SD: β = −0.24, NS; at mean: β = 0.21, NS). However, when mothers' T was high (+1 SD), a positive correlation between OT and *Affectionate Touch* emerged (β = 0.658, $p < 0.01$). Mothers' *Parent-Infant Synchrony* was best predicted by hormones from t_2 ($R^2 = 0.225$, $F(3,31) = 2.99$, $p < 0.05$), with a significant main effect for OT, and with no significant effect for T or the interaction between OT and T (see Table 3).

Fathers' *Parent-Infant Synchrony* was best predicted by hormones from t_1 ($R^2 = 0.171$, $F(3,36) = 2.47$, $p < 0.1$), with a significant negative association to T (see Table 3). Fathers' *Affectionate Touch* was best predicted by hormones from t_2 ($R^2 = 0.401$, $F(3,23) = 5.13$, $p < 0.01$),

with a significant negative main effect for T and a significant interaction effect between OT and T (see Table 3). Simple slope analysis revealed that as T increased, a negative correlation between OT and *Affectionate Touch* emerged. When fathers' T was low (−1 SD) or medium, there was no significant correlation between OT and *Affectionate Touch* (at −1 SD: β = 0.199, NS; at mean: β = −0.15, NS). However, when fathers had an above average T (+1 SD) a negative correlation between OT and *Affectionate Touch* emerged (β = −0.507, $p < 0.05$). Graphic presentation of the two interaction effects are presented in Fig. 2.

4. Discussion

Results of our study, among the first to examine the relationship between OT and T and the development of human mothering and fathering across the postpartum months, highlight both the independent and combined effects of the two hormones on key parenting behaviors – affectionate touch and parent-infant synchrony. We found that while T is independently related to paternal behavior, its role in mothers was subtler and it appears that T was related to tightening of the effect of OT on

Table 3
Regression analyses predicting parental interaction behaviors with parents' T and OT, and the interaction between the two.

Interaction behavior:	Mothers									
	Hormones from Time 1					Hormones from Time 2				
	Affectionate touch					Synchrony				
	B	B	SE	T	p	B	β	SE	T	p
Breastfeeding status	1.33	0.04	5.01	0.27	0.79	18.32	0.3	24.78	0.73	0.47
OT	0.06	0.26	0.04	1.48	0.15	0.22	0.45	0.08	2.81	0.009
T	−8.37	−0.12	11.08	−0.76	0.45	17.65	0.16	34.06	0.52	0.61
OT × T	0.28	0.44	0.13	2.14	0.04	−0.43	−0.36	0.27	−1.6	0.12
Model summary	$R^2 = 0.19$, $F(3,43) = 3.38$*					$R^2 = 0.23$, $F(3,31) = 2.99$*				
Interaction behavior:	Fathers									
	Hormones from Time 1					Hormones from Time 2				
	Synchrony					Affectionate touch				
	B	β	SE	T	p	B	β	SE	T	p
OT	0.07	0.28	0.05	1.46	0.15	−0.07	−0.21	0.05	−1.45	0.16
T	−5.35	−0.39	2.55	−2.09	0.04	−7.62	−0.42	2.34	−3.26	<0.001
OT × T	−0.01	−0.21	0.1	−1.02	0.31	−0.03	−0.34	0.02	−2.11	0.04
Model summary	$R^2 = 0.17$, $F(3,36) = 2.47$+					$R^2 = 0.40$, $F(3,23) = 5.13$**				

+ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, ***$p < 0.001$.
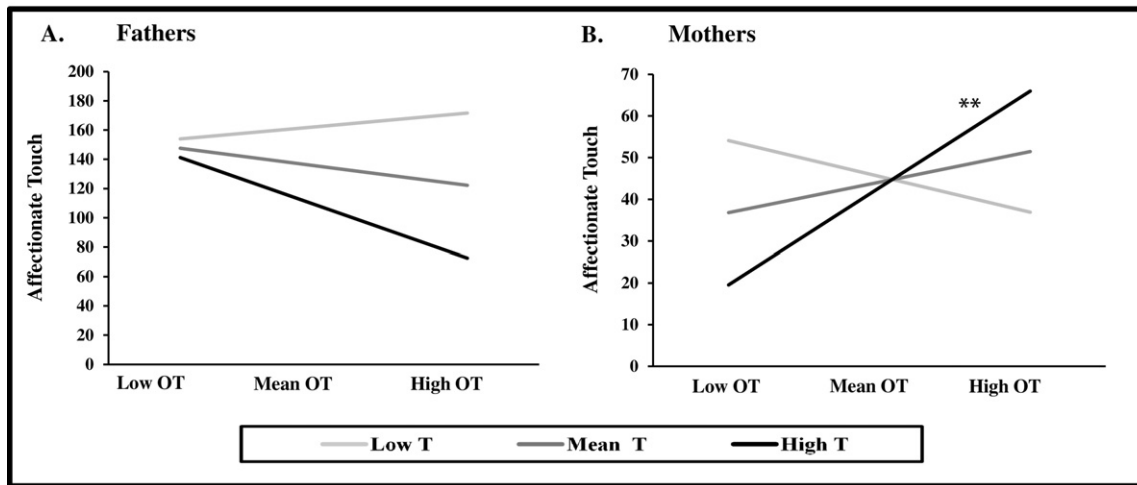
Fig. 2. Simple slope analysis of interaction effects between testosterone, oxytocin and affectionate touch.

maternal behavior. In fathers, T levels were naturally higher than in mothers, but also individually stable across the first six months of parenthood and predictive of lower parent-infant synchrony. In mothers, T was neither stable nor predictive of behavior, yet, in the context of higher than average T, the associations of OT and mother-infant synchrony were tighter. Thus, while lower T in fathers may represent a trade-off between mating and fathering (Wingfield et al., 1990), in mothers, T may provide a neuroendocrine milieu that supports vigilance and social engagement.

Parent-infant synchrony was negatively associated with T in fathers and showed positive associations with OT in mothers. This is consistent with research demonstrating associations between OT and positive maternal behavior (Carter, 2014; Insel, 1990) and reduction of T with positive paternal behavior (Gettler et al., 2011a, 2011b, 2015). Previous studies showed that fatherhood is negatively related to T levels (Edelstein et al., 2015; Gray et al., 2002) and suggest that this decrease may help facilitate the emergence of paternal behaviors that involve empathy and caregiving (Mascaro et al., 2014). The experience of paternal caregiving in of itself may reduce T levels, such an hypothesis is consistent with Gettler et al.'s (2015) findings that fathers who increased their involvement with childcare exhibited a decline in T. It appears that endogenous changes in T levels interact with the caregiving experiences of new fathers to create a biopsychological background for the development of adaptive fathering.

OT and T were not directly related in our sample, perhaps suggesting that these two systems have complex, rather than linear associations that may involve other biological processes (Israel et al., 2014). For example, T was found to induce OT receptor binding in the hypothalamus (Okabe et al., 2013) and this process is thought to result from the combined action of T and its metabolites: estradiol and dihydrotestosterone (Johnson et al., 1991; Okabe et al., 2013). In addition, intra-cerebral ventricular injections of OT induced maternal behavior in female virgin rats specifically after they were primed with estrogen - a metabolite of T (Pedersen et al., 1982). These findings point to complex joint action of OT and T in the support of parenting behavior. Similar findings, for instance, are reported for OT and cortisol. Although both hormones are critical for the establishment of maternal care, studies assessing OT and cortisol in relation to observed parenting rarely find direct correlations between the two but complex interactions in the prediction of parental behavior (Gordon et al., 2010a, 2010b; Feldman et al., 2007).

In contrast to the gender-specific effects of T, OT showed a more consistent effect across genders. Levels of peripheral OT did not differ in mothers and fathers; OT was individually stable in both genders. The stability of OT over time has been previously shown for periods ranging from several months to several years (Feldman et al., 2007, 2013), and the current findings are consistent with this literature. Hormonal

attunement between attachment partners has been reported for OT, but also for other hormones that play a role in the development of parental behavior, such as vasopressin, cortisol, progesterone and prolactin (Edelstein et al., 2015; Kiecolt-Glaser et al., 2003; Robles and Kiecolt-Glaser, 2003; Schreiber et al., 2006; Young et al., 2001). T levels were not found to be correlated among partners and this is consistent with a recent study, which found no associations between T levels in expecting partners (Edelstein et al., 2015). Animal studies indicated that the coordination of T between partners can dynamically change across time and context. For instance, in geese, coordination of T across partners is related to reproductive success and bi-parental care, and yet there is a reduction in T coordination during egg-laying and as the relationship bond endures (Hirschenhauser, 2012). In humans, T levels between new romantic partners were not correlated, but, on the contrary, higher T in one partner combined with lower T in the other was associated with greater behavioral empathy during a conflict discussion (Schneiderman et al., 2014). With regards to the coordination between OT levels in mothers and fathers, while our study cannot imply causality, the findings are consistent with evidence indicating hormonal attunement between attachment partners in OT as mediated by affiliative behavior. It has been shown that high levels of OT in both parents predicted higher levels of behavioral synchrony during triadic mother-father-infant interactions at six months (Gordon et al., 2010a). Associations were found between OT levels in parents and children (Apter-Levi et al., 2013; Pratt et al., 2015), pointing to a cross-generation transmission of OT as mediated by synchronous behavior (Feldman et al., 2010a, 2010b), consistent with research in rodents (Francis et al., 2000). Thus, circulating OT levels may have a trait-level quality that can index aspects of the parent-infant relationship (Gordon et al., 2010a, 2010b).

Slope analysis indicated that among mothers, only in the context of high T levels, positive associations were found between OT and affectionate touch. In contrast, among fathers, high T levels provided the background for negative associations between OT and paternal touch. This is in line with previous studies showing that increased T can be adaptive for mothers (Bos et al., 2010; Cho et al., 2015a, 2015b; Edelstein et al., 2015), while reduced T is adaptive for fathers (Edelstein et al., 2015; Gettler et al., 2011a, 2011b, 2015). These interactions also highlight the gender-specific manner by which T provides the context for OT's function as a modulator of parenting behavior. These findings underscore the importance of assessing both OT and T for a broader understanding of maternal and paternal behavior and the need to examine the neuroendocrine basis of parental care separately for mothers and fathers. Importantly, the interaction of OT and T predicted only affectionate touch, not synchrony, a parental behavior that was not contingent upon the infant's behavior. Possibly, the more evolutionary-ancient mammalian general

parental behavior – touch – evolved in the context of a greater mutual dependence of OT and T, whereas the later-evolving human-specific phenomenon of synchrony more flexibly draws on the independent actions of each system, but this hypothesis requires much more comparative research.

Our findings may contribute to the Steroid/Peptide Theory of Social Bonds (Van Anders et al., 2011), which suggests that the action of T is integrated with that of affiliative neuropeptides in the formation of social attachments. According to this theory, high OT combined with low T support enhanced nurturing intimacy, whereas high OT combined with high T is related to enhanced sexual intimacy. In this way, T is thought to represent the trade-offs between reproduction and care giving. Our results indicate that high T combined with high OT can also predict nurturing behaviors, but in a gender-specific and behavior-specific manner. This suggests that T may have complex moderation effects on the relationship between OT and parenting behavior that are different in each gender and require much further research. Taken together, theory and research suggest that the complex interplay between OT and T during the transition to parenthood is dependent on gender, time, and context. Moreover, two recent studies showing actor-partner effects of T levels on the relationship between other biomarkers and bonding behaviors lend further support to the complex bi-directional effects of T. Cho et al. (2015b) report that higher maternal T together with higher infant OT was associated with more positive and more frequent maternal interactive behaviors. Additionally, in romantic partners, the association between one partner's T and expressed hostility was positive only when the other partner also had high T, but correlated with low hostility when the other partner had low T (Schneiderman et al., 2014). Future studies are thus needed not only to examine the interactions between OT and T in predicting parenting behaviors but also to consider the mutual effects of the co-parent's and the infant's hormonal levels in shaping dyadic behaviors.

Limitations of the study primarily relate to the measurement of hormonal data. First, OT and T were measured only once during a home visit at each age and future research should include several measures. Although several studies report important associations of hormones with other hormones and behavior using a single plasma measurement (Elmadih et al., 2014; Weisman et al., 2012) and in specifically when testing T (Bos et al., 2010; Kuo et al., 2012; Mascaro et al., 2014), future studies should incorporate multiple measurements of T within individuals to reveal sources of variance and to replicate our findings. Additionally, as the time of measurement varied across subjects, the effect of the time of day on the hormonal data could potentially be a covariate in our analysis. Though, as the correlations between the hormonal data and the time of measurement were very low, this is unlikely. Furthermore, the reliance on circulating levels of OT and T are a potential limitation of the current study, as the relationship between central and peripheral OT is not yet fully understood (Valstad et al., 2016). Several studies in animals and humans point to a certain degree of concordance between OT in the brain and the periphery (Burri et al., 2008; Carson et al., 2014; Carter et al., 2007; Neumann et al., 1993; Wotjak et al., 1998). These results strengthen our use of peripheral measures, and yet it is important to note here that several studies also point to a lack of association between central and peripheral OT (See Valstad et al., 2016). We propose that the stability in OT concentrations across several months of the transition to parenthood period, together with studies that demonstrate associations between central and peripheral OT measures (Weisman et al., 2012; Feldman et al., 2012) provide support to the validity of utilizing peripheral OT as a biomarker of parenting in humans, but much further research is required on the topic. Finally, since parental behavior and hormones were measured at the same time, it is not possible to infer causality. Much further research is required to describe the complex interactions of OT and T in shaping parenting behavior as they are expressed across children's development, particularly during periods of developmental transitions such as school entry, the pubertal transition, and leaving home.

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