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The cross-generation transmission of oxytocin in humans

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ABSTRACT

Animal studies demonstrated that the neuropeptide oxytocin (OT), implicated in bond formation across mammalian species, is transmitted from mother to young through mechanisms of early social experiences; however, no research has addressed the cross-generation transmission of OT in humans. Fifty-five parents (36 mothers and 19 fathers) engaged in a 15-min interaction with their infants. Baseline plasma OT was sampled from parents and salivary OT was sampled from parents and infants before and after play and analyzed with ELISA methods. Interactions were micro-coded for parent and child's socio-affective behavior. Parent and infant's salivary OT was individually stable across assessments and showed an increase from pre- to post-interaction. Significant correlations emerged between parental and infant OT at both assessments and higher OT levels in parent and child were related to greater affect synchrony and infant social engagement. Parent–infant affect synchrony moderated the relations between parental and infant OT and the associations between OT in parent and child were stronger under conditions of high affect synchrony. Results demonstrate consistency in the neuroendocrine system supporting bond formation in humans and other mammals and underscore the role of early experience in shaping the cross-generation transmission of social affiliation in humans.

Introduction

Among the central features of the oxytocinergic system, which plays a key role in processes of bond formation across mammalian species, is its sensitivity to early social experience, particularly to variations in parental care (Gimpl and Fahrenholz, 2001; Keverne and Curley, 2004; Lee et al., 2009; Meaney, 2001; Pedersen, 2004; Ross and Young, 2009). Studies in rats, voles, sheep, and non-human primates have shown that maternal Oxytocin (OT) is associated with the provision of maternal behavior and the amount of maternal behavior, in turn, shapes the infant's OT expression and bears long-term consequences for the development of social competence, aggressive behavior, and the infant's ultimate skill as a parent (Carter, 1998; Francis et al., 2000; Keverne and Kendrick, 1992; Maestripieri et al., 2009; Meaney, 2010; Neumann, 2008; Ross and Young, 2009). Rat mothers who provided high levels of licking-and-grooming showed higher OT receptor densities in brain areas central for parenting, including the medial preoptic area, lateral septum, the paraventricular nucleus of the hypothalamus, and the nucleus accumbens. Their female infants similarly engaged in high licking-and-grooming parenting to their own infants and exhibited the brain profile typical of the high licking-and-grooming dams (Champagne, 2008; Francis et al., 2000; Meaney, 2001). Among rhesus monkeys, mothers who provided more grooming and contact had higher levels of plasma OT (Maestripieri et al., 2009), while infant monkeys reared by their mothers showed greater CSF OT concentrations as compared to nursery-reared animals and displayed more social behavior toward conspecifics (Winslow et al., 2003). OT knockout mice expressed less ultrasonic vocalizations in infancy and more aggression and social dysfunction in adulthood (Winslow et al., 2000). Overall, these studies suggest a bio-behavioral feedback loop of OT, parenting, and infant social competence: between maternal OT and the mother's parenting behaviors, between maternal behavior and the infant's OT expression, and between infant OT and the child's life-long capacity for social affiliation, stress management, and adaptation to the social group, a cycle which repeats in the next generation (Ahern and Young, 2009; Champagne et al., 2008; Francis et al., 2000, 2002).

Searching for the mechanisms that underpin the cross-generation transmission of the OT bio-behavioral feedback loop, studies have shown that the transmission of OT and parenting from one generation to the next are based on behavioral and ecological mechanisms to a greater extent than on genetic ones. The seminal work of Meaney and colleagues with cross-fostered animals demonstrated that female infants bred to a high licking-and-grooming brand and reared by low licking-and-grooming dams and vice versa exhibited both the brain profile and ultimate parenting behavior typical of the adopted strain, underscoring the central role of early experience in organizing the structural and functional features of the oxytocinergic system (Champagne and Meaney, 2001; Meaney, 2001). In general, the body

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of research on the cross generation transmission of OT and social affiliation in mammals highlights three main points. First, variations in the early social environment, in maternal behavior, alloparental care, and the nature of the rearing environment (e.g., single mothers versus couple rearing), are related in systematic ways to both the amount of positive parenting behavior the infant receives and the level of parenting the infant will ultimately provide as a parent (Ahern and Young, 2009; Gimpl and Fahrenholz, 2001). Second, parenting behavior shapes the infant's social adaptation through complex gene-by-environment interactions and epigenetic influences that augment the expression of certain genes while downplaying the role of others (Champagne, 2008; Meaney, 2010; Weaver et al., 2004). Finally, the species-specific repertoire of parenting behavior the infant experiences is closely related to the first social behaviors the infant expresses. These early social behaviors are thought to initiate a cascading bio-behavioral process that shapes the infant's lifetime socialization and sets the long-term expression of stress and affiliation neuroendocrine pathways (Feldman, in press; Fleming et al., 1999).

Although less research examined the associations between OT and parenting in humans, recent studies point to consistencies in the neuroendocrine systems that support bond formation in humans and other mammals. For instance, maternal OT levels measured across pregnancy and the postpartum showed high individual stability over time and OT levels at the first trimester predicted the amount of maternal postpartum behavior, including maternal gaze at infant face, "motherese" vocalizations, expression of positive affect, and affectionate touch (Feldman et al., 2007). Similarly, maternal OT was associated with the mother's sensitive behavior toward her infant and with an increased BOLD fMRI response to infant stimuli in brain areas rich in OT receptors (Strathearn et al., 2009). Comparable levels of plasma OT were found in mothers and fathers across the first 6 months of parenting and maternal and paternal OT were related to the parent-specific set of parenting behavior (Gordon et al., 2010). Mothers and fathers who provided high levels of tactile contact to their infants showed an increase in salivary OT following parent–infant interactions but such an increase was not observed among parents who provided low tactile contact (Feldman et al., 2010), echoing the high and low licking-and-grooming patterns of rat mothers and their differential impact on OT expression. OT inhaling increased fathers' response to their toddlers, particularly the father-specific pattern of exploratory play (Naber et al., 2010), and variations in the OXTR gene were related to the degree of maternal sensitivity (Bakermans-Kranenburg and van Ijzendoorn, 2008). Taken together, these studies demonstrate that measures of both central and peripheral OT are reliably linked to meaningful differences in parenting behavior in humans, similar to their role in other mammals.

In addition to its contribution to human parenting behavior, research has demonstrated the relations between lower levels of OT or blunted OT response and conditions associated with disrupted parenting or maladaptive early environments. Lower urinary OT was found in children reared in severely neglectful orphanage conditions as compared to children reared in typical environments (Fries et al., 2005). Women with a history of childhood abuse had lower CSF OT concentrations (Heim et al., 2009), cocaine abusing mothers showed lower plasma OT and more negative affect toward their infants (Light et al., 2004), and maternal postpartum depressive symptoms were related to lower plasma OT and less maternal behavior (Feldman et al., 2007). Studies employing the OT inhaling paradigm showed the effects of OT on social adaptation throughout life, including increased trust (Kosfeld et al., 2005), more responsive couple interaction (Ditzen et al., 2009), decreased social fear (Kirsch et al., 2005), and improved social skills among autistic individuals (Andari et al., 2010). Combined with the well-known links between sensitive parenting in infancy, infant attachment security, and the child's social adaptation up until adulthood (Sroufe, 2005; Bakermans-Kranenburg and van Ijzendoorn, 2007), these studies support each component of the OT bio-behavioral feedback loop: between OT and parenting, between parenting behavior and the infant's social repertoire, and between OT and the individual's social adaptation throughout life. However, the links between all components of the cross-generation transmission cycle in humans have not yet been tested in a single study.

In light of the above, the present study had two goals. First, we examined whether OT levels in human parents and infants are interrelated as they are in other mammals. The second goal was to assess whether OT in parent and child is associated with the parenting behavior the infant receives and the early social repertoire the infant expresses. In addition, we tested whether parenting behavior moderates the relations between the parent's and the infant's OT. Parents (mothers and fathers) and their 4- to 6 month-old infants were observed in a 15-min play session and salivary OT was sampled from parent and child before and after interactions, in addition to baseline plasma OT sampled from the parents. Carter and colleagues (2007a,b) showed that salivary OT is a reliable biomarker of peripheral OT and studies have demonstrated that salivary OT increases after massage in adults (Carter et al., 2007a,b), following affectionate touch between couples (Holt-Lunstad et al., 2008), and after a session of parent–infant contact (Feldman et al., 2010), pointing to the links between salivary OT and processes of social affiliation.

Several hypotheses were proposed. Consistent with research in animal models (Champagne and Meaney, 2001), we hypothesized that parental and infant's OT, at both the baseline and post-interaction assessments, would be significantly correlated and higher parental OT would be related to higher infant OT. It was further expected that more sensitive parenting behavior would be associated with higher parental and infant OT. Specifically, we expected correlations between parent–infant synchrony and higher levels of parental and infant OT. Parent–infant synchrony indexes the parent's capacity to carefully monitor and adapt to micro-level shifts in the infant's socio-affective signals and to enter into a matched social dialogue with the child (Feldman, 2007a,b). In addition, the infant's social engagement, addressing the infant's early non-verbal social repertoire, is an important marker of social development and has shown to predict greater social competence with peers (Feldman and Masalha, 2010; Marshal and Fox, 2006). We thus expected that higher parental and infant OT would be related to more infant social engagement. Finally, studies in animals indicate that infants reared in positive environments benefit more from environmental enrichment (Curly et al., 2009; Ross and Young, 2009), suggesting that positive early experience may enhance the cross-generation transmission of OT. We thus examined whether parent–infant synchrony would moderate the relations between the parent and infant's OT so that among infants reared under conditions of high affect synchrony a closer relationship would be observed between the parent's and the infant's OT as compared to infants reared under conditions of low affect synchrony.

Method

Participants

Participants were 55 parents, including 36 mothers and 19 fathers (not couples) and their 4- to 6-month-old infants (M = 157.1 days, SD = 11.9). All parents were healthy with at least 12 years of education and were of middle-class SES. Mothers were on average 28.3 years (SD = 5.11), completed on average 15.45 (SD = 2.83) years of education, and 82.5% of the mothers were breastfeeding. Fathers' age averaged 29.6 years (SD = 4.78) with an average education of 15.58 (SD = 2.82) years. Infants were born at term, mainly (92%) by vaginal delivery, and received an Apgar score of 9.12 (SD = 1.43). Sixty-one percent of the infants were firstborn. Fathers reported at least medium-level participation in childcare. To screen for parental mood disorders, parents completed the Beck Depression Inventory (Beck,