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THE SOCIAL NEUROENDOCRINOLOGY OF HUMAN PARENTING

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Introduction

Nonhuman mammalian mothering is hormone-dependent; hormonal changes occurring during pregnancy and labor causally determine the expression of maternal behavior. Studies in animal models have shown that experimental manipulations on the expression of key hormones markedly alter or totally eliminate the expression of maternal care (Feldman, 2012b, 2016; Lonstein, Lévy, and Fleming, 2015; Pryce, 1996; Rosenblatt, 1994; Rosenblatt, 2003). Research in rodents describes the critical role of oxytocin (OT) and prolactin (PRL), which undergo substantial changes during late pregnancy (PRL) and surge at birth (OT), for the onset of maternal behavior. In parallel, hormones associated with the stress response, particularly corticosterone (cortisol in humans), modulate maternal vigilance and active protection of offspring (Brummelte and Galea, 2010; Mann and Bridges, 2001; Pedersen and Prange, 1985). Finally, animal studies point to the involvement of vasopressin (AVP) and testosterone (T) in the emergence of fatherhood and the expression of mammalian paternal care (Carter, 2014; Wynne-Edwards, 2001). In combination with sex-related hormones (estradiol, progesterone), these hormones establish the neuroendocrine milieu that enables rodent mothers—and fathers in the 3%–5% of mammalian species who are biparental (Braun and Champagne, 2014; Kleiman, 1977)—to parent. The hormones of parenting enable parents to recognize infants as rewarding stimuli, protect infants from harm, nurse, express species-typical parental behavior, and provide external regulation for the infant's immature regulatory systems, including sleep organization, thermoregulation, autonomic functions, attention, and exploration (Feldman, 2016; Hofer, 1995a,b; Numan and Stolzenberg, 2009). These hormones also help parents usher their young into the social niche and accommodate its distinct features. Finally, the neuroendocrinology of parenting promotes the infant's ability to manage life in harsh ecologies via mechanisms of endocrine fit and the effects of parental hormones on the infant's brain maturation and social fittedness (Feldman, Monakhov, Pratt, and Ebstein, 2016).

Human parenting is not hormone-dependent; however, hormonal changes during pregnancy, birth, and the postpartum period prime and accompany the expression of parenting, sculpting the development of the parent-child attachment and its long-term effects on the infant's brain and behavior (Apter-Levi et al., 2016; Galbally, Lewis, IJzendoorn, and Permezel, 2011; Feldman, 2016, 2017; Gordon, Zagoory-Sharon, Leckman, and Feldman, 2010b, 2010c). Humans' large associative cortex, neural plasticity, and massive limbic-cortical projections enable bottom-up, behavior-based processing so that committed parental care can trigger the hormones of parenting even without pregnancy

and childbirth; for instance in primary-caregiving fathers or adoptive parents (Abraham et al., 2014; Bick, Dozier, Bernard, Grasso, and Simons, 2013). Yet, as parenting is the only social phenomenon observed across species and taxa, there is no other sociobiological process that can provide a clearer lens into evolution as it occurs and shed light on the roots of humans' collaborative, empathic, and relational abilities (Feldman, 2015a, 2015b; Rilling and Young, 2014). Furthermore, the parent-infant interface marks the arena where Darwin (1859) has initially proposed structural and functional brain adaptations take place. The neuroendocrinology of human parental care, addressing the hormonal changes that accompany parenting and their neural, behavioral, and mental correlates, may thus afford a unique perspective on the evolution of human sociality, highlighting both its conserved and human-specific features (Feldman, 2015b, 2016).

In addition to a special viewpoint on human sociality, the neuroendocrinology of parenting provides a unique angle on neural plasticity not available from other topics in neuroscience. Pregnancy and the postpartum mark the period of greatest plasticity in the adult brain (Leuner, Glasper, and Gould, 2010), and such plasticity is observed not only in the maternal but also in the paternal brain, with fathers' investment in childrearing increasing plasticity not only in the father's brain but also in the brain of his offspring (Braun and Champagne, 2014). Parenting, therefore, enables the investigation of endocrine systems and neural networks as they reorganize in the parent's brain and research on how successful versus less optimal reorganization directly impacts the infant's emerging endocrine systems and neurobiological outcomes. Furthermore, parenting is perhaps the most highly conserved social phenomenon, accompanied by similar species-typical behaviors that are triggered by the same neuroendocrine events across mammalian evolution (Feldman, 2015a, 2015b; Rilling and Young, 2014). This is particularly the case with regards to the ancient oxytocin system, which supports parenting, group cohesion, and stress management in species ranging from nematodes to humans, including birds, fish, and *Caenorhabditis elegans* (Feldman et al., 2016; Goodson, 2013). In comparison with the neuroscience of parenting, assessing the brain basis of emotions, memory, or categorization involves a much greater conceptual leap; these constructs are heuristic, much farther away from their biological underpinnings or evolutionary origins, and are constructed online by humans' higher-order representations. When research on the neurobiology of parenting is coupled with detailed observations of parental behavior in the natural habitat, it provides a closer setting to that of nonhuman mammals as compared to most other domains in neuroscience. Yet, notwithstanding the similarity of human parental care with that of other mammals, human parenting is also greatly influenced by humans' higher-order cognitive abilities and cultural construals. Thus, research on the neurobiological basis of parenting affords a unique view on the integration of mammalian-general and human-specific features on key biological processes. Because parenting is triggered by the same hormones across mammalian species, the hormonal basis of human parenting provides a scientifically plausible tool for mechanistic research as compared to other domains of inquiry (e.g., the neurobiology of psychiatric illness); hence, the neuroendocrine basis of parenting is among the few topics that offer a uniform trajectory of empirical investigation across the evolutionary ladder.

The social neuroendocrinology of human parental care comprises four main lines of research. The first assesses the hormonal basis of parenting in healthy parents. Most of this line of research focuses on the hormones of motherhood; the typical hormonal changes occurring in mothers during pregnancy, the postpartum period, and across the early years. Often, these studies examine not only mean-level changes but also individual differences in hormonal levels and their links with maternal behavior, attitudes, or personality traits. To date, the hormone receiving the most research in relation to mothering is cortisol (CT), possibly due to its reliable bioassay in saliva that has been available for some time. Yet, with the development of more sensitive bioassays, studies have also looked at OT, PRL, AVP, T, salivary alpha amylase (sAA), beta endorphin, and immune biomarkers (IL-6, salivary IgA). Another area of research within this global line is the hormones of fatherhood. Fathering in general, and the neurobiology of fathering in particular, has received much less research

as compared to mothering in both humans and other mammals, but the hormonal basis of fathering is a developing area of research and a growing body of literature is beginning to assess fathers' hormones in relation to observed paternal behavior.

The second line of research on parental hormones examines "endocrine fit"—the "match" or synchrony between parent and child hormonal levels. Such biological synchrony is conceptualized as one mechanism by which the parental affiliative system is transferred to the child or as a way in which parents signal environmental danger to their offspring (Feldman, 2016, 2017; Pratt et al., 2017; Bornstein, 2013). Our *biobehavioral synchrony* model contends that such hormonal synchrony, while genetically informed, matures in the context of coordinated social behavior and shared parent-child social experiences (Feldman, 2012c, 2015a, 2016, 2017).

A third line views the neurobiology of human parenting as a global area of research, which includes the brain networks, hormonal systems, and specific behaviors that activate in mothers or fathers with the birth of an infant. Several studies in this line test associations between activations of specific brain areas in the parental brain with parenting-related hormones, including OT, AVP, CT, or T (for a review see Feldman, 2015b). It is hypothesized that the "mammalian parenting network", the brain regions that support mammalian parenting, initiates its activation through sensitization by the hormones of pregnancy (Numan and Young, 2016), thus indicating that hormonal changes trigger neural alterations that define the neurobiology of parenting.

The last area of research in the neuroendocrinology of parenting, and by no means the least abundant, addresses parental hormones under high-risk conditions, whether the risk stems from mother-related conditions (e.g., maternal depression, anxiety), child-related conditions (prematurity, autism spectrum disorders), or contextual adversities (poverty, abuse, war exposure). Several studies of high-risk parenting compared a high-risk cohort to a typical group, whereas others use a correlational design within the high-risk sample. Of note, very few studies examine fathers' hormones in high-risk contexts, and a smaller number of studies address the fit between high-risk parents and children.

The following literature reviews the hormonal basis of human parenting keeping in mind its evolutionary origins. Due to the extensive literature on the topic, this review is by no mean comprehensive and addresses mainly parental hormones in the first years of life, with a focus on infancy, and follows the four lines of research outlined above. Consistent with the comparative approach, only studies that measure hormones in relation to observed parental behavior are reviewed. This approach accords with the view that in humans the neurobiology of parenting may trigger, not only through pregnancy and lactation, but via commitment to caregiving and active involvement in daily interactions with the child. Thus, similar to the long line of "cooperative breeding" in primates, the human "village" (grandparents, "aunties", male partners, adoptive parents, godparents) can rear the child through bottom-up, behavior-based activation of the neurobiology of parenting, consistent with Hrdy's (2007) suggestion that in species such as mammals parenting *is* behavior (Feldman, 2012d). This conceptualization of a bottom-up activation of the neurobiological systems that support parenting via parenting behavior is consistent with findings that mother-child synchrony expresses in the brain as brain-to-brain synchrony of gamma-band oscillations, with gamma marking a distinct bottom-up, behavior-based mechanism (Levy, Goldstein, and Feldman, 2017).

Hormonal Basis of Human Mothering and Fathering in Low-Risk Contexts

This section describes each hormonal system separately and addresses findings related to mothering and fathering for each hormone. Following, a section discusses endocrine fit. Overall, hormones of parenting are divided into the "affiliative hormones" module, which includes mainly OT but also AVP and PRL, hormones that support the formation of parent-infant bonding, maintain attachments, and buttress human sociality (Carter, 2014; Fleming, Ruble, Krieger, and Wong, 1997;

Numan, 2006). The other group involves stress-related hormones, mainly CT but also salivary alpha amylase (sAA) or immune biomarkers (IL-6, IgA). A third group considers sex-related hormones (T, progesterone, estradiol). These three classes of hormones are not independent in their action, and studies have shown co-dependence and mutual influences of these hormones on each other, mainly in complex, nonlinear ways that require much further research (Gordon, Zagoory-Sharon, Leckman, and Feldman, 2010a; Gordon et al., 2017). Research in rodents has further shown that the expression of maternal behavior functions on both the affiliation and stress neuroendocrine systems, with maternal licking and grooming building the expression of both oxytocin receptor densities in the nucleus accumbens (Francis, Champagne, and Meaney, 2000) and glucocorticoid receptors in the hippocampus of the infant's brain (Liu et al., 1997).

Figure 6.1 describes OT and CT as the main, most well-research hormones of parenting, their mutual influences on other hormones, and their behavioral correlates.

Oxytocin

Oxytocin is considered the main neuroendocrine system supporting the formation and maintenance of the parent-infant bond and a central trigger for the expression of parental behavior

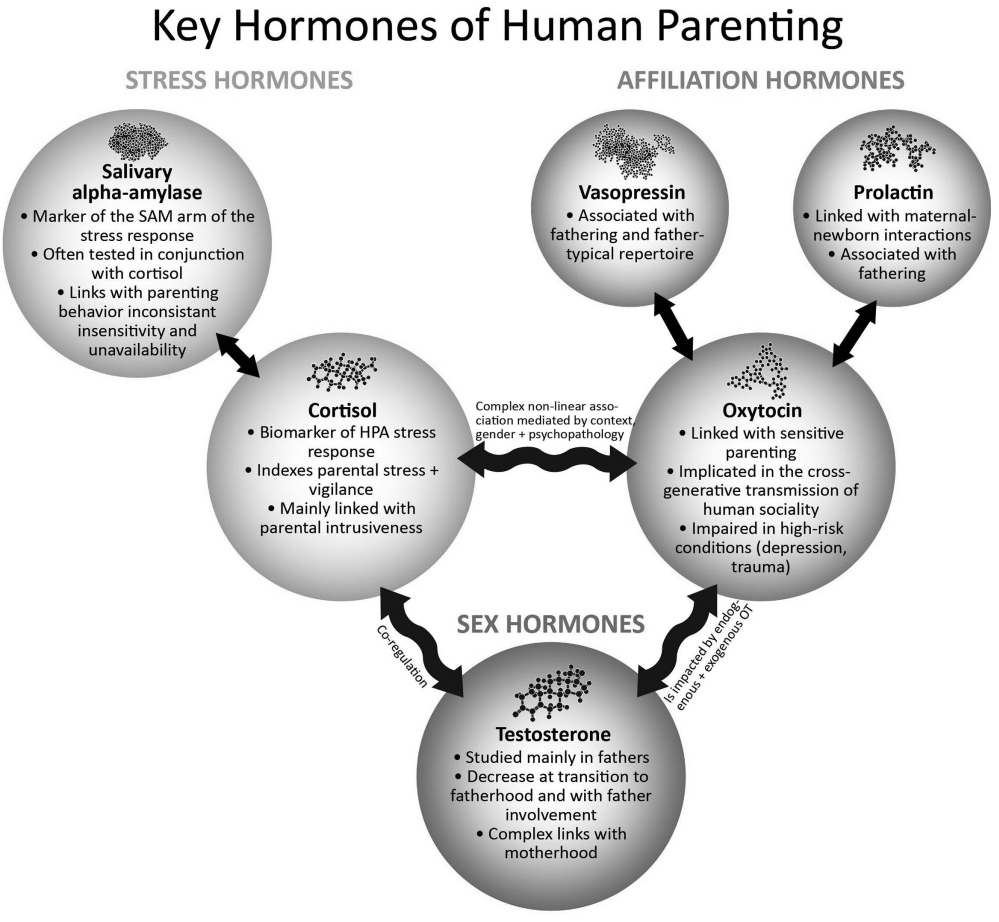

Figure 6.1 Key hormones of human parenting.

(Feldman, 2015b, 2016, 2017). It is an integrative system that provides a neuroendocrine milieu for the functioning of multiple hormones. Numerous hormones operate in concert to support parental care, but OT maintains crosstalk with other hormones in the context of parenting. We found that OT links and interacts with a range of hormones in supporting parenting behavior, including AVP (Apter-Levi, Zagoory-Sharon, and Feldman, 2014), CT (Gordon et al., 2010a), T (Gordon et al., 2017; Weisman, Zagoory-Sharon, and Feldman, 2014), beta endorphin, and IL-6 (Ulmer-Yaniv et al., 2016), highlighting the role of OT in integrating the affiliation, reward, stress, and immune systems in support of parenting.

OT is a nine-amino-acid neuropeptide hormone, which presumably evolved from the ancient vasotocin molecule via gene duplication in jawed fish approximately 650 million years ago (Feldman et al., 2016). OT is implicated in sociality across vertebrate evolution and substantial research in rodents has pinpointed its role in birth, lactation, and maternal care in mammals (Carter, 2014; Feldman et al., 2016; Lee, Macbeth, Pagani, and Young, 2009; Lim and Young, 2006). Studies have examined peripheral levels of OT—in plasma, saliva, urine, and to a lesser extent in cerebrospinal fluid—in relation to human parenting, aided by the availability of new and more reliable immunoassay kits. Associations between brain OT and its peripheral indices are not fully clear, but human studies have lent support to the use of peripheral OT by demonstrating marked increase in peripheral OT when individuals inhale OT, which has shown to impact the brain's OT system (Neumann, Maloumby, Beiderbeck, Lukas, and Landgraf, 2013; Weisman, Zagoory-Sharon, and Feldman, 2012), associations between plasma OT and more efficient variants of the oxytocin receptor gene (OXTR; Feldman et al., 2012), and correlations between plasma and salivary OT with brain activations in areas rich in oxytocin receptors, including the hypothalamus or the amygdala (Abraham et al., 2014; Atzil, Hendler, and Feldman, 2011; Strathearn, Fonagy, Amico, and Montague, 2009). The distributions of OT receptors in the brain are species-specific (Stevens, Wiesman, Feldman, Hurley, and Taber, 2013) and the nature of the relation between central and peripheral OT is a matter of ongoing debate, but an accumulating body of research has shown that variability in peripheral OT is meaningfully linked with the expression of maternal and paternal behavior in ways that are consistent with research on central OT in rodents.

In the first longitudinal study of OT and parenting behavior, we followed healthy women across pregnancy and the postpartum and measured plasma OT and cortisol (CT) at three time-points; first trimester of pregnancy, third trimester, and the first postpartum month when we also observed mothers interact with their infant in the home environment. We used an in-depth interview to measure maternal thoughts, preoccupations, and attachment representations. OT levels increase in early pregnancy and stay stably high across pregnancy and the early postpartum. OT levels during the first trimester predict the expression of the human species-typical maternal behavior, suggesting a priming effect of OT in humans. In addition, OT and CT across pregnancy are unrelated at any time-point, but CT levels independently predict a decrease in the expression of maternal postpartum behavior, indicating a joint effect of the two main hormonal systems on maternal postpartum behavior similar to that found in rodents (Feldman, Weller, Zagoory-Sharon, and Levine, 2007). Another evidence for a priming effect was found when mothers with higher OT during late pregnancy reported greater bonding to their fetus (Levine, Zagoory-Sharon, Feldman, Lewis, and Weller, 2007). It has been suggested that mothers develop clear representations of their unborn child during the last weeks of pregnancy and a failure to do so, due to depression or risk for preterm delivery, impairs the emerging attachment (Hart and McMahon, 2006; Pisoni et al., 2016). OT in late pregnancy also predicts increased maternal preoccupations and more positive representations of the infant and the attachment relationship. Others found similar links between attachment representations and higher OT levels in pregnancy and the postpartum (Eapen et al., 2014). These findings, therefore, add the representational component to the priming effect in other mammals and show that in humans the higher-order cognitive dimension of parenting is similarly triggered by the oxytocinergic system.

We next followed first-time mothers and fathers from the first postpartum month to 6 months postpartum and measured plasma OT in relation to maternal and paternal parenting behavior. Postpartum parents had much higher OT levels as compared to individuals who were not parents or in a romantic relationship, indicating that OT levels increase when individuals become attached. In addition, no difference was found between mothers' and fathers' baseline OT, even when mothers were breastfeeding. Similar to the first study, OT levels in individuals were highly stable over time, and mutual influences between partners' OT were observed both within and across time-points (Gordon, Zagoory-Sharon, Leckman, and Feldman, 2010b). This result suggests that plasma OT may tap a "trait-like" dimension of the individual which is individually stable yet shaped by close attachment relationships (Schneiderman, Kanat-Maymon, Ebstein, and Feldman, 2014). OT levels in mother and father were related to the parent-specific behavioral repertoire (Feldman, Gordon, Schneiderman, Weisman, and Zagoory-Sharon, 2010). Maternal OT was related to the "affiliative parenting" constellation typical of mothers, including gaze to infant face, expression of positive affect, "motherese" high-pitched vocalizations, and affectionate touch, the human parallel of "licking-and-grooming" (Meaney, 2001). In contrast, fathers' OT was linked with "stimulatory parenting", a style typical of mammalian fathering, which included directing attention to the environment, stimulatory contact, and high, unpredictable positive arousal (Gordon et al., 2010b; Naber, van IJzendoorn, Deschamps, van Engeland, and Bakermans-Kranenburg, 2010). These findings, the first to test plasma OT in new fathers, show comparable OT levels in mothers and fathers and indicate that fathers may be just as biologically prepared to care for infants. In comparison with mothers', fathers' parenting style is expressed via a distinct set of behaviors that prepare infants to explore their physical environment, rather than focus on the dynamics of face-to-face relationships, and this paternal repertoire is linked with father's OT. Finally, observing triadic family interactions between these parents and their 6-month-old infants we found that OT predicted triadic synchrony, the coordination of behavior among the three family members (Gordon et al., 2010a), highlighting the role of OT as an integrator of social behavior among affiliative units.

Comparing OT in plasma, saliva, and urine in a group of mothers and fathers (not couples) and their 4- to 6-month-old infants, we found no differences in baseline OT levels in plasma, saliva, or urine between mothers and fathers. Of note, OT levels in saliva and plasma showed mid-level correlations, and similar associations were found in several other samples, but no correlations emerged between these indices and urinary OT, possibly since urinary hormone concentrations travel through a different bodily route. Both plasma and salivary OT were related to higher parent-infant synchrony (Feldman, Gordon, and Zagoory-Sharon, 2011). Similar associations obtain between mothers' plasma OT response (change from baseline to post-interaction) and gaze coordination and gaze duration between mothers and their 7-month-old infants (Kim, Fonagy, Koos, Dorsett, and Strathearn, 2014).

In contrast to plasma and salivary OT, urinary OT predicts greater parental stress and attachment anxiety, highlighting the dual role of OT in linking to both the affiliative and the anxiety/vigilance components of parenting (Feldman, Gordon, et al., 2011). These findings are consistent with data from a large cohort of women and men, both parents and nonparents, which showed that in women plasma OT levels are positively associated with measures of attachment anxiety (Weisman, Zagoory-Sharon, Schneiderman, Gordon, and Feldman, 2013) as well as with research in animal models pointing to the role of OT in modulating stress and anxiety (Neumann and Slattery, 2016). Urinary OT has been linked with infant caregiving behavior in cooperative-breeding marmoset monkeys (Finkenwirth, Martins, Deschner, and Burkart, 2016), and listening to mother's voice during a stress paradigm elevated children's urinary OT and enabled better stress management (L.J. Seltzer, Ziegler, and Pollak, 2010), validating urinary OT as a biomarker of parental care.

In the first months of life, parental plasma OT levels are associated with allelic variability on the OXTR on key SNPs associated with attachment, including *OXTR* (rs2254298 and rs1042778) and *CD38* (rs3796863), as well as with more parental touch and greater gaze synchrony, the two

main features of close attachment bonds (Feldman et al., 2012). These findings are consistent with numerous studies showing associations between more functional *OXTR* variants with sensitive parenting and attachment security throughout life (Bakermans-Kranenburg and van IJzendoorn, 2008; Feldman et al., 2016; Raby, Cicchetti, Carlson, Egeland, and Collins, 2013).

Consistent with findings on the cross-generational transmission of OT functionality in rodents, which is mediated by maternal behavior (Champagne, 2008; Champagne, Diorio, Sharma, and Meaney, 2001), parental OT in the first months of life shapes the infant's OT system and this cross-generation transmission is similarly moderated by synchronous parenting; links between parent and child OT are found only when parents engage in synchronous interactions, but not when minimal synchrony is observed (Feldman, Gordon, and Zagoory-Sharon, 2010). In another study, following parents and infants from the first month of life to the preschool stage, we similarly found cross-generational transmission over time and attachment bonds. Parents' plasma OT in the postpartum predicted child salivary OT at preschool as mediated by early parental behavior. Furthermore, parental OT and synchronous parenting shaped not only the child's OT but also the degree of reciprocity and positive engagement during interactions with the first best friend at 3–4 years, consistent with attachment theory's predictions that parental care shapes children's ability to enter subsequent attachments in their lives, with friends, mentors, and romantic partners culminating in their ability to parent the next generation (Feldman, 2012b; Feldman, Gordon, Influs, Gutbir, and Ebstein, 2013).

The OT response is sensitive to parental touch. Mothers and fathers were tested in the 10-minute "play and touch" paradigm, where a parent interacts with the infant freely and is instructed to "touch your infant as you normally do". Mothers who provided abundant amounts of affectionate touch, but not those who provided little touch, showed an OT increase following the interaction. In parallel, fathers who had high levels of stimulatory contact, but not those who showed little touch, increased their OT levels (Feldman et al., 2010). Furthermore, infants as young as 4 months displayed OT increases following synchronous interactions with their parents (Feldman, Gordon, and Zagoory-Sharon, 2010). Like rodents, human parent-specific touch, when provided in abundance, elicits OT response in parents, which, in turn, elicits a parallel OT response from the infant, priming the infant's OT system to respond to pleasurable social touch within future attachment relationships.

Finally, animal studies have suggested that neuroendocrine changes in mothers during pregnancy and the postpartum provide a template for pair bonding, and, thus, there is continuity between hormonal processes implicated in parental and pair bonding (Numan and Young, 2016). We measured plasma OT, beta endorphin, and IL-6—biomarkers of the affiliation, reward, and immune systems—in a group of first-time parents and their 3-month-old infants, a group of new romantic partners who had been together for 3 months, and unattached singles. Synchrony between parents and infants and among new lovers was microcoded. We found that all hormonal systems underwent changes with the formation of new attachment bonds. OT increased in parents but was highest in new lovers. In contrast, both beta endorphin and IL-6 were highest in parents, lowest in singles, and at mid-level in lovers. In addition to increase, biomarkers of affiliation, reward, and stress management coalesced, and the correlations between them became tighter during periods of bond formation. Finally, the effects of beta endorphin and IL-6 on behavioral synchrony were mediated by the oxytocin system (Ulmer-Yaniv et al., 2016). These findings, combined with the aforementioned continuity between parental and filial attachment (humans' attachment to their close friends) highlight the integrative role of OT across human affiliative bonds, as mediated by sensitive parenting (Feldman, 2012a, 2012c).

Research has also investigated the effects of intranasal OT administration on a plethora of human social functions. Several studies showed effects of OT administration on increasing fathers' energetic and object-focused interactions with their toddlers (Naber et al., 2010) or on brain response to infant cry and laughter among nonparents (e.g., Riem et al., 2011, 2012).

In the context of parental hormones and behavior, we administered OT to 35 fathers of 5-month-old infants in a double-blind placebo-controlled within-subject design, examined paternal and infant

hormones, and microcoded social behavior. As expected, intranasal OT administration markedly increased fathers' salivary OT; however, surprisingly, OT administration to parent increased the infant's salivary OT by 30-fold, although infants were taken out of the room where fathers inhaled OT and remained outside for the 45-minute waiting period. This measurable increase in infant OT may point to mechanisms of chemosignaling between parent and child which require much further research. Under the OT condition, subtle differences in parent and child's social behavior were observed; fathers touched infants more and gently reoriented infants back to the joint play when they averted gaze. Infants gazed at their fathers for longer durations and engaged in longer episodes of joint exploration. Autonomic signs were also higher in the OT condition, and both father and infant increased cardiac vagal tone, a biomarker of social engagement (Weisman et al., 2012).

OT administration to fathers also impacted the infant's CT levels as mediated by father-infant synchrony. Among infants experiencing high synchrony, paternal still-face increased CT production and elevated infants' social gaze to the nonattentive parent. However, among infants experiencing low paternal synchrony, OT reduced the infant's stress response and decreased social gaze to the father during the still-face phase (Weisman, Zagoory-Sharon, and Feldman, 2013). As OT increases the social salience of events (Shamay-Tsoory and Abu-Akel, 2016), it is possible that among infants who internalized an engaged and available paternal style, the OT condition enhanced their social attention to father's communicative failure.

Vasopressin

AVP is a structurally similar neuropeptide to OT, both originating from the ancient vasotocin molecule, and both implicated in mammalian fathering (Carter, 2014), but little research has examined peripheral AVP in relation to human parenting. Studies in rodents suggest that AVP is involved in physiological changes in AVP in fathers may mediate changes in energy balance and stress reactivity that are required for the onset of fathering (for review: Bales and Saltzman, 2016; Saltzman and Ziegler, 2014). AVP is associated with male bonding and defensive and territorial behavior (Bielsky, Hu, Ren, Terwilliger, and Young, 2005), and AVP promotes social recognition in both rodents (Caldwell, Lee, Macbeth, and Young, 2008) and human males (Guastella, Kenyon, Unkelbach, Alvares, and Hickie, 2011). Regions characterized as part of the AVP circuitry are implicated in socio-cognitive processes in both humans and rodents (Goodson and Thompson, 2010). This AVP-brain associations may represent elevated AVP-dependent vigilance, which supports father's ability to read the intention of others to defend mother and young (Thompson, George, Walton, Orr, and Benson, 2006). In contrast, AVP supports the mother's ability to befriend others. Thus, AVP may prompt differential social strategies in social contexts in women and men (Thompson et al., 2006).

Research on AVP is predominantly male oriented as AVP has been mostly studied in the context of autism and aggression. Variability on the AVP receptor gene has been associated with observed parenting in healthy parents (Avinun, Ebstein, and Knafo, 2012) as well as the context of continuous trauma exposure (Feldman, Vengrober, and Ebstein, 2014). OT administration to males and females increases both AVP (Weisman, Schneiderman, Zagoory-Sharon, and Feldman, 2013), indicating affinity between the expression of the two neuropeptides.

Only two studies, to our knowledge, measured plasma AVP levels in parents. In the first, OT and AVP were measured in relation to neural activations in the maternal and paternal brain (Atzil, Hendler, Zagoory-Sharon, Winetraub, and Feldman, 2012). AVP correlated with fathers', but not mothers', amygdala response to infant stimuli, supporting the links between fathering and AVP in humans. In the second study, OT and AVP levels in mothers and fathers of 4-month-old infants were measured in relation to parent-infant interactions. No mean-level differences emerged in AVP between mothers and fathers, but plasma OT and AVP were associated with distinct configurations of parental behavior. Parents with higher OT directed their infants toward a social focus, enhancing

behaviors such as gaze coordination and affectionate contact, behaviors that were more prevalent in mothers. In contrast, parents with high AVP engaged in stimulatory contact and tended to increase object-salience when infants showed bids for social engagement, a behavioral profile more common in fathers. Thus, synchronous processes with mother and father within the family unit distinctly prepare children to join the larger social world (Apter-Levi et al., 2014). (Another study followed parents and infants across the first 6 years of parenthood in relation to brain activations and assessed salivary AVP and is described below in the section on hormones and the parental brain.)

Prolactin

Prolactin (PRL) is a peptide hormone originating mainly in the anterior pituitary lactotroph cells (Freeman, Kanyicska, Lerant, and Nagy, 2000) that has multiple effects on reproduction and lactation and is thought to mediate the formation of affiliative bonds (Neumann, 2009). PRL is released within the hypothalamus and other limbic areas during mother-infant contact in rodents (Torner et al., 2004) and its administration stimulates maternal care in rats (Bridges, DiBiase, Loundes, and Doherty, 1985). PRL has been examined in relation to fatherhood in a number of animal species (Storey, Delahunty, McKay, Walsh, and Wilhelm, 2006; Wynne-Edwards, 2001; Ziegler, Wegner, Carlson, Lazaro-Perea, and Snowdon, 2000). In humans, studies have shown that both men and women exhibit elevated levels of plasma PRL before childbirth, and fathers who report being more affected by infant cues show higher PRL (Fleming, Corter, Stallings, and Steiner, 2002; Storey et al., 2006). Experienced fathers show greater increases in PRL when listening to infant cries as compared to first-time fathers (Fleming et al., 2002). In contrast to single men, fathers' PRL does not decline following interaction with their toddler (Gray, Parkin, and Samms-Vaughan, 2007). Among fathers to 6-month-old children, plasma PRL correlates with OT levels and higher paternal PRL is associated with greater attention to the environment and joint father-child exploratory play (Gordon et al., 2010c).

In mothers, on the second post-birth day, a rise in PRL was found 20 minutes after infant suckling (Jonas et al., 2009). Infant stimulation of nipple induces both OT and PRL responses (McNeilly, Robinson, Houston, and Howie, 1983). Finally, between 4–6 weeks postpartum, higher PRL correlates with lower stress and better mood only among formula-feeding mothers (Groër, 2005), and following cesarean delivery OT and PRL are related to lower anxiety (Nissen, Gustavsson, Widström, and Uvnäs-Moberg, 1998). Overall, early animal studies on the neurobiology of maternal care described the contribution of both OT and PRL, but human studies have placed much greater emphasis on the role of OT, with less research devoted to the links between PRL and observed parenting.

Testosterone

Testosterone is an androgenic steroid produced by the hypothalamic-pituitary-gonadal (HPG) axis that modulates reproductive behavior and plays a key role in human social behavior, particularly in behaviors associated with social status, at times in combination with aggressive behavior (Eisenegger, Haushofer, and Fehr, 2011; Mazur and Booth, 1998; Wingfield, Hegner, Dufty, and Ball, 1990). Testosterone's involvement in parenting and pair bonding has been described in human and other mammals (Kuzawa, Gettler, Muller, McDade, and Feranil, 2009; van Anders and Goldey, 2010), and alterations in T levels in males are thought to reflect a shift between conflicting reproductive strategies, from mating efforts to parenting efforts (Gray and Anderson, 2010). Studies in more than 60 bird species support the "challenge hypothesis", which suggests that T levels increase when males compete for food and territory and decrease when males must care for offspring (Wingfield et al., 1990).

Research in biparental species shows that fathers' T levels decrease in the presence of a dependent offspring (Wynne-Edwards, 2001). For example, marmoset males who carried infants the most had

the lowest urinary T levels (Nunes, Fite, Patera, and French, 2001) as well as the greatest declines in gonadal steroids (Nunes et al., 2001), and exposure to infant scent lowered serum testosterone in father common marmosets (Prudom et al., 2008). In the monogamous and biparental California mouse (*Peromyscus californicus*), greater T-increase during courtship is associated with paternal cuddling and a protective repertoire towards their pups (Gleason and Marler, 2010).

Similar findings have emerged in human fathers. High T was found in single and divorced men, and low T in men and women within a committed relationship as well as in new fathers (Booth and Dabbs, 1993; Burnham et al., 2003; Gettler, McDade, Feranil, and Kuzawa, 2011; Mazur and Michalek, 1998; van Anders and Goldey, 2010). During the transition to fatherhood, men decrease their T levels (Berg and Wynne-Edwards, 2001; Perini, Ditzen, Fischbacher, and Ehlert, 2012), and such decrease is associated with positive paternal behavior (Fleming et al., 2002). A study in the Philippines assessing men before and after becoming fathers showed a decline in T levels in fathers, which correlated with the degree of father involvement in childcare (Gettler, McDade, Agustin, Feranil, and Kuzawa, 2013). In our study of intranasal OT administration to fathers, we found that lower baseline paternal T was associated with more optimal father and infant social behavior, including gaze, vocalizations, and touch (Weisman et al., 2014). Furthermore, OT-induced changes in T correlate with more positive affect, social gaze, and synchrony, consistent with the perspective that neuroendocrine systems in human males evolved to support committed and flexible fathering (Ziegler, 2000).

Very few studies test T in mothers. An increases in T was found in pregnant women (Edelstein et al., 2015; Fleming et al., 1997), and mothers' T levels were associated with infants' physical and socioemotional health and lower maternal depression (J.I. Cho, Carlo, Su, and McCormick, 2012; J. Cho, Su, Phillips, and Holditch-Davis, 2016). We found that across the first months of parenting, fathers' T is associated with lower behavioral synchrony, and mothers' T is not directly related to maternal behavior (Gordon et al., 2017). However, in the context of high T, maternal OT predicts greater mother-infant synchrony, further supporting the mutual influences of OT on T, which require much further research. Assessing diurnal T in mothers and fathers of two preschool-aged children, among fathers more diurnal variability in T was associated with more sensitivity and respect for autonomy, whereas for mothers greater diurnal variability correlated with less sensitivity, further indicating that T carries differential effects on mothering and fathering (Endendijk et al., 2016). Higher maternal testosterone and infant cortisol are associated with more positive and more frequent maternal interactive behaviors (J. Cho, Su, Phillips, and Holditch-Davis, 2015). It thus appears that the direct and mediated effects of T on parenting, particularly mothering, requires much further research both in relation to the effects of T on behavior and the effects of T on other hormones.

Cortisol

Cortisol is a steroid hormone secreted by the hypothalamic-pituitary-adrenal (HPA) axis in conditions of physical and psychological stress (Lupien, McEwen, Gunnar, and Heim, 2009). Cortisol is a key component of the stress response, and as parenting is a highly stressful evolutionarily adaptive process, research has pointed to CT's participation in the vigilant component of parenting. A large body of research in humans and animal models links CT with the regulation of maternal behavior, and, to a lesser extent, with paternal caregiving (Fleming et al., 1997; Wynne-Edwards, 2001; Ziegler, 2000). Most research on cortisol in the context of parenting is related to maternal stress, and the vast majority of studies utilize CT as an index of stressed parenting, associated with maternal early or current life stress.

The various components of the stress response are indexed in parenting research by multiple CT indices, including basal cortisol, cortisol reactivity to stressful paradigms, diurnal CT production, and hair cortisol (Levine et al., 2007). Overall, the stress response involves complex interactions between

the sympathetic nervous system and the HPA axis, allowing to both prepare for danger and return to baseline once threat is removed (Laurent, Ablow, and Measelle, 2012; Lupien et al., 2009). The HPA axis comprises the hormones CRH, ACTH, and cortisol, which interact with contextual factors to shape both momentary stress reactivity and long-term stress physiology (Ellis and Essex, 2007; Romeo, 2010). Cortisol plays an important role in the stress response by preventing over-reaction of the immune system to threats and acting on the hypothalamus and pituitary gland via negative feedback loops to foster homeostasis once safety is achieved (Kudielka, Hellhammer, and Wüst, 2009; Miller, Chen, and Zhou, 2007; Smyth, Hucklebridge, Thorn, Evans, and Clow, 2013).

Extant evidence in humans and animals has shown that maternal care provides social buffering of HPA axis activity in offspring (Hostinar, Sullivan, and Gunnar, 2014; Jessop and Turner-Cobb, 2008; Moriceau and Sullivan, 2006; Shionoya, Moriceau, Bradstock, and Sullivan, 2007). Beginning in infancy, when the child's HPA system is labile, and across childhood and adolescence, sensitive parenting attenuates children's HPA reactivity, expressed in smaller cortisol increases or quicker returns to baseline following stress (Albers et al., 2008; Blair et al., 2008; Berry et al., 2016; Feldman, Singer, and Zagoory, 2010). In contrast, insensitive parenting, expressed in intrusive, unavailable, and fragmented parental style, alters the development of children's stress response and threat-detection neurobiological circuits (Hostinar et al., 2014) and correlates with higher CT production (Ahnert et al., 2004; Berry et al., 2016; Bosquet Enlow et al., 2014; Marceau et al., 2015) or inflexible cortisol response and reduced variability (Apter-Levi et al., 2016). Thus, a central line in the study of CT relates to how the nature of parental care shapes the development of children's HPA axis functioning.

Less research on CT in the context of parenting addresses CT in the parent, and some of these studies measures parental CT in conjunction with child CT. The bulk of this research focuses on high-risk conditions (see below), with less research assessing parental CT in low-risk samples. Thus, from the extant literature and reviews available on the cross-generational transmission of human stress physiology (for review see Bowers and Yehuda, 2016) less research has focused on CT in relation to observed parental behavior in low-risk mothers, and even less research has tested paternal CT in relation to paternal behavior in typically developing families.

Regarding CT and mothering, in the newborn period, reports are mixed on the relations of CT to maternal behavior. Some found the expression of maternal behavior to correlate with higher CT (Fleming, Steiner, and Anderson, 1987), but our assessment of plasma CT across pregnancy and the postpartum month showed that CT increased in late pregnancy and higher CT predicted restricted maternal behavior (Feldman et al., 2007). Starting at 3–4 months, research has measured CT in mothers and infants in stressful paradigms, such as the "still-face", and most studies across infancy, childhood, and adolescence describe links between higher maternal CT, expressed in higher basal levels, greater stress reactivity, and slower recovery from stress, and less optimal parenting, expressed in lower sensitivity, decrease reciprocity, and greater intrusiveness (for review, Gunnar, Talge, and Herrera, 2009).

Although most studies on CT and stress-inducing paradigms focus on infant CT, few also test maternal CT. For instance, higher maternal basal cortisol and greater reactivity to the "still-face" at 6 months are related to higher intrusiveness and lower second-by-second synchrony (Feldman, Singer, and Zagoory, 2010). Similarly, mothers with higher parenting-focused mindfulness show steeper cortisol recovery slopes following the still-face at 6 months (Laurent, Duncan, Lightcap, and Khan, 2017). Maternal blunted cortisol awakening response (CAR), the typical increase in CT from wakening to 30 minutes post-wakening, during pregnancy predicts lower infant emotion regulation as mediated by maternal sensitivity (Thomas, Letourneau, Campbell, Tomfohr-Madsen, and Giesbrecht, 2017). Similarly, higher diurnal cortisol production is linked with maternal retrospective report of early life stress and predicts lower sensitivity to their 2–6 months (Gonzalez, Jenkins, Steiner, and Fleming, 2012). Of note, among mothers and infants aged 6–12 months, those of low socioeconomic status (SES) had higher diurnal CT production compared to high-SES mothers and infants, as well

as lower adrenocortical synchrony (Clearfield, Carter-Rodriguez, Merali, and Shober, 2014). Overall, these studies indicate that across CT biomarkers more attuned parenting and greater maternal abilities to allocate resources to the child are associated with lower CT.

In fathers, CT declines following father-toddler interaction, as does fathers' PRL, and the decline in CT is greater in experienced, compared to first-time, fathers (Gettler, McDade, Agustin, and Kuzawa, 2011). Testing fathers of 22-month-old toddlers following father-child interactions on a day they spent several hours alone with the child prior to testing versus days without the child, it was found that CT generally declined following interaction, but a greater decline was observed when fathers spent time alone with the child (Storey, Noseworthy, Delahunty, Halfyard, and McKay, 2011). We found greater diurnal CT production in mothers of 6-month-old infants compared to fathers and both parents' CT was negatively related to warmth and sensitivity during triadic mother-father-infant interaction (Gordon et al., 2010a). These studies highlight the stress-reducing function of positive father-child interaction on the father's overall cortisol production and CT response.

The use of hair cortisol analysis in humans provides a measure of more chronic aspects of the stress response (Burnard, Ralph, Hynd, Edwards, and Tilbrook, 2016; Russell, Koren, Rieder, and Van Uum, 2012; Stalder and Kirschbaum, 2012; Staufenbiel, Penninx, Spijker, Elzinga, and van Rossum, 2013). Each centimeter of hair approximates one month of cortisol secretion, thus measuring CT in hair presumably integrates free steroids over the time of growth (Russell et al., 2012; Stalder et al., 2016), and thus hair cortisol concentrations (HCC) are thought to provide a retrospective month-by-month measure of cumulative cortisol secretion and serve as a reliable biomarker of chronic stress (Hinkelmann et al., 2013; Ouellette et al., 2015; Simmons et al., 2016; Steudte et al., 2013; Vanaelst et al., 2012).

HCC has been studied mainly in the context of chronic stress, trauma, and psychiatric illness, and very few studies have integrated this measure into parenting research. In children, HCC is associated with lifetime trauma (Simmons et al., 2016), fearfulness upon school entry (Groeneveld et al., 2013), the number of major childhood traumatic life events (Vanaelst et al., 2012), and lower SES, which likely involves greater chronic stress (Rippe et al., 2016; Vliegenthart et al., 2016). Higher parenting stress and greater child socioemotional difficulties are linked with children's elevated HCC (Palmer et al., 2013). Similarly, mild perinatal adversity, such as late preterm birth, moderates the links between maternal harsh parenting and HCC in 6-year-old children (Windhorst et al., 2017). These studies suggest that, if little research has integrated hair measurement in parents, HCC may be a unique biomarker of the stress response that requires much further research in the context of low- and high-risk parenting.

Salivary Alpha Amylase

Salivary alpha amylase (sAA) has been integrated into research on parenting and child outcomes an index of the sympathetic-adrenal-medullary (SAM) arm of the stress response (Hellhammer, Wüst, and Kudielka, 2009; Nater and Rohleder, 2009). The stress response involves the coordinated functioning of two major anatomically distinct systems, the SAM, which initiates the fight-or-flight response by increasing blood flow, respiration, cardiovascular activity, and the release of catecholamines (Nater and Rohleder, 2009), and the HPA system, which has a more gradual onset and is associated with physiological and behavioral withdrawal (Bauer, Quas, and Boyce, 2002; Tarullo and Gunnar, 2006). Whereas momentary stress induces immediate changes in each system, chronic stress exerts a lasting effect and may alter the balance between the functioning of the SAM and HPA systems (Wolf, Nicholls, and Chen, 2008). Salivary alpha amylase has mainly been tested in children and less commonly in parents in the context of stress, both alone and in relation to CT (Wolf et al., 2008).

In children, sAA has been tested in relation to physical health (Wolf et al., 2008), negative emotional reactivity (Spinrad et al., 2009), and attachment under stress (Frigerio et al., 2009). Similar to

CT, the bulk of sAA studies have been conducted in high-risk samples (see below). Lower sAA was found among maltreating mothers and reduced reactivity to infant crying compared to nonmaltreating mothers (Reijman et al., 2015). Insecure-avoidant 1-year-old infants had higher sAA levels following the strange situation paradigm and their mothers, who showed no differences in sAA, exhibited less vagal withdrawal in the reunion episode (Hill-Soderlund et al., 2008). Parent-child relationship quality predicts the associations between marital conflict and higher child sAA reactivity (Lucas-Thompson and Granger, 2014), and smoking mothers have higher salivary CT and lower sAA compared to nonsmoking mothers (Granger et al., 2007). In fathers of adolescent girls, higher interparental aggression is related to lower father sAA (Gordis, Margolin, Spies, Susman, and Granger, 2010). Overall, it appears that sAA may be a useful marker of the SAM arm of the stress response, but much further clarifications are required to integrate it as a measure of optimal versus high-risk parenting.

Summary

As seen, the hormones of parenting in humans function in a comparable way to those supporting parental care in nonhuman mammals and enable the expression of the unique evolution of parental care across human societies. OT, AVP, and PRL appear to ignite the expression of parenting behavior, CT, sAA, and immune biomarkers to manage the stress involve in parenting, and T plays a special role in development of fathering.

Endocrine Fit: Synchrony in Parent and Child's Hormones

Synchrony or attunement between the parent and infant's physiological and behavioral processes enables mammalian parents to promote sociality and regulate stress in their young. Hormonal concordance or synchrony, the match between parent and child's hormones, is a central aspect of such biobehavioral attunement and a link between parent and child's hormonal levels has been observed in most studies reporting on the associations between parent and child's hormones measured concurrently. Hormonal synchrony is thought to stem from both genetic similarity and shared environment; yet research has tested the degree in such linkage in different contexts and conditions and its association to parent-child relational variables. According to our *biobehavioral synchrony* model (Feldman, 2012c, 2015b, 2016, 2017), biological synchrony is an important mechanism in the development of mammalian young by which the parent's mature physiological systems externally regulate the infant's immature system through the coordination of biological and behavioral processes during moments of social contact. We showed in multiple physiological systems, such as heart rate coupling (Feldman, Magori-Cohen, Galili, Singer, and Louzoun, 2011), brain-to-brain synchrony in neural oscillations (Levy et al., 2017), and endocrine systems (e.g., Feldman et al., 2010; Pratt et al., 2017), that synchrony in biological processes is anchored in behavioral synchrony and increases during moments of concordance in parent and child nonverbal behavior in the gaze, affect, vocal, and touch modalities.

Consistent with findings in animal models (Hofer, 1995a), we found that biological synchrony operates in a system-specific manner. Thus, the following reviews the two main parenting-related hormonal systems, oxytocin and cortisol, in healthy and high-risk populations, with more empirical data available for CT compared to OT. The distinction between the two hormones as the main neuroendocrine systems supporting the affiliation and stress/vigilance components of parenting is also expressed in a distinction between the developmental goal of hormonal synchrony in OT and CT. For OT, higher parental sensitivity, synchrony, and reciprocity are associated not only with higher parental OT and higher infant OT, but in a closer match between their OT levels, which promotes more optimal social-emotional outcomes in children. In contrast, tighter cortisol synchrony

is associated with greater child stress physiology and lower parental sensitivity and dyadic reciprocity (Pratt et al., 2017).

Parent-Child Oxytocin Synchrony

Among 4- to 6-month-old infants, we found hormonal synchrony of oxytocin both prior to and following a "play and touch" paradigm, and such endocrine synchrony was observed when social synchrony was high, not when it was low (Feldman et al., 2010). The endocrine fit of parent and child's OT only in cases of high behavioral synchrony suggests that the fit between parent and child is based on parental behavior, consistent with research in animal models.

In three high-risk samples we found OT synchrony between parent and child. In a study comparing preschoolers with autism spectrum disorders (ASD) with typically developing children (TD), OT synchrony in both the ASD and TD group emerged between children with both their mothers and fathers, with no significant differences in the magnitude of OT synchrony between parents or among the two groups (Feldman, Golan, Hirschler-Guttenberg, Ostfeld-Etzion, and Zagoory-Sharon, 2014), despite the fact that levels of OT differed between ASD and TD preschoolers but not among their mothers or fathers (see below).

Following mothers diagnosed with Axis-I depression across the child's first 6 years of life and their children, we found that depressed mothers had lower salivary OT as did their children. Fathers in families of depressed mothers also had lower OT, and low OT was related to the diminished maternal touch and social gaze in depressed mothers (Apter-Levy, Feldman, Vakart, Ebstein, and Feldman, 2013). Lower baseline OT and attenuated OT response to mother-child interaction was also found in urinary OT in mothers and children whose urinary OT levels were correlated. As stated above, such urinary OT concordance was sensitive to stressful aspects of the interaction and correlated with greater maternal intrusiveness and higher child withdrawal. Of note, among depressed mothers, those who still had higher OT were able to transmit a functional OT system to their child, and their children's OT differed from that of controls, highlighting the protective role of the mother's oxytocin functionality (Pratt et al., 2015).

Finally, in a group of children exposed to continuous war-related trauma, we found lower OT in war-exposed mothers and OT synchrony between mother and child. Such OT synchrony mediated the effects of war on the child so that high maternal OT led to higher mother-child behavioral synchrony leading to reduced child's anxiety disorders by age 10 (Ulmer-Yaniv et al., 2017).

Parent-Child Adrenocortical Synchrony

The coordination between parent and child cortisol production has been entitled by several terms, including cortisol coregulation, hormonal concordance, stress contagion, or adrenocortical synchrony (Atkinson et al., 2013; Mörelius, Örtenstrand, Theodorsson, and Frostell, 2015; Papp, Pendry, and Adam, 2009; Pratt et al., 2017; Ruttle, Serbin, Stack, Schwartzman, and Shirtcliff, 2011; Saxbe et al., 2014; Stenius et al., 2008). The vast majority of studies examined the coordination of CT following stress paradigms and found that, when stress is elevated in mother or child, both partners increase CT in a coordinated fashion (Atkinson et al., 2013; Hibel, Granger, Blair, and Finegood, 2015; Mörelius, Broström, Westrup, Sarman, and Örtenstrand, 2012; Mörelius, Theodorsson, and Nelson, 2009; Neu, Laudenslager, and Robinson, 2009; Ruttle et al., 2011; Sethre-Hofstad, Stansbury, and Rice, 2002). Much less research has focused on the coordination of diurnal CT patterns between mother and child (Hibel, Trumbell, and Mercado, 2014; LeMoult, Chen, Foland-Ross, Burley, and Gotlib, 2015; Papp et al., 2009; Schreiber et al., 2006; Stenius et al., 2008; Williams et al., 2013), a distinct aspect of HPA axis functioning that is often uncorrelated with CT reactivity to momentary stressors (Edwards,

Clow, Evans, and Hucklebridge, 2001). Even fewer measured parent-child linkages between hair cortisol concentrations in mother and child have been examined, yet another dimension of HPA reactivity, typically unrelated to salivary response to stress (Halevi et al., 2017).

Synchrony of diurnal CT within the family is related to the amount of shared experience (Mörelius et al., 2012, 2015; Schreiber et al., 2006; Stenius et al., 2008). For instance, preterm infants placed in family care and exposed to maternal-infant skin-to-skin contact exhibit cortisol concordance, whereas no correlations between maternal and infant CT was found among infants placed in standard incubator care (Mörelius et al., 2012, 2015). Six-month-old infants show greater diurnal adrenocortical synchrony with their mothers as compared to their fathers (Stenius et al., 2008). Among preschool-aged children mother-child morning CT levels show linkage only on nonwork days (Hibel et al., 2014); and among adolescents, shared environment is a better predictor of afternoon CT linkage than genetic factors (Schreiber et al., 2006).

Synchrony in diurnal CT was found between mothers and children, above and beyond time of measurement. Mother-child reciprocity is related to lower adrenocortical synchrony, whereas father-child tension is marginally predictive of greater adrenocortical synchrony. Higher child diurnal CT production predicts a stronger linkage between maternal and child diurnal CT, suggesting that greater physiological stress may render children more susceptible to the effects of maternal stress physiology. Maternal depression, although related to attenuated child diurnal CT decline, does not affect adrenocortical synchrony. Adrenocortical synchrony may tap a unique aspect of HPA axis functioning, potentially linked with the cross-generation transfer of stress physiology. Results highlight mothering and fathering family subsystems as moderators of adrenocortical synchrony and point to the role of parent-child relational stress in shaping diurnal CT linkage.

Compared to a healthy control group, synchrony in diurnal CT was found between depressed mothers and children, and the degree of mother-child reciprocity was related to lower adrenocortical synchrony. When children's CT production during the day was higher, there was also a tighter synchrony between maternal and child CT, suggesting that greater physiological stress may render children more susceptible to the effects of maternal stress physiology. Maternal depression, although related to attenuated child diurnal CT decline, did not affect adrenocortical synchrony. These findings highlight the role of parent-child reciprocity in shaping diurnal CT linkage (Pratt et al., 2017).

In a group of preschoolers with ASD compared to TD children, we found CT synchrony between children and both their mothers and their fathers at the three measurement points following the SF paradigm (Ostfeld-Etzion, Golan, Hirschler-Guttenberg, Zagoory-Sharon, and Feldman, 2015). Furthermore, father-child cortisol linkage is stronger in dyads that show less reciprocity, when fathers were less sensitive and when children showed less self-regulation. Consistent with the prior findings, mother-child linkage is stronger in dyads that show less reciprocity and lower maternal sensitivity, demonstrating that higher CT linkage is observed in less functional dyads (Saxbe et al., 2017).

Finally, in the war-exposed group, early childhood adrenocortical synchrony is present in maternal and child CT levels at both baseline and reactivity to stressors in early childhood (Feldman, Vengrober, Eidelman-Rothman, and Zagoory-Sharon, 2013). In late childhood (9–11) years, adrenocortical synchrony appears in both salivary cortisol and hair cortisol concentrations, and mothers' reduced CT in the face of chronic trauma initiates a cascade of biobehavioral synchrony, linking to lower child CT, greater behavioral synchrony, and higher child social engagement, which, in turn, decreased child externalizing and internalizing symptoms (Halevi et al., 2017).

Overall, adrenocortical synchrony is thought to be a mechanism by which, beginning in utero, mothers signal to the developing fetus the amount of danger the environment will likely contain. Studies in rodents indicate that the mother's species-typical behavior carries a unique effect on consolidation of the pup's HPA reactivity (Gubernick and Alberts, 1983; Rosenberg, Denenberg, and Zarrow, 1970) and that mothers with lower corticosterone display more maternal behavior and their infants show lower HPA axis reactivity in adulthood (Francis and Meaney, 1999; Dong Liu et al.,

1997). Cross-fostering studies show that maternal behavior has epigenetic effects on pup neural and behavioral responses to stress and the effects of maternal behavior exceed those of genetic dispositions (Champagne and Meaney, 2001; Kundakovic and Champagne, 2015). These findings provide mechanistic evidence for the concordance between maternal and child HPA axis functioning and suggest that variability in maternal caregiving may play a role in shaping the infant's cortisol production and degree of their adrenocortical synchrony (Macrì, Zoratto, and Laviola, 2011).

Parents' Hormones and the Parental Brain

Hormonal Correlates of Parent Brain Activations

Research in rodents has shown that hormones of pregnancy prepare brain structures which are sensitized by childbirth and form the "mammalian caregiving network", including the amygdala, hypothalamus (particularly the MPOA), and the dopamine-rich subcortical ventral tegmental area (VTA) (for review; Numan and Stolzenberg, 2009; Numan and Young, 2016). Imaging studies of the human parental brain, exposing parents to auditory, visual, or multimodal stimuli of their infants, have revealed that the same network activates, in addition to other cortical networks implicated in empathy, interoception, embodied simulation, mentalizing, and emotion regulation to form the "global human caregiving network" (for Review, Feldman, 2015b; Swain and Ho, 2017).

Work on the parental brain points to associations between parent's brain activations and parents' hormones. Regarding maternal brain-hormone relations, mothers' plasma OT levels correlate with two nodes of the subcortical mammalian network; amygdala, mediating maternal vigilance, and Nucleus accumbens, linked with the subcortical dopamine reward system (Atzil et al., 2011). Salivary OT in mothers relates to maternal dorsal anterior cingulate cortex (dACC), a component of the empathy-embodied simulation network (Abraham et al., 2014), and to the hypothalamus and ventral tegmental area of the subcortical mammalian network (Strathearn et al., 2009). Finally, mothers showing less CT reactivity have higher brain activation to their infant cry in the PAG, insula, ACC, and OFC, areas implicated in interoception (perception of bodily milieu) and empathy (Laurent, Stevens, and Ablow, 2011).

Fathers' OT is associated with activations in the superior temporal sulcus, a key node of the social brain integrating mirror and mentalizing properties (Abraham et al., 2014). Fathers' amygdala activity correlates with fathers' plasma AVP levels (Atzil et al., 2012). Finally, fathers' testosterone, known to decrease in men at the transition to fatherhood (Gettler, McDade, Feranil, et al., 2011), correlates with lower VTA activation and higher left caudate activation (Kuo, Carp, Light, and Grewen, 2012; Mascaro, Hackett, and Rilling, 2013).

Long-Term Prediction Of Parental Brain and Hormones for Children's Social Development

In several studies, we measured parental neural and hormonal response in infancy in relation to child outcomes across the first years of life. Among primary-caregiving mothers and fathers, we found that the coherence of the parent's embodied simulation network, integrating structures implicating in mirror and empathy functions, and parental OT predicted children's OT in the preschool stage as well as their capacity to use advanced strategies for regulating negative emotions (Abraham, Hendler, Zagoory-Sharon, and Feldman, 2016).

Another study assessed parent brain response to coparental stimuli—stimuli depicting the partner as parent, in relation to observed coparental behavior, hormones, and child outcomes. Coparental stimuli activated the caudate, a critical node in supporting motivational goal-directed social behavior. Caudate-ventromedial prefrontal cortex (vmPFC) vmPFC connectivity, linking caudate with the

prefrontal area implicated in intersubjectivity, mentalization, and affect sharing, is associated with collaborative coparenting and the link between caudate-vmPFC connectivity and reduced child behavior problem at 6 years was mediated by the parent's OT. Caudate connectivity with the dACC, which has been linked with pain perception, envy, and vigilant monitoring of social and aggressive response, predicts undermining coparenting across time and is linked with AVP (Abraham, Gilam, et al., 2017). Greater functional connectivity between the two empathy networks in the parental brain, the embodied simulation and mentalizing networks, predicts lower child CT reactivity and better emotion regulation at preschool (Abraham, Raz, Zagoory-Sharon, and Feldman, 2018).

Parental Hormones in High-Risk Conditions

A comprehensive review of parental hormones in high-risk populations is beyond the scope of a single chapter. The following reviews studies on OT and CT in high-risk populations, focusing mainly on two systems—OT and the affiliative system and CT and indices of the stress response.

Oxytocin and Affiliative Biomarkers Markers

Postpartum Depression

Several studies have addressed OT functionality in mothers suffering from depression, with few studies addressing mothers with clinically diagnosed Axis-I depression, not just self-reported depressive symptoms. Lower OT during pregnancy and the postpartum goes with greater depressive symptomatology in the neonatal period and less maternal behavior (Feldman et al., 2007). Similar findings were reported by Skrundz, Bolten, Nast, Hellhammer, and Meinlschmidt (2011), who showed that higher depressive symptoms during pregnancy predict lower plasma OT in the postpartum.

A longitudinal study followed a community cohort of depressed mothers and their families from birth across the first decade of life. At 6 years, depressed mothers, their husbands, and their children had lower salivary OT levels and greater prevalence of the more evolutionary-recent protective A allele on the *OXTR*. Lower OT was linked with reduced maternal touch and sensitive parenting (Apter-Levy et al., 2013). Measuring OT in urine in mother and child showed that in both depressed mothers and their children there was lower baseline OT and lower OT response to mother-child interactions. Such reduced urinary OT was related to higher maternal intrusiveness and child withdrawal (Pratt et al., 2015). At 10 years, depressed mothers and children as a group no longer had lower salivary OT, but child OT mediated links between maternal depression and child externalizing and internalizing symptoms as well as child lower empathy as measured by two home-based paradigms (Priel et al., 2018).

Administration of OT to postnatally depressed mothers did not increase the level of sensitive parenting (Mah, van IJzendoorn, Smith, and Bakermans-Kranenburg, 2013) nor improve depressive symptoms, but increased their protective behavior to infants in the presence of an intrusive stranger (Mah, Bakermans-Kranenburg, van IJzendoorn, and Smith, 2015).

With regards to other hormones of the affiliation system, plasma prolactin levels are significantly lower in depressed mothers who were breastfeeding (Harris et al., 1989). Similarly, depressed mothers show lower serum prolactin levels (Groer and Morgan, 2007). To date, no study has tested maternal AVP in the context of depression.

Stress and Trauma

Following a cohort of children exposed to repeated wartime trauma and their mothers from early childhood to adolescence, we found that by 9–11 years war-exposed mothers had lower OT, but children as a group did not have lower OT, only those with PTSD. These mothers also had much

higher prevalence of psychiatric disorders, particularly anxiety disorders, PTSD, and depression, their children had higher levels of anxiety symptoms as well as greater prevalence of psychiatric diagnosis. War-exposed mothers also exhibited lower sensitivity and empathy, and their children displayed less social engagement, which was related to lower maternal OT (Ulmer-Yaniv et al., 2017). Children with ASD exhibit lower baseline OT levels, which are momentary normalized during parent-child contact (Feldman et al., 2014). There is evidence that OT increases during skin-to-skin contact between parents and premature infants (Cong et al., 2015), findings which are consistent with the links between maternal proximity and licking-and-grooming with the oxytocin system in animal models.

Cortisol and Stress Biomarkers

Within the family of stress-related biomarkers, numerous studies assess diurnal or reactive cortisol as well as other stress biomarkers in relation to high-risk parenting. Most studies on CT and high-risk parenting address the effects of maternal stress, trauma, depression, or premature birth on the infant's CT, but few studies also measure maternal hormones. Importantly, there are studies following children from birth to adolescence demonstrating that maternal postpartum depression or perinatal stress alter various aspects of children's HPA axis functioning including baseline levels, diurnal patterns, and variability (e.g., Halligan, Herbert, Goodyer, and Murray, 2007).

Postpartum Depression

During pregnancy and 3 months postpartum, higher depressive symptoms are associated with lower cortisol awakening response and flatter diurnal patterns (Scheyer and Urizar, 2016). In one study, at 8 weeks postpartum, breastfeeding mothers underwent a social stressor while breastfeeding. Among depressed mothers, the surge of OT during nursing was reduced and CT levels were higher, suggesting that depression attenuates the anxiolytic effects of breastfeeding on the maternal stress response (Cox et al., 2015). Mothers with a history of major depression combined with child abuse showed steeper CT decline and their infants had lower baseline CT, and more maternal comorbid conditions on top of the depression, such as abuse history or PTSD, augmented the disruptions to HPA functioning (Brand et al., 2010). At 4–6 weeks postpartum, depressed mothers show downregulated HPA functioning, expressed as lower salivary CT (Groer and Morgan, 2007). In contrast, both clinically depressed and clinically anxious mothers at 9 months have higher CT, augmented CT response to stress, and slower CT recovery, and these alterations in CT production were associated with their diminished sensitivity and lower infant social engagement (Feldman et al., 2009).

Following the cohort of depressed mothers and their children from birth to 10 years, we found that at 6 years, mothers and children did not have altered cortisol levels—both diurnal and reactive, but had diminished CT variability in daily patterns and in response to stress (Apter-Levi et al., 2016; Pratt et al., 2017). Similar findings emerged at 10 years of age (Priel et al., 2018), with less flexible CT patterns (lower AUCi index) at both ages associated with less optimal mothering, including maternal intrusiveness and diminished sensitivity, and greater child social withdrawal.

Trauma

Mothers with a history of early trauma show less positive affect and flatter cortisol patterns during a home visit at 6 months (Juul et al., 2016). In a longitudinal study of children exposed to war-related trauma, we found in early childhood that, compared to nonexposed controls, children exposed to trauma since birth had reduced CT variability in response to stress. However, exposed children with PTSD had low and flat CT patterns, suggesting a "shut down" response, but exposed children who

were more resilient had elevated nonflexible levels, indicating high arousal of the system. These differential patterns were related to differences in maternal depression, anxiety, and PTSD symptoms, which were higher in mothers of PTSD children, and greater proximity-seeking behavior in the more resilient exposed child group. Mothers and children also manifest altered patterns of salivary alpha amylase, and for both CT and sAA there were close links between maternal and child's hormonal levels (Feldman, Vengrober, et al., 2013). These findings—which differentiate trauma survivors or trauma-exposed individuals with and without PTSD—are consistent across several samples and various traumas, such as survivors of the 9/11 attack, the Holocaust, and abuse (Yehuda and Bierer, 2007).

At 10 years of age, we measured both hair cortisol and salivary CT response from mothers and children in the same sample. Mothers who lived in a war zone for over a decade had higher hair CT, indicating greater chronic stress, as well as greater salivary CT production during a home visit. These altered maternal patterns impacted the child's pattern via mechanisms of cortisol linkage, charting a pathway from trauma exposure to higher psychopathology in children (Halevi et al., 2017).

Autism Spectrum Disorders

Mothering children with ASD involves high levels of stress, yet few studies have assessed maternal CT in the context of ASD, and even fewer compared CT levels with observed parenting. Mothers and fathers of children with ASD have lower morning cortisol levels, indicating effects of the increased stress on daily stress response (Foody, James, and Leader, 2015). Similarly, 89% of mothers of ASD children display a blunted diurnal CT response, indicating decreased flexibility of the system (Dykens and Lambert, 2013), and another study reported lower CT production throughout the day in mothers of adolescents with ASD (Seltzer et al., 2010).

We assessed CT production in 3- to 6-year-old children during a home visit with mother and a parallel home visit with father, where they faced the same experimental stress manipulations (emotion regulation tasks and "still face"). We found no differences between the CT response of mothers and fathers to children with ASD as compared to control parents; however, children with ASD showed blunted CT responses during interaction with mothers, but typical responses during the visit with father. We interpreted the findings in terms of fathers' pushing children to act more in age-appropriate ways and mothers providing social buffering to children's stress response in a similar manner to mammalian neonates (Ostfeld-Etzion et al., 2015).

Prematurity

Kangaroo care (KC), or skin-to-skin contact, is an intervention aimed to reduce maternal-newborn separation and enhance contact among infants born preterm. Skin-to-skin contact decreases maternal CT following premature birth (Janevski, Vujičić, and Đukić, 2016). Another study showed reduction of infant CT in a group receiving kangaroo care and linkage between maternal and infant CT at 4 months only in the KC group (Mörelius et al., 2015). Reduced CT levels across the first month following birth were also observed in a full-term sample (Bigelow, Power, MacLellan-Peters, Alex, and McDonald, 2012). In our study of kangaroo care and its long-term impact, by 10 years of age children who received kangaroo care as neonates had attenuated CT responses to social stressors (the TSST-C) and their mothers similarly had lower CT production (Feldman, Rosenthal, and Eidelman, 2014).

Hormones of parenting provide biomarkers for stressed or high-risk parenting, hormonal levels are associated with the parent psychological state, history, psychiatric condition, and observed behavior, and hormones demonstrate the utility of using neuroendocrine measures to expand our understanding of at-risk parenting.

Conclusions

Individual variations in hormones play a key role in the development of parenting and are meaningfully associated with variations in maternal and paternal behavior. There is much we do not know which requires future research. First, there are currently no normed curves for hormones across pregnancy and the first year following childbirth. With the growing incorporation of hormones into parenting research, there is a critical need for large-scale studies that can define normative curves across multiple cultures for future research. Second, changing role of fathers and the growing involvement of fathers in childcare prompts much research to understand the neuroendocrinological basis of fatherhood. Third, much research is needed to compare hormonal profiles across a variety of high-risk conditions and to tease apart single from multiple risk, for instance maternal depression in the context of low-risk environment, from maternal depression occurring in the context of poverty, premature birth, or child abuse. Finally, much more research and theory-building are needed to test the hormones of parenting within a global bio-psycho-social theory of parenting that investigates endocrine systems from a comparative perspective and across levels of analysis, incorporating studies of the cellular, genetic, and neural levels with behavioral and representational levels, into a theoretical frame that can define more precisely how hormones of parenting contribute to the successful rearing of human children.

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