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The neurobiology of mammalian parenting and the biosocial context of human caregiving

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ABSTRACT

This article is part of a Special Issue "Parental Care".

Research on the neurobiology of attachment, pioneered by scholars in the generation that followed the discovery of social bonding, examined the biological basis of mammalian parenting through systematic experiments in animal models and their application to theories on human attachment. This paper argues for the need to construct a theory on the neurobiology of human attachment that integrates findings in animal models with human neuroscience research to formulate concepts based on experimental, not only extrapolative data. Rosenblatt's (2003) three characteristics of mammalian parenting – rapid formation of attachment, behavioral synchrony, and mother-offspring attachment as basis of social organization – are used to guide discussion on mammalian-general versus human-specific attributes of parental care. These highlight specific components of attachment in rodents, primates, and humans that chart the evolution from promiscuous, nest-bound, olfactory-based bonds to exclusive, multi-sensory, and representation-based attachments. Following, three continua are outlined in parental behavior, hormones, and brain, each detailing the evolution from rodents to humans. Parental behavior is defined as a process of *trophallaxis* – the reciprocal multisensory exchange that supports approach orientation and enables collaboration in social species – and includes human-specific features that enable behavioral synchrony independent of tactile contact. The oxytocin system incorporates conserved and human-specific components and is marked by pulsatile activity and dendritic release that reorganize neural networks on the basis of species-specific attachment experiences. Finally, the subcortical limbic circuit underpinning mammalian mothering extends in humans to include multiple cortical networks implicated in empathy, mentalizing, and emotion regulation that enable flexible, goal-directed caregiving. I conclude by presenting a philosophical continuum from Hobbes to Lorenz, which illustrates how research on the neurobiology of attachment can put in the forefront the social-collaborative elements in human nature and afford a new perspective on the mind-brain polarity.

…"Critical characteristics of mammalian parental behavior are: Simultaneous onset of birth, lactation, and maternal care, **rapid formation of an attachment** of the mother to her offspring, **synchrony in the behavioral interaction** between mother and young during their development until weaning, and the significance of the mother-offspring unit as **the basis of social organization**".

[J.S. Rosenblatt, 2003, p. 265 (my emphasis)]

In what was to become his last major conceptual paper, Rosenblatt summarizes his perspective on the field he pioneered: the neurobiology of mammalian mothering. Coming of age in a period heavily influenced by psychoanalytic thinking when human mothering was considered mainly a mental phenomenon beginning when mothers first met their newborns (Rosenblatt, 1989, 1994), his creative research program and conceptual clarity helped redirect attention to the physiological basis of parenting. It placed human mothers in a long line of evolutionary progress and emphasized inter-species comparability in the central function of evolutionary adaptation: the successful rearing of offspring. From research and conceptualization developed by Rosenblatt and his contemporaries (Bowlby, 1953, 1967; Denenberg and Bell, 1960; Denenberg et al., 1962; Harlow, 1958; Hofer, 1970, 1987; Levine, 1957, 1967; Schneirla, 1946, 1958, 1971) – the generation that followed Lorenz' discovery on the biological basis of social bonding in 1935 – a new perspective on mothering and its central role in shaping infant biology and behavior emerged and new understanding of attachment bonds as the basis for social organizations was formulated. In addition to new theories, these researchers also advocated a new methodology to study attachment, one that is based on careful observations, hypothesis testing, and step-by-step uncovering of relevant physiological processes. Following their cumulative effort, the notion of "mothering" as a scientific area of inquiry flourished, became anchored in specific hormonal changes and brain structures, and was seen as a long process that begins with pregnancy and undergoes stage-by-stage preparation for the

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maternal–infant encounter at birth, from which it develops through reciprocal mother–infant exchanges (Feldman, 2012a, 2015a; Rosenblatt, 1980). This generation was also the first to utilize animal models, particularly rodents, to study the biological basis of maternal care.

As can be expected, a research program based on animal models highlights the conserved components of parenting. Two conserved processes were particularly emphasized as markers of mammalian caregiving. First, it was suggested that in all mammals parenting is expressed primarily via behavior; in fact, in species such as mammals *parenting is behavior* (Feldman, 2012b; Hrdy, 1999; Rosenblatt, 1989). This definition of "parenting as behavior" touches upon a central divide of mammals (and some birds) from lower species that accompanied the emergence of viviparity and its concomitant increase in maternal investment (Curley and Keverne, 2005; Hogarth, 1976; Larsson, 1994). The focus on behavior altered the field by postulating that in order to understand parenting one must look closely at bonding-related behavior, find ways to quantify it with precision, and define the physiological systems that support its species-specific expression. The second important contribution inserted a temporal dimension into the neurobiology of parenting by describing gradual processes occurring across pregnancy (Rosenblatt, 1989). The emphasis on time provided a template for later research, which added the generational time-line and showed how mothering is prepared not only across pregnancy but by the cross-generation cycles of females, including Champagne and Meaney's (2001) "like mother like daughter" on the cross generation transmission of maternal behavior, Keverne's (2013) work on matriline effects through the maternal–placental–fetal interface, and epigenetic studies on non-genomic transmission of stressful life events via DNA methylation (Meaney and Szyf, 2005; Meaney, 2010; van IJzendoorn et al., 2011). Overall, this generation not only redefined parenting but placed it in the forefront; parenting became the most important topic for understanding mammalian social life and was described as rooted in biology and anchored in evolution. Moreover, these studies "demystified" mothering, advocating that the poetic notion of "maternal love" can be given to rigorous science, systematic experiments, and incremental – not only holistic – knowledge.

In the following, I wish to pay tribute to Rosenblatt, whose research has been instrumental to my theory on *bio-behavioral synchrony* (Feldman, 2007a, 2007b, 2012a, 2012c, 2012d, 2014, 2015a, 2015b), by highlighting the relevance of his work to current models on the neurobiology of human parenting. The three principles of mammalian parenting he outlined – the rapid formation of attachment, the behavioral synchrony, and the role of synchrony as providing the basis for social organization – will guide our discussion on parental care. Yet, this paper focuses on the neurobiology of *human* parenting and discusses it not only as comparable to mammalian parenting but also as distinct from it. It appears that the pendulum has swung far into the biological and away from the mental, and current models on the neurobiology of parenting emphasize the conserved elements while paying much less attention to the uniquely human. Current technical and empirical advances enable us to study the neurobiology of human parenting without the split faced by previous generations, between human studies relying solely on self-reports and low-tech observations while only animal models can provide a window into the underlying physiological mechanisms. New imaging studies of the human parental brain, genetic and epigenetic human research, and the exponential increase in research on the role of oxytocin in human social functions, whose central role in priming the maternal brain for parenting was discovered by Rosneblatt and colleagues, among others (Kendrick and Keverne, 1989; Pedersen et al., 1982; Poindron et al., 1988; Rosenblatt et al., 1988), afford new integration of insights from animal research with human neuroscience experiments. Future technological advances will undoubtedly allow an even greater precision in human neurobiological studies. Such biologically-based human research requires a new theoretical framework, one that is based on prior conceptualization and findings in animal models yet addresses the neurobiology of human parenting from an experimental, not only extrapolative standpoint. The polarity of mind and brain, body and soul, the physical and the mental has puzzled philosophers and scientists since the ancient Greeks. Each generation drafts a somewhat different answer that reflects, in my opinion, how that generation perceives what it means to be human. The neurobiology of human parenting, by providing a central framework to address the biological basis of human social life, may afford one integrative perspective particularly relevant to our generation.

As such, the following discussion is divided into four sections, each presenting a continuum of polarized opposites. The first three describe continua from animal models to human parenting in the three central aspects of parenting; Parenting behavior, oxytocin (in crosstalk with other hormones), and the parental brain. The fourth addresses a philosophical continuum from Hobbes to Lorenz, depicting the polarity between viewing the biological basis of human nature as solipsistic, self-serving, and directed toward accumulating power and resources to models that highlight the social and collaborative elements in Man's biology.

The model on the human parental caregiving context, based on Rosenblatt's three principles derived from research in rodents, is presented in Fig. 1.

As seen, components of the mammalian-general constellation are uniquely expressed in humans in each of the three principles, and their inter-connections are depicted in both red/dotted arrows (mammalian-general) and blue/filled arrows (human specific). The immediate formation of attachment is expressed in humans by the exclusive bond, which is not observed in rodents (Feldman, 2015b), the expression of human-specific parenting behavior immediately after birth, the openness of the human infant's physiological systems to organization by maternal contact, and the special role of oxytocin in this process (Feldman, 2012a; Galbally et al., 2011). These elements, in turn, lead to the development of interaction synchrony (red/dotted and blue/filled arrows), which in humans is dyad-specific, based on the pace and rhythms of each parent and child, and assembles from the same behavioral building blocks in the gaze, affect, vocal, and touch modalities in culture-specific ways (Feldman and Masalha, 2007; Feldman et al., 2006). Interaction synchrony supports the formation of human social life via multiple mechanisms that are both general (red/dotted arrows) and human-specific (blue/filled arrows) as shown in cross-sectional and longitudinal research from infancy to adolescence (Feldman, 2007c, 2012a, 2012c, 2012d). However, in humans there is also a feedback loop from social organization back to attachment formation, which is not so clearly seen in other mammals. This implies that humans, more flexibly than non-human mammals, adapt attachment patterns to diverse social organization, such as permanent versus nomadic habitat, nuclear versus extended family constellation, single versus multiple caregivers, and minimal versus extensive father involvement. Such human-specific arrow also leads from the module of social organization, which is mammalian-general, to the human-specific module of culture, which serves as an overarching organizing principle of human attachment. Large brain primates, particularly humans whose associative cortex is significantly larger than that of chimpanzees, our closest relatives (Rilling, 2014), live in complex social organizations composed of multi-level social relationships, and navigating such complex social ecologies rely on later-evolving associative, executive, and mentalizing brain networks that enable the diversity of human cultural societies (Broad et al., 2006; Dunbar, 2014). Culture-specific factors involving both immediate living conditions, such as co-sleeping, continuous contact, or culturally-accepted amounts of parent–child gaze, touch, and positive arousal, as well as cultural meaning-systems and perceptions of optimal parenting, are both shaped by the neurobiology of attachment and shape it in return, rendering the parent–child interface a flexible platform for evolutionary adaptation.

Our discussion is based on the wealth of research in animal models that described the neuroendocrine and brain networks implicated in parental care and the expression of parental behavior (Numan and Insel, 2003; Numan et al., 2006). These studies highlight the unique

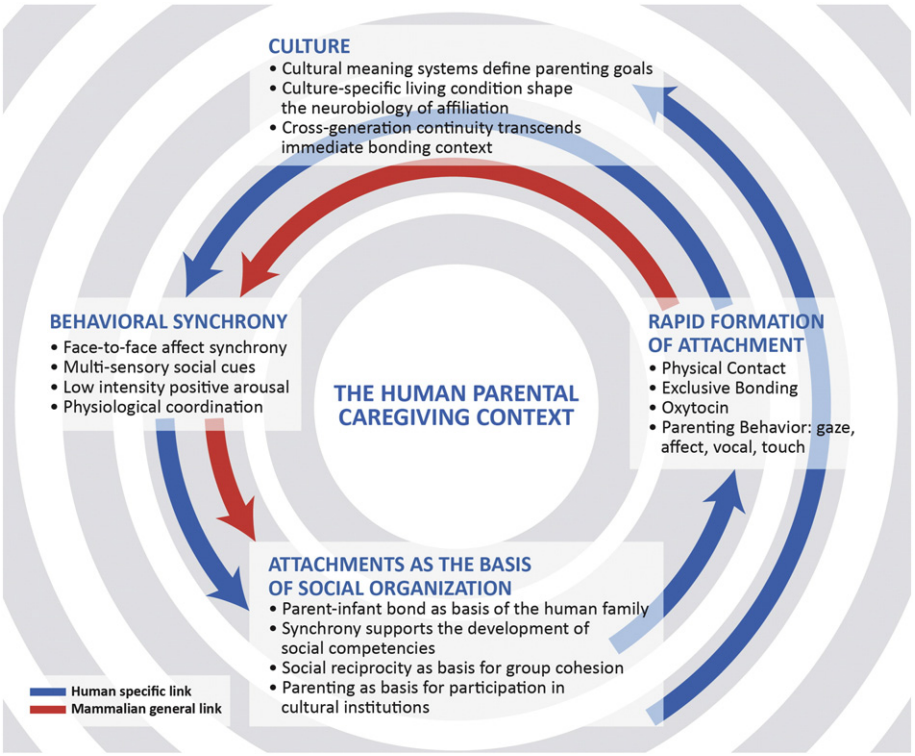

Fig. 1. Human-Specific Components of Parental-Infant Bonding Based on Rosenblatt's Three Characteristics of Bonding in Mammals.

stage of plasticity in the parental brain across the postpartum period, the special opportunities it affords for the parent's cognitive, executive, and emotional functioning, and the special integration of hormonal and brain systems into a neuro-endocrine envelop specifically suited for heightened vigilance to survival of the young, expression of the species-typical parenting behavior, and reward drawn from infant cues (Kinsley and Amory-Meyer, 2011; Kinsley et al., 2015; Bridges, 2015; Fleming et al., 1994). These studies also underscored the openness of the infant's brain to that of the parent's, describing the intricate neurobiology of biobehavioral synchrony in each species. Importantly, while the current review focuses on oxytocin (OT), this neuropeptidergic system functions on the background of hormones known to influence the onset of mothering, including shifting levels of the steroid hormones estradiol and progesterone and the lactogenic hormones prolactin and placental lactogens in stimulating maternal behavior (Bridges et al., 1978a, 1978b, 1985; Mann and Bridges, 2001; Siegel and Rosenblatt, 1975, 1980). Similarly, while the focus here is on fMRI studies of the human parental brain, this recent area of inquiry is based on the pioneering research that described the critical role of subcortical structures, such as MPOA, nucleus accumbens, amygdala, and ventral tegmental area in the emergence of maternal care in rodents (Fleming and Korsmit, 1996; Li and Fleming, 2003; Numan, 2007).

Behavior; from trophallaxis to interaction synchrony

Troxphallaxis and maternal behavior in animal models

Life within social groups requires constant exchange of social signals among members. The famous entomologist Wheeler (1928), investigating how social insects maintain complex social organizations, accomplish collaborative goals, or signal a joint path of journey, coined the term "trophallaxis" to denote the exchange of sensory signals among members of a social group. Schneirla (1946, 1958, 1971), studying the army ants, extended the term to include social, in addition to sensory stimuli and suggested that trophallaxis describes the reciprocal multisensory stimulation of low intensity that elicit approach response. Following, Schneirla and Rosenblatt (1961) suggested that parenting behavior represents a form of "trophallaxis" and this definition highlighted three important elements of parenting behavior, each of which carries human-specific features as discussed below: the low intensity, the social reciprocity, and the trophallaxic process as charting a line from the parent–offspring synchronous exchange during its critical period to life within social groups.

An important conceptual frame for understanding parental effects on social development is that of "social ontogeny" (Schneirla and Rosenblatt, 1963). Social ontogeny addresses the interchange between maturational processes in the infant and the experiences it can draw from the environment at each stage and describes how the infant-context unit enables infants to meet evolutionary challenges and manage the stress response. This perspective foreshadowed the application of dynamic systems' theory, originating in the biological sciences, to human social development, particularly blurring the distinction between infant and context and emphasizing the emergent nature of social abilities from child and environmental inputs (Feldman, 2015c; Fogel, 1993). Moreover, social ontogeny theory underscored an important aspect of parenting – that of "critical periods" – and was among the first to emphasize that sensitive periods apply not only to discrete sensory systems (e.g., the classic "ocular dominance") but also to the entire social envelop parents construct for their infants (Feldman, 2015a). Schneirla and Rosenblatt (1963) emphasized that some inputs must be provided by mother and nest at specific moments in development to assure proper maturation of the social brain. Furthermore, they maintained that the stage-by-stage effects of the social environment on brain maturation can be understood only within a given species and only in relation to variations that alter experiences between mothers and their infants, further supporting the hypothesis that behaviors within early attachments provide the biological basis for social organization. Social ontogeny theory is echoed in recent models in social neuroscience. For instance, Goodson's (2013) idea of "deconstructing sociality" contends that "sociality" evolved from loosely-coupled "modules" that uniquely describe social life in each species, such as flocking, monogamy, social hierarchies, seasonality, or bi-parental rearing.

Thus, understanding the parent–offspring context, its impact on the infant's later social adaptation, and its contribution to global social organizations must be conducted *within a given species*, consistent with our emphasis on the need to formulate a social neuroscience theory based on the neurobiology of *human* parenting.

Two additional features described by Rosenblatt in rodents may be useful to the study of human parenting. The first involves the distinction between two phases of mothering – initiation and maintenances – the first primed by hormones of pregnancy (progesterone and estradiol) and triggered by birth hormones (oxytocin and prolactin); the second depends on ongoing inputs from infant and nest (González-Mariscal et al., 1998, 2000; Numan et al., 1977; Rosenblatt, 1989, 1994). Thus, although rodent mothers do not form exclusive bond with their infants, the second phase of mothering is less automatic and requires "trophallaxis" in the form of social reciprocity and mutual exchanges of stimuli between mother and young for its establishment and later impact on social life. Interestingly, while Rosenblatt mainly investigated maternal behavior in rodents, his work on mother–infant synchrony in the hamster (Siegel and Rosenblatt, 1980) and the rabbit (González-Mariscal et al., 1998) indicated that trophallaxis can appear in multiple forms from momentary to intense, short to longer-lived, expressed across single or multiple contexts, and guided to various extent by olfactory cues, thereby setting the stage for the wide variability of trophallaxis in humans.

The second feature relates to the initiation of maternal care as the "resolution of an approach-avoidance conflict" (Rosenblatt, 1994), a conceptualization that resonates with clinical theory. Virgin rats find infant stimuli aversive, and thus, the initiation of maternal care requires a two-stage process, first suppressing the innate aversion to pups and then placing an incentive value on infant via MPOA-dopamine connectivity (Numan, 2007). Whether such approach-avoidance conflict typifies human bond formation is questionable – imaging studies show that human adults, parents and non-parents alike, find infant stimuli rewarding and respond with activation of dopamine reward circuits to stimuli involving infant pictures or videos (Caria et al., 2012; Mascaro et al., 2014; Montoya et al., 2012; Strathearn et al., 2008) – but it is possible that some echo of this ancient conflict plays a role in the neurobiology of high-risk parenting where the bonding process may be underpinned by conflict, such as postpartum depression or the cross-generation transmission of child abuse and neglect. Better understanding of this approach-avoidance conflict in humans may help construct interventions that can address it when the natural bonding process is disrupted.

Human parental behavior as a trophallaxis process

Human mothers, like rodents, are primed for the expression of maternal behavior and show it immediately after birth. The human species-specific parental repertoire includes gaze at infant face and body, expression of positive affect, "motherese" high-pitched vocalizations, and affectionate touch, which marks the human parallel of "licking and grooming" (Feldman and Eidelman, 2007; Feldman, 2012a, 2012c). Like rodents, the mother's postpartum repertoire is impacted by the oxytocin system and is related to factors such as breastfeeding (Feldman and Eidelman, 2003) and levels of peripheral oxytocin (Gordon et al., 2010a). Finally, like rodents, experiences within the mother-infant unit enable young to become members of their social niche, partly via the effects of maternal behavior on the organization of the infant's oxytocinergic system (Hammock, 2015; Weisman et al., 2012). The buffering effects of maternal presence and behavior on the infant's stress response, glucocorticoids receptor distribution in the hippocampus, and amygdala activation patterns (Hofer, 1995; Meaney, 2010; Sullivan and Holman, 2010) are similarly echoed in human children's amygdala response to maternal presence (Tottenham, 2012) and cortisol patterns shaped by early maternal touch-and contact (Feldman et al., 2010d, 2014a).

Yet, human parenting follows a long line of evolutionary progress and the expression of parental behavior in humans differs from that of other mammals in substantive ways, not only in discrete behaviors. Unlike other mammals, human mothers coordinate the expression of their postpartum behavior with the infant's social readiness. There are large individual differences in the expression of human mothers' postpartum behavior, which are impacted by a range of maternal factors, such as depression (Feldman and Eidelman, 2003; Goodman, 2007), infant factors, such as neurodevelopmental maturation, particularly inborn regulatory abilities or regulatory support systems, such as cardiac vagal tone and sleep organization (Feldman, 2006; Feldman et al., 2004), and cultural contexts (Feldman et al., 2006; LeVine, 2002; Tronick, 1995). Longitudinal studies of mother-infant interaction that follow mothers and infants from the neonatal stage and across the first months of life describe how the maternal repertoire in the first days of life is transformed into interaction synchrony within the parent–infant unit during the third months of life in human-specific ways that underpin the development of the infant's social brain and maturation of neuroendocrine and autonomic systems critical to support participation in social life (Feldman and Eidelman, 2007; Feldman et al., 2010d, 2012; Gordon et al., 2010a; Lavelli and Fogel, 2002).

In several longitudinal studies we found that the amount of maternal postpartum behavior and its coordination with infant social readiness predict better child social outcomes across childhood, including greater child symbolic play and cognitive development at one year (Feldman et al., 2004), emotion regulatory capacities across the first five years (Feldman, 2006, 2009), more optimal trajectories of cognitive and social-emotional development across the first five years of life (Feldman and Eidelman, 2009), and higher executive functions, more adaptive cortisol stress response, and a more flexible autonomic response to stress by ten years (Feldman et al., 2014a). Most importantly, the amount of maternal postpartum behavior and its coordination with newborn state was found to predict greater behavioral synchrony in both mother-child and father-child interactions during the critical period for the development of social synchrony in humans: between 3 and 9 months of age (Feldman and Eidelman, 2007; Feldman, 2007d). This period, from the time human infants begin to take active part in social exchanges to the emergence of symbols in word and gesture, marks the most social period of human life (Stern, 1985; Trevarthen, 1993), when the infant's active involvement in the world can occur only through the sharing of social signals, particularly before the second six months when infants are not yet able to grasp, crawl, or manipulate objects. Coordination of social signals at that stage supports maturation of the social brain, enables a sense of initiation and agency, and helps consolidate the infant's cortisol and oxytocin response (Feldman, 2007a, 2015a; Feldman et al., 2010a, 2010d).

Interaction synchrony

Synchrony provides the basis for the human infant's capacity to participate in social life and charts the line described by Rosenblatt (2003) from "synchrony in the behavioral interaction between mother and young during their development until weaning" to participation in "social organizations". In multiple studies, our lab and others found that mother-infant synchrony during the critical period of three to nine months predicts higher emotion regulation, attachment security, symbolic competence, physiological organization of key support systems, and greater capacity for empathy across childhood and up to adolescence (Beebe et al., 2010; Feldman, 2007c, 2015a). This line from synchrony to social life charts the mammalian-general "trophallactic" process as expressed in human-specific ways.

Low intensity

The other two features of "trophallaxis" are also uniquely expressed in humans. First, Schneirla (1946, 1958, 1971) maintained that trophallaxis in the behavior of mothers and young requires "low intensity", possibly as only low intensity contexts enable the cross-generational

transmission of those unique signals that assemble into the social repertoire of each species, whereas more intense exchanges communicate danger, mark stress, or accompany the fulfillment of survival functions and activate other neurobiological systems. Such "low-intensity" exchanges highlight an important attribute of synchronous interactions between human parents and infants — the co-construction of positive emotions (Feldman, 2003). Although human infants can express negative emotions from birth and can regulate negative arousal via self-soothing behavior or gaze aversion from the first days of life, infants are only able to experience positive emotions within social contexts, during synchronous interactions that both build the infant's positive arousal, maintain it through reciprocal coordination, and regulate it by providing a matched framework that contains these highly arousing social moments. Furthermore, we found differences in the intensity levels infants experience during synchronous interactions with mother and father; mother-infant dyads cycle around states of neutral affect ("low intensity"), whereas father-child interactions contain quick, random peaks of positive arousal (Feldman, 2003, 2007c). Such low-intensity "trophallaxis", particularly with mother, may be required for the human infant to form the "secure base" described by Bowlby (1969), from which exploration of the outside world can emanate.

Low intensity may also construct a platform for biobehavioral synchrony between the physiological and behavioral processes of mother and young and may be needed for the release of oxytocin. OT has well-known anxiolytic effects in the brain (Neumann and Landgraf, 2012) and its effect on reducing arousal to "low intensity" may assist in initiating the first experiences of synchrony. This is observed, for instance, in Hofer's (1987) eloquent description of the moment-by-moment synchrony between mothers and pups' slow-wave sleep which is required for the mother's oxytocin release and the initiation of lactation.

Social Reciprocity

The final aspect of "trophallaxis" in humans, social reciprocity, defines a social relationship that integrates inputs from multiple partners and molds them into an interpersonal bond (Schneiderman et al., 2011; Feldman, 2015c). As social reciprocity provides the basis for social collaboration within groups, it is considered as a cornerstone of social life that must be experienced within the parent–infant bond during a sensitive period (Feldman, 2015a; Hauser et al., 2009; Rosenblatt, 1965). The main distinction between "interaction synchrony" and "social reciprocity" — two constructs that highlight the integration of two living organisms into a single functional unit, is the focus on microlevel temporality. Whereas synchrony defines a temporal relationship (concurrent or sequential) between events, particularly the second-by-second concordance of social signals between affiliated partners, reciprocity describes a more global mutual process that shapes infant development through long-term, large scale bidirectional influences of parent on child and child on parent (Sameroff and Rosenblum, 2006). Human research described long-term reciprocal processes by which the child dispositions and the global "parental context", including a range of factors from contextual conditions such as poverty to parental personality and relational style, shape each other over time from infancy to adulthood. Extent evidence demonstrates longitudinal cross-lagged parent-to-child and child-to-parent effects on children's self-regulation, executive control, emotional development, and psychopathology (Essex et al., 2002; Feldman, 2015c; Fox and Calkins, 2003; Kochanska, 2001; Sroufe, 2005).

Parent–offspring reciprocity as providing the interface of evolutionary adaptation is highlighted already in the work of Tinbergen (1963) and discussed in relation to multiple levels of inquiry including ontogenetic and phylogenetic reciprocal processes and causal as well as functional levels of explanations (Bateson and Laland, 2013). New evolutionary perspectives (Muller, 2007) describe the social transmission of traits as one pathway for the systematic generation of variations and emphasize reciprocal behavior among members, particularly within the parent–offspring exchange, as a central pathway of evolutionary adaptation.

Within the context of the immediate social interaction, social reciprocity addresses the "give-and-receive" components of social life that are formed in age-specific, person-specific, and culture-specific ways. Reciprocal interactions undergo substantial modifications from infancy to adulthood. In the first months of life, parents adapt to their infant's non-verbal signals to form the first social exchange. During the second year, parents and toddlers learn to engage in verbal-symbolic dialog, and in the preschool years increasing language skills enable dyads to co-construct affect-laden narratives. With the emergence of conceptual thought, parent–adolescent reciprocity marks the capacity to discuss conflicts with empathy and perspective-taking and accomplish joint action with pleasure. Finally, individuals develop reciprocal adult–adult relationships with children, friends, and partners that build on familiarity with the partner's nonverbal patterns and are expressed by mutual self-disclosure, empathy, and care (Feldman, 2007d; Feldman et al., 2013a; Schneiderman et al., 2012). Phenomenologically, reciprocal exchanges across the lifespan are defined by a give-and-receive quality, construct online from the inputs of both partners, and promote positive affect, security, and intimacy, charting the line from the first parent–infant reciprocal exchange to close social relationships in adulthood. In a recent study, we followed parents and infants at seven time-points from birth to ten years and assessed both parent–child reciprocity and child emotion regulation capacities using age-appropriate paradigms. We found that not only social reciprocity was stable over time, the degree of reciprocity at each time-point predicted the child's emotion regulation at the next assessment and vice versa, and this field of mutual influences between infant regulatory skills and parent–child reciprocity predicted child social outcomes at ten years, included greater empathy, higher RSA, lower behavior problems, and less accident proneness, further supporting the line from early reciprocity to social competencies (Feldman, 2015c).

Cultural variability and the trophallactic process

The wide cultural variability in the expression of human parental care attests to the immense flexibility and adaptiveness of the neurobiology of human parenting. Such variability supports our hypothesis that the adaptive human parental brain integrated primitive mammalian-general survival-related functions with large associative cortex not only to enhance survival across multiple contexts but also to buttress human-specific functions such as transmitting values, forming crossgenerational meaning systems, and preserving rituals. Because humans are among the very few species capable of forming habitats throughout Earth, the neurobiology of parenting that enables a unique state of neuroplasticity (Kinsley et al., 2015), evolved to accommodate multiple group living conditions, seasonal parameters, food availability, and population dispersion to ensure the successful rearing of infants.

Cultures shape the social brain of their members through the earliest interactions between caregiver and child. Parent–infant interaction patterns in different societies allow for more or less soothing contact, social gaze, active touch, or high positive arousal, thus shaping the environment-dependent brain mechanisms for social collaboration and affect regulation. Different levels of ongoing parent–infant contact are customary in different societies, with caregiving in traditional societies involving more contact in the form of co-sleeping, infant carrying during the day, and immediate response to infant cry, patterns that shape the infant's stress physiology (Bornstein, 2013; Kagitcibasi, 1996; LeVine, 2002; Rogoff, 2003; Super and Harkness, 1986; Shweder, 2003; Tronick, 1995; Whiting and Whiting, 1975). Although the development of global social milestones is universal, there are "cultural pathways" to the achievement social skills (Greenfield et al., 2003), implying that the specific parenting behaviors embedded in each culture support the emergence of general social competencies (e.g., sharing, modulation of aggression) in ways that enable children to navigate their social ecology (Jahoda, 1986; Werner, 1988).

Studies assessing distinct, micro-level parental behavior across cultures demonstrate marked differences in the three aspects of trophallaxis; *interaction synchrony*, *low intensity*, and *social reciprocity*. In our cross-cultural studies, we compared parent–child and triadic family interactions in Israeli and Palestinian families, cultures guided by independent versus interdependent philosophies (Kitayama, 2002) and individualistic versus collectivistic orientations (Triandis, 1989). We followed young, educated, dual-earner couples and their firstborn child in the two cultures from infancy to preschool age, highlighting not only differences in parenting behavior but also cultural pathways to social outcomes. As for *interaction synchrony*, in Western cultures guided by individualistic philosophies, parent and infant interact as two independent agents that match discrete social behaviors in the gaze, touch, vocal, or affect modalities. Interactions are clearly demarcated from the stream of daily life and parents use coordinated behavior to engage infants in active social moments or teach infants new skills, encouraging through such behaviors the independence, agency, and initiation required for social life in such societies. Even the position of social interactions differs— in Western societies parent and infant sit facing each other whereas in more traditional cultures parent and child maintain full physical contact but are not in face-to-face. Thus, whereas interaction synchrony occurs in individualistic societies through the coordination of visuo-facial social cues, in more traditional societies synchrony is expressed to a greater extent via touch, contact, and physical proximity and possibly involves processes of theromoregulation or transmission of olfactory cues (Feldman et al., 2006; Tronick, 1995).

With regards to *low intensity*, we and others found that in more individualistic societies interactions aim to elicit high positive arousal and contain frequent shifts between positive and neutral affect and more negative emotionality, whereas in more traditional cultures interactions are marked by "low intensity" neutral affect and their goal is to soothe infants. Thus, the degree of "affect matching", which involves more energy, is more predictive of social competencies in the preschool stage in individualistic as compared to collectivistic societies. On the other hand, factors such as the family's social support network, indexing its place in the social hierarchy, or the father's involved but controlling behavior predict greater child social competence in kindergarten in collectivistic societies (Feldman and Masalha, 2010).

Finally, we found that the overall degree of *social reciprocity*, harmony, coherent functioning, and collaboration in both parent–child interactions and the family microsystem was comparable in the two cultures, albeit achieved via different concrete behaviors (Feldman et al., 2001). For instance, the way families resolved daily conflicts – among spouses and between parents and preschoolers – was different, via dialog and compromise in the Israeli group and through mutual respect in the Palestinian group. Conflict dialog among spouses also differed: more emotion-focused among Israelis and more solution-focused among Palestinians. However, children growing in homes where spousal and parent–child dialog was more reciprocal according to the culture's norms showed less aggression toward peers in kindergarten, were able to resolve peer conflict without resorting to fights or withdrawing, and showed greater self-regulation across various daily activities (Feldman et al., 2010c). Such immense cultural variability in the parenting behavior *within the same species* is observed only in humans and demonstrates how discrete parenting behaviors fine-tune the parents' brain, the parent's behavior, and the infant's brain and social behavior, thereby preparing children to life within the social ecology.

Fig. 2 describes critical determinants of the parent–offspring bond that are differentially expressed in rodents, non-human primates, and humans.

As seen, the *context* of bonding in rodents in nest-bound, dependent on hormones of pregnancy, draws on maternal–infant physical contact, and is short-lived. In contrast, primates live in social groups that require navigation of multiple ranked relationships and bonding draws on recognition of extended social relationships and the formation of social expectations, which are based on memory of behavioral patterns among members and guide future behavior within a social order (Dunbar, 2014; Keverne and Curley, 2004). In addition, bond formation in rodents relies on *hormones* of pregnancy, birth, and lactation. Human bonding, while similarly initiated and supported by hormones, evolved to include multiple, more flexible pathways for the initiation of bonding that are based on bottom-up processes of hormonal release and may be triggered by active caregiving and mental commitment to the child and the parental role. This enables the formation of attachment bonds by individuals whose brain has not been primed by hormones of pregnancy, such as fathers, grandparents, adoptive parents, and non-kin caregivers and mentors. Such bonds based on large associative cortex can extend to social bonding within families, neighborhoods, cultures, and nations with each bond defining a unique process of social synchrony built on exclusive and gradually-acquired associations. Similar in this context is the role of breastfeeding. Although much research emphasized the positive effects of breastfeeding on the formation of mother-infant synchrony, the infant's social gaze (Feldman and Eidelman, 2003; Klahr et al., 2015) and the development of cognitive competencies up to adulthood (Johnson et al., 1996; Mortensen et al., 2002), while bonding in rodents critically depends on lactation, human mothers can bond to their infants in the absence of breastfeeding via multiple alternative pathways and other forms of caregiving.

In terms of *timing* and length of the social bond, the short bond of rodents (and the extremely brief bond in other species such as rabbit) extends in primates to form predictions of relationships among group members who may remain bonded. Human bonding, in comparison, is informed by the past and projects to the future and its representational nature enables the cross generational transmission of attachment patterns and the resonance of cultural heritage within current bonds in dyad-specific ways which are formed from the interplay of the familiar and the novel. Differences are also noted in the *sensory* basis of attachment bonds, which depend on olfactory cues in rodents, are visually-guided and touch-based in primates, and are visually-guided and multi-sensory in humans, where the initial touch-based interaction between parents and newborns in the postpartum period gives way to face-to-face interactions that are human-specific, build on the exchange of visuo-affective cues, and can impact the physiology of the interacting partners without physical contact (Feldman, 2015b). It is important to note here that such clear-cut distinction of vision from touch and olfaction, while potentially informative is schematic and over-simplified. For all mammals, maternal–infant touch and contact serve a primary role for biobehavioral maturation and provide the setting for lactation. In non-human primates, as well as in humans, olfactory and tactile cues serve a key role in the formation of attachment, may function as "hidden regulators" of maternal care (Hofer, 1987, 1995), and initiate a cascade that lead to the supremacy of social gaze reciprocity. For instance, Doucet et al. (2007) found that among 3–4 day-old infants odor from breast led to greater infant social gaze and less crying, and 4-month old infants looked longer at faces when exposed to their mother's odor (Durand et al., 2013), suggesting that olfactory cues direct and provide an underlying support to the infant's social gaze behavior. In a decade-long study, we provided full maternal-infant bodily contact in a Kangaroo Care position (a position that integrates touch, odor, proprioception, vision, and audition) to premature neonates who were deprived of full maternal contact and found profound effects of early contact on the development of maternal-infant bonding, gaze synchrony, social outcomes, and stress management until ten years of age (Feldman et al., 2014a, 2014b, 2014c, 2014d). Yet, by the time human infants reach their third month, face-to-face interactions guided by gaze become the prototypical platform for social exchange and mother and infant can coordinate physiological processes, such as synchronizing heart rhythms, through visuo-affective social cues without the need for physical contact (Feldman et al., 2011b). Finally, in both affiliation *hormones* and the parental *brain*, the human-specific expression is based on processes observed in rodents, upon which more

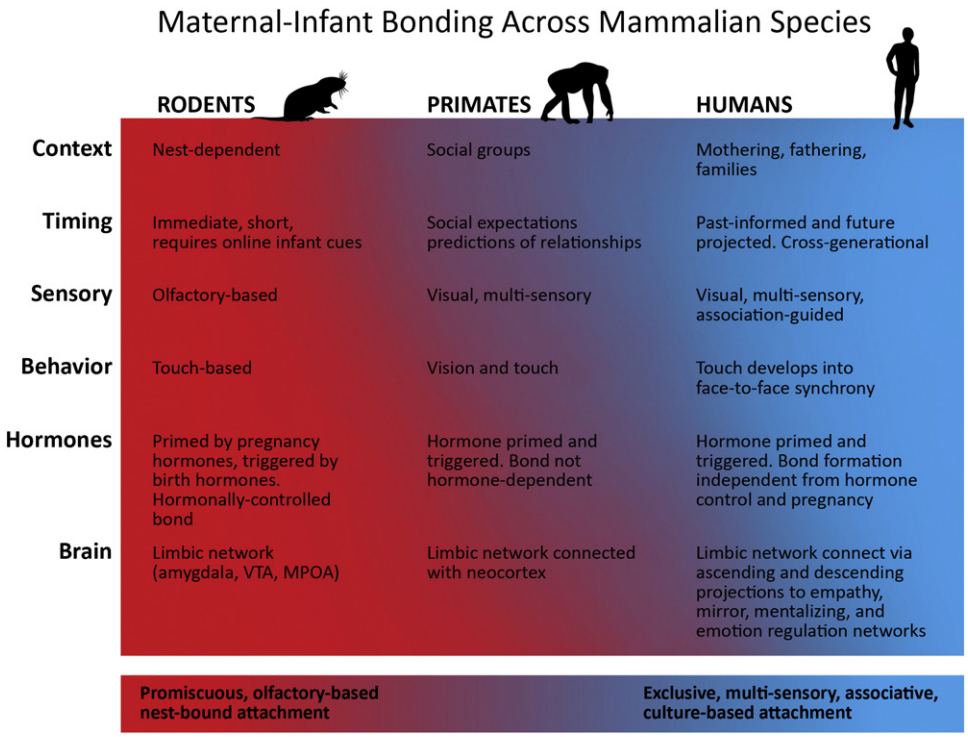

Fig. 2. Features of Maternal-Infant Bonding in Rodents, Primates, and Humans.

complex processes are constructed, and the system maintains some evolutionary-ancient features, which are integrated and extended in multiple ways, as discussed below.

Oxytocin and bonding: from vole to man

Much research on the neurobiological underpinning of maternal care in animal models emphasized the dynamic feedback loop of endocrine and neural processes, what Bridges (2015) calls an endocrine-neurological link that supports the expression of maternal care. Thus, while the following discussion is divided to hormones and brain, it is clear that they are intimately linked and mutually influencing. Similarly, the OT system discussed here does not work alone and a host of hormones and neuroendocrine systems, including hormones of pregnancy and parturition (estradiol, progesterone, prolactin), serotonin, dopamine, noradrenaline, cortisol/CRF, testosterone, and vasopressin interact to support bond formation in mammals and the complex interactions among these systems is only beginning to be investigated. Finally, brain and hormones function within a feedback cycle in relation to sensory and motor stimuli the mother receives from her infant, and these should receive much further research.

Oxytocin and bonding in animal models

Current studies detailing the pervasive involvement of OT in human social functions mainly originated from two lines of research; studies implicating OT in bond formation in rodents and herding animals (Keverne and Kendrick, 1992; Lévy and Keller, 2009; Lévy et al., 1995; Neumann et al., 2013; Pedersen et al., 1982; Rosenthal, 1991) and comparative research of the vole, particularly studies addressing differences in OT receptor distributions in monogamous and polygamous closely-related vole species that show marked differences in sociality, including gregariousness, father involvement, promiscuous versus monogamous pair bonds, and extended versus limited parental care (Donaldson and Young, 2008; Insel and Young, 2001). These studies established the critical involvement of OT in mammalian sociality (Carter, 2014) and opened a plethora of research linking OT with human social functions as well as in psychiatric conditions associated with social dysfunctions, including autism, schizophrenia, social anxiety, and depression (Bakermans-Kranenburg and van Ijzendoorn, 2013; Heim and Binder, 2012; Macdonald and Feifel, 2012; Preti et al., 2014).

Following two decades of research, however, it became clear that OT receptors are highly species specific, displaying not only large species variability between rodents, primates, and humans but also within a rodent species in relation to living conditions, seasonality, and various social "modules" related to social life within that species (Hammock, 2015; Stevens et al., 2013). Since the mechanisms by which OT supports bonding and social life are species-specific, they should be tested in humans. Yet, several important features of the OT system chart mammalian-general mechanisms that underpin the formation of attachment bonds. The first is the time element, addressing both the temporal organization of processes during pregnancy and parturition and the pulsatile nature of OT release, which serves a critical role in neural plasticity (Feldman, 2015a). During pregnancy the OT system undergoes significant transformation. In late pregnancy K-opiods, co-produced by OT neurons, inhibit OT release in the posterior pituitary to prevent premature labor, which decreases toward the end of pregnancy to enable action-potential trigger of OT release during parturition. During labor the OT system undergoes major reorganization that results in OT release from magnocellular neurons in the hypothalamus coordinated with dendritic release that occurs via binding of OT autoreceptors and coordinated burst-firing. OT pulsatile release from the posterior lobe is controlled by opioid-based mechanisms, which can coordinate birth according to favorable environmental conditions, charting the first integration of environmental events and the OT system in the life of the newborn (Brunton and Russell, 2008). OT during birth causes GABA signaling to change from excitatory to inhibitory and the OT surge at birth enables synchrony of fetal hippocampal neurons and the transition from prenatal to postnatal life (Bali and Kovacs, 2003; Blyth et al., 2000). Following childbirth, the maternal OT system reorganizes

on the basis of ongoing stimuli from the infant. OT release in the maternal brain functions to sensitize a limbic network implicated in reward and emotionality, including the ventral tegmental area (VTA), nucleus accumbens (NAcc), insular cortex, hypothalamus, and amygdala, structures implicated in human parental care (Ebner et al., 2005; Feldman, 2015b; Neumann et al., 2006; Li and Fleming, 2003). OT functions as a modulator within this network, which is critical for survival, emotionality, and motivation (Sokolowski and Corbin, 2012).

Another expression of the temporal component in OT functionality is pulsatility. OT is released in burst-firing pattern from magnocelular neurons and the synchrony of bursting neurons in the paraventricular nucleus (PVN) and supraoptic nucleus (SON) – the two major sites of OT production in the hypothalamus – facilitates neural plasticity (Lightman et al., 2001; Uvnas-Moberg, 1997). The rhythmic nature of OT activity supports maturation of circadian rhythms, enables connectivity of OT with CCK, glutamate, and GABA neurons, and supports OT effects on regulating the HPA stress system (Theodosis et al., 1986). In juvenile rats, the surge and decline of the pulsatile release of OT during play provides the biological platform for the formation of social preferences that enable navigation in the social world (Nelson and Panksepp, 1996). It is suggested that the pulsatile nature of OT release plays an important role in enabling neural development, particularly during critical periods in the maturation of the social brain (Feldman, 2015a).

Recent research has implicated OT in processes of experience-dependent plasticity, particularly as related to the development of social recognition, which in rodents is olfactory-based and supports the formation of olfactory-dependent bonds. Gur et al. (2014) examined the role of OT in the acquisition of long-term social recognition memory through connectivity between the olfactory system and the medial amygdala (MeA) and described the role of OT in memory consolidation via mechanisms of synaptic long term depression. Exogenous OT administration increased long-term depression in the olfactory-MeA pathway whereas OT antagonist inhibited this process. It thus appears that plasticity at the molecular level requires first depression of general input and then activation of a specific synaptic connection. These findings lends support to Rosenblatt's notions (1994) that bond formation involves, as a first step, reduction of response to aversive social stimuli and then approach and bonding, and to studies that implicates OT in this process by reducing aversion detected by the olfactory system, prior to increasing network connectivity to enable a specific response to the attachment target (Bosch et al., 2005, 2006). Although, as described above, olfactory cues may not be as central to human bonding, the same limbic network supporting olfactory-based bonding, including the hypothalamus, NAcc, bed nucleus of stria terminalis, lateral septum, and MeA, also underpins human social behavior and OT functions as a modulator of neural activity within this system. Sokolowski and Corbin (2012) suggest that humans are wired for social behavior via activity of this limbic network that functions to regulate critical survival-related behaviors in the service of social bonding.

Finally, the special mode of OT peptidergic dendritic release is a key feature in its priming effect that enables the reorganization of the social brain on the basis of early attachment experiences, particularly the limbic network modulated by OT. Such mode of functioning in the brain –as both a neuropeptide and hormone – enables a very crude administration of OT without temporal or spatial sophistication to cause coherent functional effects on behavior that are long-lasting and self-sustaining. While neurotransmitters transmit information from one neuron to another, peptides can transmit information between populations of neurons and can act across great distances. This enables experiences occurring during an early sensitive period for social growth to reorganize neural networks. Thus, the priming of social experiences during sensitive periods may be the mechanism by which a diffuse signal releasing OT, such as interactive synchrony, can cause a coherent, long-lasting effect on the development of the mature animal and its social functioning (Ludwig and Leng, 2006).

Oxytocin and bond formation in humans

Consistent with the focus on human-specific aspects of attachment, I present a very brief summary of our studies on OT and human bonding (for more extensive reviews see Feldman, 2012a, 2015a). This selective review describes how mammalian-general features are interspersed with human-specific components to define OT's support of human social bonds.

The involvement of OT in human attachment bonds has been tested across multiple expressions of the system; peripheral OT levels in plasma, saliva, and urine; OT administration to parents and couples; genetic variability on the oxytocin receptor gene (*OXTR*) that supposedly tap a more "efficient" functioning of the brain oxytocin system through allelic variations; and imaging the parental brain and measuring activations in OT-rich brain areas. Overall, it was found that periods of bond formation, such as becoming a parent or falling in love, are accompanied by increased OT production which is expressed in higher baseline plasma OT (Gordon et al., 2010a; Schneiderman et al., 2012); that baseline OT levels in plasma are highly stable within individuals throughout pregnancy (Feldman et al., 2007) and across the first years of parenting (Feldman et al., 2013b); and, consistent with the propositions of attachment theory and research in rodents, OT functionality is transmitted from parent to child (Feldman et al., 2010b; Weisman et al., 2012) and is transferred from the parent–infant attachment to the first attachment relationship the child forms with a close friend outside the family (Feldman et al., 2013b).

Importantly, OT support of human bond formation – as described by the "parenting as behavior" approach – is behavior-based, employs bottom-up mechanisms, and depends on the degree of interaction synchrony within attachment bonds. Mother and father peripheral OT in plasma and saliva and variability on the *OXTR* were found to be associated with greater parent–child reciprocity and synchronous behavior (Feldman et al., 2011a, 2012). However, OT is related to the parent–specific repertoire, in mothers to more affectionate parenting that includes medium arousal (low intensity trophallaxis), mutual gaze, "motherese" vocalizations, and affectionate touch, while in fathers to more stimulatory touch, high positive arousal, and exploratory focus (Gordon et al., 2010a). Moreover, high levels of affectionate contact in mothers and stimulatory contact in fathers increased maternal and paternal OT levels respectively during a fifteen minute "play and touch" interaction (Feldman et al., 2010a). OT administration to fathers dramatically increased father salivary OT, but, in parallel, also increased the child's OT levels and this synchronous increase of OT was mediated by subtle changes in social reciprocity, including longer durations of mutual gazing, touch, and joint exploration (Weisman et al., 2012). Similar behavior-based OT production was found during pair-bond formation in humans. We found significant increase in plasma OT during the first three months of falling in love, which correlated with observed social reciprocity between lovers, including emotional attunement, affectionate touch, and expression of positive emotions (Schneiderman et al., 2012). Similarly, more "efficient" allelic variation on five *OXTR* SNPs combied into a cumulative OXTR index was associated with more empathic behavior during a support giving paradigm between new lovers (Schneiderman et al., 2014a). Finally, in the third attachment bond in humans – close friendships – a similar link of OT and reciprocal social behavior was found. Three-year old children displaying more social reciprocity during interactions with their best friends had higher salivary OT (Feldman et al., 2013b).

Another important function of the OT system is providing a template for the integration of multiple neuroendocrine systems that jointly support bond formation and its impact on health, stress management, and autonomic functioning (Carter, 2014). Possibly, this integrative function renders the OT system a key factor in the support of attachment bonds. Several examples for such integration emerged from our research. Maternal postpartum behavior was triggered, as in rodents, by OT levels observed throughout pregnancy, but at the same time, the amount of

maternal behavior was independently predicted by lower cortisol across the same period and the two systems likely interacted across pregnancy to prime maternal behavior while protecting the fetus from the effects of maternal glucocorticoids (Feldman et al., 2007). In fathers, associations were found between levels of OT and prolactin. Both hormones supported father-child social play in different ways, OT correlated with person-oriented social play and prolactin with object-oriented exploratory play (Gordon et al., 2010b). OT administration to fathers, in addition to dramatically increasing OT levels in father and child, also altered father's testosterone and cortisol levels, both as a function of father interactive behavior in the gaze, affect, vocal, and touch modalities and the amount of social reciprocity between father and infant (Weisman et al., 2013, 2014). Finally, while the important role of arginine vasopressin (AVP), a closely related nonapeptide, in mammalian bonding has been emphasized (Donaldson and Young, 2008), little research addressed the role of AVP in human parenting. Measuring plasma OT and AVP in mothers and fathers, we found that the two hormones showed mild but significant correlation. OT correlated with more affectionate touch, social gaze synchrony, and parental (maternal and paternal) response to infant social bids by augmenting social salience (e.g., inducing high joint laugh). On the other hand, parental AVP was associated with stimulatory contact, joint attention to object, and response to infant social bids by increasing object salience (Apter-Levi et al., 2014). We similarly found that the more efficient variant on the AVPR1a in war-exposed young children, as well as in their mothers and fathers, functioned as a resilience buffer and was associated with lower PTSD chronicity from early to middle childhood (Feldman et al., 2014b).

Bi-directional effects of multiple hormones and relational behavior during bond formation were also found in new lovers. Plasma levels of five hormones — oxytocin, prolactin, cortisol, DHEA, and testosterone, were measured in new lovers, and their behavioral empathy and hostility were coded during a conflict discussion. We were particularly interested in how the interchange of hormones and behavior during this pair bonding period leads to the consolidation or termination of the romantic bond nine months later. Results showed that cortisol and DHEA had direct actor effects; the higher the levels of cortisol and DHEA, the greater hostility that individual expressed during conflict discussion. Testosterone and cortisol had a combined actor-partner effect; High testosterone predicted greater hostility only when the partner also had higher testosterone but not when the partner had low testosterone. Similarly, cortisol predicted low empathy only in the context of high partner's cortisol, highlighting the cross-dependence between partners' hormones and social behavior. However, OT was the only hormone to show a partner effect only: individuals whose partners had higher OT showed greater empathy, thus OT impacted the partner's not the individual's behavior. Interestingly, relationship breakup was predicted by low empathy, not by increased hostility. While these findings do not show causality and it is possible that individuals select partners whose OT levels match their behavior, the findings highlight the OT system as particularly sensitive to social behavior among attachment partners (Schneiderman et al., 2014b).

Finally, disruptions in OT functionality were found to mediate, in part, the cross-generation transfer of stress and psychopathology. For instance, maternal postpartum depression has been associated with lower peripheral OT, as observed in plasma, saliva, and urine and high-risk variant on *OXTR* (Apter-Levi et al., 2013; Meaney, 2001; Skrundz et al., 2011). Consistent with the notion that OT functionality is transferred from parent to child via the expression of parenting behavior, we found that children of chronically depressed mothers had lower salivary and urinary OT, that maternal OT correlated with more sensitive and less negative parenting, and that children of depressed mothers were four times more likely to receive a psychiatric diagnosis by the time they entered school. However, when mothers' OT functionality was more intact, as observed in higher urinary OT or more efficient variant on the *OXTR*, the negative impact of maternal depression on child's propensity to psychopathology and disruptions to the child's OT response was significantly attenuated (Apter-Levi et al., 2013; Krol et al., 2013). Low salivary OT has also been found in children diagnosed with anxiety disorders, particularly separation anxiety (Lebowitz et al., 2015); orphanage-reared children showed lower urinary OT response to parent–child interactions (Fries et al., 2005), and the increase in urinary OT following interactions among foster children was associated with foster-parent sensitivity (Bick et al., 2013). These findings suggest that the OT system may provide one pathway for the cross generation transfer of psychiatric vulnerability, alongside other more well-researched pathways such as HPA-axis functioning. Interestingly, assessing salivary OT in mothers, fathers, and preschoolers with autism spectrum disorders (ASD), we found that while no differences in parental OT was found children with ASD had significantly lower baseline OT. However, after 20 min of parent–child social contact, these low levels were normalized, but returned to baseline 10 min after contact terminated, further supporting the link between parental presence and the child's OT response in the case of a well-known biologically-based disruption to the OT system (Feldman et al., 2014c).

Oxytocin receptor gene (OXTR) and human parenting

The ancient OT molecule is thought to originate from an ancestral vasotocin peptide via gene duplication in jawed vertebrates more than 600 million years ago and appears in different variants in all vertebrates and some invertebrate species (Beets et al., 2013; Donaldson and Young, 2008; Grimmelikhuijzen and Hauser, 2012). The OT-family molecule affects both peripheral tissues implicated in reproduction, homeostasis, and energy balance as well as neuromodulation of social behavior, stress regulation, and associative learning in species ranging from nematodes to humans. Cells producing OT-related peptides are found in similar neurosecretory brain centers across species and taxa and are characterized by a typical “molecular fingerprint”(Chang et al., 2013). Gene regulatory features of the ancient OT-type neuronal cell suggest dual sensory-neurosecretory properties, implying that the ancient OT signaling system functioned to convert sensory inputs into online behavioral response supported by peptidergic secretion. In humans, the oxytocin receptor gene (*OXTR*) is a 389-amino acid polypeptide with 7 transmembrane domains and belongs to class I G protein-coupled receptors that is located at 3p25–3p26.2 (Gimpl and Fahrenholz, 2001). The length of the gene region is 17 kb and it consists of three introns and four exons.

Several tagging single nucleotide polymorphisms (SNPs) have been associated with parenting behavior in humans. Mothers carrying the *OXTR* rs53576 GG genotype displayed greater sensitivity during interactions with their children (Bakermans-Kranenburg and van Ijzendoorn, 2008). Two neurophysin-I (OXT) SNPs, rs2740210 and rs4813627, were linked with more “motherese” vocalizations during mother-infant interactions (Mileva-Seitz et al., 2013). Risk alleles on two OT-pathway genes *OXTR* (rs2254298 and rs1042778) and *CD38* (rs3796863), an ectoenzyme critical for the release of peripheral OT, were each associated with lower plasma OT, demonstrating some coordination between central and peripheral indices of OT. Reduced plasma OT and *OXTR* and *CD38* risk alleles predicted less parental touch and the interaction of high plasma OT and low-risk *CD38* alleles predicted longer durations of parent–infant gaze synchrony (Feldman et al., 2012). In a family-based study of 1000 twins and their parents, *OXTR*rs53576 AA homozygous mothers were less warm compared to G carriers (Klahr et al., 2015). Following a cohort of parents and their firstborn infants from birth to three years, we found that parent–infant synchrony at 1 and 6 months and mothers' *CD38* alleles predicted children's peripheral OT and higher social reciprocity during interactions with their best friend at three years (Feldman et al., 2013b). Finally, following a cohort of children from infancy to adulthood continuity in attachment security from 1 to 26 years and transfer from parental to romantic attachment was found only among *OXTR* rs53576 GG homozygous

(Raby et al., 2013). *OXTR*rs2254298 A allele was associated with infant attachment security, but only among non-Caucasian infants (Chen et al., 2011). These findings point to the involvement of OT-pathway genes in parent–child interaction, parental quality, and the continuity of attachment and suggest that some OXTR genotypes may open children to greater susceptibility to environmental influences, for better and for worse (Belsky and Pluess, 2013).

Overall, it appears that the neuroendocrine underpinnings of parent–infant bonding combines highly conserved elements and human-specific features, similar to the pattern observed for parental behavior. The increased OT level across pregnancy primes human mothers for the expression of maternal behavior, and in the second phase of bonding that involves the maintenance of attachment bonds, OT and synchronous behavior mutually shape each other over time. However, the initiation of parenting in humans is not dependent on hormones of pregnancy and emerges in fathers and other caregivers via bottom-up behavioral processes and cortical, not subcortical brain networks. Bonding is molded by cultural patterns transmitted across generations and is controlled by vision that integrates multi-sensory inputs into a synchronous dialog that can alter biology and behavior through dyad-specific careful adaptations of the parent to a specific child at a particular moment of their relationship.

The parental brain; from mammalian maternal brain to human caregiving network

Evolution of the parental brain – from the subcortical structures that support mammalian mothering to the extensive integration of limbic, paralimbic, and cortical structures that chart the human parental caregiving network – resembles that of the oxytocinergic system: evolutionary-ancient conserved components are integrated with higher-order human-specific functions to enable flexibility, variability, and independence from the constraints of time and context.

The parental brain in animal models

The following presents a very brief summary of the mammalian maternal brain and more extensive discussions appear elsewhere (for review see; Feldman, 2015b; Kinsley et al., 2015; Neumann and Landgraf, 2012; Olazábal et al., 2013). Rodent studies on the maternal brain — originating with Rosenblatt's studies (Rosenblatt and Lehrman, 1963; Rosenblatt, 2003; Rosenblatt et al., 1994), addressed the critical role of the medial pre-optic area (MPOA) in the hypothalamus for the initiation of maternal behavior. Primed by the hormones of pregnancy and triggered by the increase in oxytocin and prolactin during parturition, the MPOA projects to the mesolimbic dopamine circuits, including VTA and NAcc, which increase maternal motivation to care for infants and place incentive value on stimuli from the child (Dobolyi et al., 2014; Numan and Stolzenberg, 2009; Shahrokh et al., 2010). The MPOA also projects to the amygdala, which increases maternal vigilance for infant safety (Been and Petrulis, 2012; Sheehan et al., 2001). These three structures, the oxytocin-producing hypothalamus, amygdala, and the limbic dopamine pathway, including both the mesolimbic and nigrostriatal pathways, constitute the central network that underpins maternal care in rodents, a network in which OT functions as a modulator (Coria-Avila et al., 2014; Insel and Young, 2001). From a comparative standpoint, however, rodent studies described maternal care as mainly subcortical, hormonally-controlled, and modulated by olfactory cues.

The human parental brain

The parental brain in healthy mothers and fathers

Investigations into the human parental brain typically used fMRI technology to test parents' brain response to auditory, visual, or multimodal infant stimuli, such as infant crying, pictures, or movies, often comparing "own infant" to a standard infant or control condition (for review see Swain et al., 2007, 2014; Feldman, 2015b). Most studies examined mothers, few tested fathers, and several examined non-parents' brain response to infant cues. From this body of research, several brain areas were shown to activate in response to infant cues and those areas globally chart a "parental caregiving" network, which integrates functioning of several interconnected networks. The subcortical mammalian caregiving network seen in rodents, involving the amygdala, hypothalamus, and dopaminergic reward circuit, was found to activate in nearly every study of human parents, pointing to the conserved nature of parental care. However, these structures were also shown to be connected via multiple ascending and descending projections to several cortical networks that form the human social brain, enabling both top-down and bottom-up processes. These include areas in the *empathy network*, consisting of structures in the anterior insular-cingulate cortex that enable parental resonance with infant pain and emotions (Fan et al., 2011), structures in the *mirror neuron* system (IPL, IFG, SMA) that enable parents to represent infant action in their own brain (Rizzolatti and Craighero, 2004), areas in the *mentalizing network* (STS/STG, precuneus, PCC, TPJ, and vmPFC) that support the parent's capacity to read the infant's nonverbal signals and infer his/her intentions (Bernhardt and Singer, 2012; Lenzi et al., 2009), and structures in the latest-evolving *emotion regulation* network (frontopolar cortex, mOFC) that allow parental inhibition, multitasking, and the selection of appropriate parental action from multiple options to implement long-term goals based on cultural philosophies, social practices, and multigenerational patterns.

Several studies showed associations between activations of areas in the parental brain with parent–infant behavioral sensitivity and synchrony and with oxytocin levels, highlighting the inter-connected nature of brain, hormones, and behavior in humans. Mother-infant synchrony – the coordination of maternal behavior with infant social readiness- and maternal intrusiveness- the excessive expression of maternal behavior when infants signal a need for rest – were observed in mothers of 4–6 month old infants during a home visit, maternal brain was imaged, and plasma OT assayed. Synchronous mothers showed greater activation of the NAcc, a key structure of the limbic dopamine circuit, and intrusive mothers displayed higher amygdala response, and only among the synchronous mothers, activation of limbic structures correlated with plasma OT. Moreover, among synchronous mothers NAcc activity was functionally coupled with areas in the mirror and mentalizing network, indicating that behavioral synchrony is associated with an underlying "reward" coloring of parenting activities and coherence among parenting-related brain, hormones, and behavior (Atzil et al., 2011). Similar associations between limbic reward areas, plasma OT, and sensitive mothering were described by Strathearn et al. (2009), and were associated with the mother's attachment representations to her own parents. Conditions that support bonding, such as vaginal versus Cesarean delivery and breastfeeding were associated with greater activations in the parental caregiving network in response to infant cry sounds and among breastfeeding mothers, such activations during the first month of parenting predicted greater maternal sensitivity at four months of age (Kim et al., 2011; Swain et al., 2008).

Only a handful of studies examined fathers' brain response to infant cues and only two studies, both from our lab, compared mothers' and fathers' fMRI responses in the same study. Both studies found greater amygdala activation in mothers and greater cortical activation in fathers, suggesting that the hormones of pregnancy may chart a unique limbic path to parenting in mothers, which in fathers is constructed via cortical networks and active caregiving behavior. In the first study, mothers and fathers observed the same video of their infant playing alone. Assessing brain-to-brain synchrony in the parents' response to their own infant, it was found that mothers and fathers synchronize activity in the right insula, which was functionally coupled with areas in the mirror, empathy, and mentalizing networks. These findings suggest that parents may coordinate brain response online to assist rapid and

appropriate parental response to the infant's needs and this may maximize their effort toward increasing infant survival (Atzil et al., 2012). We suggest that mechanisms of brain-to-brain coupling, which likely have human-specific features, probably played a critical role in the evolution of the human family.

In the second study (Abraham et al., 2014) we attempted to separate the effects of parents' sex from that of primary caregiving role. Three groups of first-time parents were recruited: mothers (primary caregivers), heterosexual fathers (secondary caregivers), and primary-caregiving homosexual fathers raising infants within a partnered relationship without maternal involvement from birth. Overall, areas in all networks of the parental brain were activated across the three groups and in most areas, no differences were found among parents. Yet, mothers showed a fivefold increase in amygdala activation compared to secondary-caregiving fathers who exhibited higher activation of the STS, a key structure of the *mentalizing* network. Intriguingly, primary-caregiving fathers showed high amygdala activation like mothers, alongside high STS activation like secondary-caregiving fathers. Furthermore, only among primary-caregiving fathers we found functional connectivity between the amygdala and the STS, indicating that the paternal pathway recruits the maternal pathway to increase infant survival in the absence of mothering. The brain-hormone-behavior correlations, however, showed parent–gender effects. In mothers, both oxytocin and synchrony correlated with limbic (amygdala) and paralimbic (ACC) areas, whereas in fathers, they were associated with structures in the mentalizing network. These findings support the hypothesis on the distinct neural paths to maternal and paternal care in humans, and highlight the flexibility of the human parental brain which enables fathers to establish the neurobiology of parenting via cortical tuning to infant needs and day-by-day involvement in active caregiving.

Another mechanism of brain plasticity in humans involves increase in gray matter, observed in mothers and fathers during the first months of parenting. Gray matter increase was found in mothers from the first to the fourth month postpartum in subcortical areas, such as the amygdala, hypothalamus, thalamus, and substantia nigra, as well as in cortical structures, including the prefrontal cortex, postcentral gyrus, and inferior parietal lobule. These gray matter increases were related to the mother's positive perception of the infant and the caregiving role (Kim et al., 2010). In fathers, gray-matter increase was found in the amygdala, striatum, hypothalamus, subgenual cortex, lateral PFC, and STG. However, fathers also showed gray-matter decrease in orbitofrontal cortex, PCC, and insula and the decrease in OFC correlated with the expression of more paternal behavior, perhaps pointing to the need for modulating cortical activity in fathers in order to engage in fathering behavior (Kim et al., 2014a, 2014b).

The parental brain and psychopathology

Research is beginning to address the effects of adversity on the maternal brain and only a handful of studies examined brain response of mothers suffering from various psychopathologies, including postpartum depression, trauma, or substance abuse. Maternal postpartum depression has mainly been linked with reduced activation in areas of the parental brain in response to infant cues, particularly in reward and empathy circuits (Laurent and Ablow, 2012, 2013; Moses-Kolko et al., 2010; Swain et al., 2008). Maternal depression has also been associated with reduced/altered connectivity, expressed as decoupling of typical connectivity patterns such as between the amygdala and PCC (Chase et al., 2014), which suggests limitations on plasticity. Maternal depression has been repeatedly associated with diminished sensitivity and synchrony and activation in these areas is linked with increased maternal sensitivity and synchrony during mother–infant interactions (Atzil et al., 2011; Feldman, 2015b; Swain et al., 2007; Strathearn et al., 2009). With regards to maternal trauma or heightened maternal anxiety, some studies showed elevated amygdala activations (Schechter et al., 2012) whereas others found blunted amygdala activation (Kim et al., 2014a, 2014b). Substance abusing mothers showed reduced activations in areas implicated in vigilance (amygdala, parahippocampus) and cognitive control, (dlPFC (Landi et al., 2011). Yet, the brain basis of pathological parenting has received extremely little attention and much further research is needed to understand how various psychopathologies are expressed in unique brain profiles.

Overall, the findings for parenting behavior, hormones, and brain activation patterns demonstrate the immense plasticity and diversity associated with human parenting. Human parental care is expressed via the entire neuroaxis, builds on a line of incremental progress, and utilizes multiple caregivers to form unique adult–infant bonds in support of childrearing. In the three main aspects of parenting – behavior, hormones, and brain – evolutionary-recent features co-opt and are superimposed upon ancient functions, which are integrated to enable the most critical role of evolutionary adaptation: the successful rearing of children.

Coda: from Hobbes to Lorenz

In a final note of reflection upon the work of Rosenblatt and his contemporaries – the generation that brought the neurobiology of parental care into the forefront – I wish to consider the new viewpoint on human nature that may arise from research on the neurobiology of parenting. This pertains specifically to the question of whether Man is by nature self-serving, egotistical, and power hungry, motivated to accumulate and control as much resources in his ecology, and only culture provides a (thin) layer to protect against these "animalistic" drives and enable social life.

Hobbes, the seventeen century philosopher and political thinker may be the person most embodying this approach, as depicted in his famous book Leviathan (Hobbes, 1968). Left to his own devises, Man's nature would lead to a state of "war of all against all" (*bellum omnium contra omnes*) that can be handled only through tight state control that permits individual protection, civil societies, and cultural and scientific progress. As Hobbes' model is deeply ingrained in Darwin's evolutionary perspective, life scientists guided by the grand theory of the biological sciences tend to view human nature as primarily ruthless and the arena where life takes place as a constant struggle where only the fittest survive. Social abilities are viewed as secondary and later-developing "garments", a collection of fragile skills that must be carefully cultivated by education, tended through cultural organizations, internalized as moral or religious laws, and maintained via strict and continuous surveillance.

While any random look at human history would attest to such grim view of human nature, perhaps the deepest contribution of this generation of scientists who directed their creative lens to the biological basis of attachment, is by demonstrating that social collaboration, interactive synchrony, and the capacity for reciprocity are no less "biological" and "primary" than the brutal acquisition of resources. With Lorenz' seminal findings (Lorenz, 1935), it became clear that bond formation, social niches, and the give-and-receive components of life in social groups are just as rooted in biology and just as primary for survival. This research not only initiated the field of ethology, but formulated a language to describe social life as fundamental, instinctual, and rooted in evolution. It put forward the notion that our social instincts stand at the same primitive level as our instinct to dominate, accumulate, and conquer. Collaboration among members of a social group and acts of "altruism" may be observed throughout the animal kingdom and across the evolutionary ladder in species ranging from nematodes to humans. Interestingly, throughout evolution, such social "abilities" are supported by the ancient oxytocin-family molecule, which originated from the initial vasotocin molecule nearly 700 million years ago (Yamashita and Kitano, 2013; Feldman et al., 2015).

From a philosophical perspective, the mind-body polarity is expressed in our generation primarily in the field of neuroscience and mainly in relation to the mind-brain duality (Bennet et al., 2007).

Current models in neuroscience tend to go back to Spinoza on this matter (see *Looking for Spinoza*, Damasio, 2003) and away from Descartes. For Spinoza, body and mind, God and nature, the physical and the mental were one and the same, and their apparent duality were related more to the observer's point of view than to a true schism. Looking at one pole makes the other recede into the background, similar to the figure-ground duality of the human visual system or the particles-wave duality of Heisenberg's uncertainty principle. One gift we received from Rosenblatt and his generation is the ability to put the social components of human biology in the foreground. This enables us to place – even for a very brief moment – the ruthless elements of Man's nature into the background.

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