



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

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