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PARENT–INFANT SYNCHRONY: A BIOBEHAVIORAL MODEL OF MUTUAL INFLUENCES IN THE FORMATION OF AFFILIATIVE BONDS

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Synchrony, a concept coined by the first researchers on parenting in social animals (Rosenblatt, 1965; Schneirla, 1946; Wheeler, 1928), describes the dynamic process by which hormonal, physiological, and behavioral cues are exchanged between parent and young during social contact. Over time and daily experience, parent and child adjust to the specific cues of the attachment partner and this biobehavioral synchrony provides the foundation for the parent–infant bond (Fleming, O'Day, & Kraemer, 1999). Affiliative bonds—defined as *selective* and *enduring* attachments—are formed on the basis of repeated exposure to the coordination between physiological states and interactive behavior within each partner, between partners, and between the physiology of one and the behavior of the other. Such social bonds, in turn, set the framework for the infant's emotional development and shape the lifelong capacity to regulate stress, modulate arousal, and engage in coregulatory interactions, achievements that are central components of the child's social–emotional growth (Feldman, 2007a). Moreover, the experience of biobehavioral synchrony in the first months of life sets the biological and behavioral systems that enable the child to provide optimal parenting to the next generation, thereby forming the cross-generation transmission of attachment patterns (Feldman, Gordon, & Zagoory-Sharon, 2010a).

During the sensitive period of bond formation, infants' brains are sensitized to the mutual influences between physiological systems, behavioral indicators, and their interactions. Studies in mammals propose that this process of synchrony—the system's sensitivity to the coordination of physiology

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and behavior in the two partners—spans the period of early gestation to weaning, which in humans is considered the period between early pregnancy and the end of the first year of life (Feldman, 2007b). During this time, infants must experience the synchrony between their own physiology and behavior and the mother's body, physical presence, and sensory cues (e.g., maternal touch, smell, heart rhythms) and the species-specific maternal repertoire for optimal social and emotional growth (Hrdy, 1999). Over the past decade, research in my lab attempted to define this process of biobehavioral synchrony; address its genetic, hormonal, autonomic, brain, behavior, and mental components; and study its implications for emotional development across childhood and up to adolescence. We examined similarities and differences between the parent–infant bond and two other processes of bond formation observed across mammalian species—pair and filial—which in humans are expressed during periods of "falling in love" with a romantic partner and in children's emerging friendships with a "best friend." The data presented here across several biobehavioral systems provide initial evidence that during periods of bond formation, parent and infant's brains transform to accommodate the inclusion of the other as an attachment partner by means of biobehavioral synchrony. Such processes enable the formation of human attachment, and attachment relationships, in turn—at least according to some perspectives—serve as the central motivating force that guide individuals throughout life and define the apex of the human condition.

From a theoretical standpoint, the focus on observed parent–infant behaviors and their physiological underpinnings as a prerequisite for theory building has been the cornerstone of Bowlby's (1969) ethological-based attachment theory. According to the early ethologists (Lorenz, 1950; Timbergen, 1963), theoretical perspectives on the nature of social adaptation in mammals must begin with a meticulous documentation of behaviors that emerge or intensify during bond formation. Indeed, Bowlby's far-reaching formulations on the attachment system across the life span were based on careful observations of infants' reactions to maternal presence and absence, daily routines, and changes in internal arousal. By focusing on concrete bonding-related behaviors, Bowlby advocated a bottom-up theory of human development that is evolutionary based. This perspective has been further elaborated by the empirical programs of Hofer and colleagues (Hofer, 1995), which spelled out the provisions embedded in the maternal physical presence and their impact on the pup's physiological systems, and Meaney and colleagues (Meaney, 2001; Szyf, McGowan, & Meaney, 2008), who detailed the effects of the mother's postpartum behavior on the offspring's brain plasticity, stress reactivity, and social behavior. Such biobehavioral coupling was thought to provide the basis for the infant's lifelong physiological regulation and social adaptation and the cross-generation transmission of attachment. In this context, it is important to note that the concept of *synchrony* describes only the *temporal concordance* between processes that occur simultaneously or sequentially and does not imply any heuristic system of symbols (e.g., "cognition" or "affect"). As such, *synchrony* as an overall framework is especially suited for a bottom-up model that centers on discrete building blocks as they cohere into a theoretical model. Conceptual perspectives in neuroscience recently addressed the process of synchrony as the mechanism that underlies consciousness and supports the brain's capacity to form a unitary event out of the simultaneous activity in discrete brain regions (Damasio, 1999; Edelman, 2004), as stated by Llineas (2001, p. 120): "timeness is consciousness." This transition from mechanisms of a "central organizer" to those of temporal synchrony marks the shift from a top-down to a bottom-up viewpoint. Such a paradigm shift has not yet been incorporated into developmental research nor has it been integrated into the wider circle of developmental thought.

BIOBEHAVIORAL SYNCHRONY FROM GESTATION TO WEANING AND INFANTS' EMOTIONAL DEVELOPMENT

Beginning in the first trimester of pregnancy, hormonal changes in the mother, especially in prolactin and oxytocin (OT), prepare for the initiation of maternal behavior (Nelson & Panksepp, 1998). In parallel, oscillator systems, such as the biological clock or cardiac pacemaker, consolidate in the fetus during the third trimester (Groome, Loizou, Holland, Smith, & Hoff, 1999; Mirmiran & Lunshof, 1996) and prepare for the engagement in social contingencies following birth. Measuring the biological clock and cardiac pacemaker weekly from 25 weeks' gestation to term, we found that individual trajectories in the two oscillators predicted infant neuromaturation at birth and mother–infant synchrony at 3 months (Feldman, 2006), suggesting that brainstem-mediated systems that support homeostasis and arousal modulation provide the basis for higher order social regulatory capacities (Feldman, 2009a; Geva & Feldman, 2008). At birth, mothers begin to engage in the species-typical set of maternal behavior, including gaze at infant face, "motherese" vocalizations, positive affect, and affectionate touch. As infants are biologically primed to detect social contingencies and mothers adapt the provision of social behavior to the scant moments of newborn alertness, infants may engage in the first experience of a contingent interpersonal dialogue immediately after birth. The engagement in social contingencies depends on the newborn's autonomic maturity, indexed by cardiac vagal tone, and has shown to predict the development of parent–infant synchrony (Feldman & Eidelman, 2007). Similarly, maternal OT level in the first trimester was found to predict the amount of maternal postpartum behavior and its coordination with infant state (Feldman, Weller, Zagoory-Sharon, & Levine, 2007). It thus appears that physiological support systems maturing in mother and child during gestation prepare for the expression of interaction synchrony.

In humans, as in mammals, the mother's postpartum behavior and its coordination with the infant state are central for emotional growth. The expression of maternal postpartum behavior is disrupted by conditions involving physical or emotional maternal deprivation, such as premature birth or postpartum depression, and is enhanced by biomarkers of bonding, such as breastfeeding (Feldman & Eidelman, 2003, 2007). In a longitudinal study, we followed premature infants at birth, 3, 6, 12, and 24 months and at 5 and 10 years. At each time point, measures of mother–infant synchrony and child emotion regulation were collected. Beginning at birth, mother–child synchrony at each time point predicted children's emotion regulation at the next assessment. At the same time, regulatory capacities at each observation predicted synchrony at the next point. It is thus possible that mother–newborn contingencies shape emotional development not only directly but also through a series of iterations that set the child's emotional trajectory to a more optimal course.

At around 3 months of age, face-to-face synchrony in its typical form is first observed, and parent and child begin to engage in the coordination of gaze, vocal, affective, and tactile signals. Face-to-face interactions contain repetitive-rhythmic sequences of social behaviors and form a couple-specific "dance" that typically includes a time-lag, occurring in seconds, between behavioral change in one partner and parallel change in the other's (Tronick, 1989). The affective contour of infants' interactions with mother and father are parent specific, with a more rhythmic contour with mother and a more jerky, highly aroused, random contour with father (Feldman, 2003), enabling infants to engage in multiple attachments simultaneously. At this age, infants also begin to engage in triadic synchrony, adjusting their behavior not only to the interacting partner but also to the nonverbal cues between the parents (Gordon & Feldman, 2008). This ability to navigate a complex multiperson system supports the development of social skills in the "filial" attachment system and predicts toddlers' social competence during interactions with peers (Feldman & Masalha, 2010).

The experience of synchrony during its first appearance at 3–4 months of age, the most social period in human life (Stern, 1985), is an example of a critical environmental input that is required not only for the maturation of brain circuits that support social engagement (Johnson et al., 2005) but also for the infant's ultimate emotional development. Parent–infant synchrony at that age has been shown to predict infants' attachment security, self-regulation, behavior adaptation, empathy, symbolic competence, and moral internalization across childhood and up to adolescence (Feldman, 2007c, 2007d, 2009b; Feldman, Greenbaum, & Yirmiya, 1999; Jaffe, Beebe, Feldstein, Crown, & Jasnow, 2001).

During the second 6 months, with the maturation of object exploration, joint attention, intentionality, and intersubjectivity, the synchrony experience transforms into a more mutually regulated process and both partners assume responsibility for matching the other's signals. As the infant's regulatory repertoire expands, synchrony becomes tightly coupled with physiological and behavioral stress regulation systems. Conditions such as postpartum depression and anxiety disrupt both the infant's capacity for social engagement, the regulation of fear and novelty, and the functioning of the hypothalamic–pituitary–adrenal-axis stress management system (Feldman et al., 2009). With the reorganization of the brain at that age that co-occurs with the first stages of prefrontal cortex maturation, regulatory abilities as well as interpersonal synchrony consolidate into relatively stable trajectories that shape the individual's regulatory structures of the mind throughout life.

Finally, with the emergence of symbolic thought and language toward the end of the first year, the synchrony experience expands to include the concordance between the partners' affective-symbolic communication into the framework of synchrony. For instance, during symbolic play between toddlers and parents, an increase in the child's symbolic complexity is often preceded by an increase in the parent's affective reciprocity (Feldman, 2007d). With time, interactions between attachment partners, across the life span, begin to contain two parallel components: the underlying nonverbal synchrony in the gaze, touch, and affect modalities and the verbal–symbolic synchrony in the expansion of closeness between partners. Observing the interactions between romantic couples during the first 3 months of falling in love, we detected both nonverbal synchrony in the gaze, touch, and affect modalities and verbal synchrony between moments of self-disclosure in the two partners. Behavioral synchrony was related to the partners' vagal tone and OT levels, echoing the physiological precursors of the mother-newborn relationship during bond formation.

EVIDENCE FOR BIOBEHAVIORAL SYNCHRONY IN THE AUTONOMIC, HORMONAL, AND BRAIN SYSTEMS

Maternal–Infant Contact Shapes Children's Autonomic Response

In two studies, we examined the effects of maternal touch and contact on the regulation of children's autonomic reactivity, following Hofer's (1995) research on the role of maternal proximity in regulating the pup's heart rhythms. In the first study, two groups of 6-month-old infants were tested in the still-face (SF) paradigm, an experimental manipulation that simulates maternal deprivation: One group experienced the standard SF, and the other received maternal touch during the SF episode (Stack & Muir, 1992). Vagal tone was measured from mother and child during the free play, SF, and reunion episodes of the paradigm. When maternal momentary unavailability was complemented by touch, infants' vagal response was milder in amplitude and the return to baseline was quicker, similar to the effects of handling on the stress response of young animals (Feldman, Singer, & Zagoory, 2010). In the second, decade-long study, mothers provided daily skin-to-skin contact (Kangaroo Care) to their preterm neonates and dyads were followed for 10 years. Children receiving maternal contact as neonates showed higher baseline vagal tone and greater vagal brake to emotional stressors at 10 years compared to a matched no-intervention group, pointing to the lasting effects of early maternal contact during periods of deprivation on the infant's physiology.

Although these data highlight the lasting impact of maternal contact on the infant's autonomic functioning, they do not demonstrate online synchrony between maternal and infant's physiology and behavior. To this end, face-to-face interactions between mothers and their 3-month-old infants were observed, while cardiac output was measured from mother and child and episodes of gaze, affect, and vocal synchrony were marked. Using bootstrap analysis, we found that mothers and infants synchronize their heart rhythms within lags of less than 1 s and the effect was specific to own infant. Moreover, during moments of vocal and affect synchrony, biological synchrony between mother and infant's heart rhythms increased substantially (Feldman, Magori-Cohen, Galili, Singer, & Louzoun, 2011). Thus, human mothers and infants coordinate their physiology and behavior through episodes of social synchrony, yet, unlike mammals, human synchrony occurs through the online matching of facial signals and does not require tactile contact.

Finally, conditions of maternal physical or emotional unavailability, such as prematurity or postpartum depression, were found to decrease both neonatal vagal tone and maternal contingent response (Feldman & Eidelman, 2003, 2007). Such findings support the hypothesis that maternal availability contributes to the emergence of bonding-related behavior, maturation of the infant's environment-dependent physiological systems, and the coupling between physiology and behavior.

Affiliation Hormones in Parent–Infant and Romantic Attachment

Bond formation is supported by a specific neuroendocrine system, and the neuropeptide OT has been shown to play a key role in processes parental bonding across mammalian species (Insel, 1997). In a series of studies, we addressed the involvement of the OT system in human bonding across the gestation-to-weaning period and beyond and its links with the partners' social synchrony. In the first study, plasma OT was measured from healthy pregnant women during the first trimester, third trimester, and first postpartum month.

OT was highly stable within individuals and levels at first trimester predicted the amount of maternal postpartum behavior and its coordination with infant state, indicating that already in the first weeks of gestation hormonal systems function to prime the mother for the expression of maternal behavior. Similar to vagal tone, maternal depression was associated with reduced OT levels at both first trimester and the postpartum (Feldman et al., 2007).

In a second study, we measured plasma OT from 160 mothers and fathers (80 couples) at the transition to parenthood and again at 6 months in relation to dyadic and triadic interactions. Surprisingly, levels of OT in fathers did not differ from those observed in mothers at both time points. Although OT has initially been implicated primarily in birth and lactation, father-infant touch and contact possibly provide additional pathways for the biological basis of fatherhood. OT was associated with maternal and paternal parent-specific behavior—affectionate play with mother and stimulatory play with father—and with parent–infant synchrony at 6 months, particularly with touch synchrony—the matching of parent affectionate touch with the parent and infant's social gaze. Consistent with the propositions of the biobehavioral model, cross-time mutual influences were found between hormones and behavior. Maternal and paternal OT in the postpartum predicted parent–infant synchrony at 6 months and vice versa; postpartum behavior predicted parental OT at 6 months, underscoring the mutual adaptation of physiology and behavior during bond formation. Interestingly, biological synchrony between attachment partners was observed and OT levels of mothers and fathers were correlated at each time point (Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010a). Possibly, in the formation of affiliative bonds, partners shape each other's physiology through a variety of processes, including social synchrony during dyadic and triadic interactions.

In a second study, 122 mothers and fathers (noncouples) engaged in an episode of parent-infant "play and touch" with their 4- to 6-month-old infants and measures of plasma, salivary, and urinary OT were collected. Results indicated that salivary OT increased following parent-infant contact, but only among mothers who provided high levels of affectionate touch and among fathers who exhibited high levels of stimulatory contact. It thus appears that the parent-specific form of touch functions to stimulate OT release, highlighting both the similarities and differences between maternal and paternal care and their differential relations to the neuroendocrine foundation of bonding (Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010). A third study assessed salivary OT in 55 parents and their infants before and after a session of social interaction. Correlations were found between parent and infants' baseline and reactivity OT, as well as in the degree of OT increase following play. Furthermore, synchrony increased the cross-generation transmission of OT and among children growing up in the context of high synchrony, a closer link between parental and child OT was observed, similar to the animal studies pointing to higher cross-generation transmission of OT in the context of environmental enrichment (Feldman , Gordon, & Zagoory-Sharon, 2010). Finally, we measured maternal and paternal plasma OT as predictors of triadic synchrony between new parents and their firstborn child. Higher triadic synchrony, defined as moments of coordination between physical proximity and affectionate touch between parents as well as between parent and infant while both parent and child are synchronizing their social gaze, was predicted by maternal and paternal OT and among mothers, also by lower cortisol (Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010b). Overall, these studies point to the important links between the neurobiological basis of bonding and moments of synchronous coordination between maternal, paternal, and coparental microlevel behaviors, particularly during the first months of the infant's life and the first period of parenting.

Interestingly, OT and social behavior were associated with two additional bonding-related hormones. OT and paternal coordination of joint exploration with the infant correlated with the father's prolactin levels (Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010c), similar to the associations described for fathers in biparental species (Wynne-Edwards, 2001), and with cholecystokinin (CCK), a hormone implicated in hunger and satiety that plays a role in maternal-infant bonding (Blass, 1996).

Two other studies examined OT in relation to social bonding at other points in the life cycle. OT and cortisol were sampled from single adults in relation to bonding to own parents. Levels of OT in singles were lower than those observed in parents, supporting the involvement of the OT system during periods of bond formation. OT was related to bonding to own parents and to lower depressive symptoms, further suggesting that the connection between OT and bonding-related internalizations can be observed throughout life (Gordon et al., 2008).

Finally, results from a study of romantic partners during the first 3 months of "falling in love" showed that OT levels in new lovers were higher than in singles, indicating increased activity of the oxytocinergic system during periods of bond formation across the life span. Levels of OT in new lovers, both men and women, were associated with the degree of interaction synchrony between the partners, including matched affect, positive arousal, joint social gazing, and affectionate touch, similar to the findings shown for new parents, and to the partners' preoccupations and anxieties regarding the partner and the relationship. These findings may suggest that falling in love involves a reorganization in which the partners' physiology, mental state, and synchronized behavior cohere to form the basis for the selective and enduring romantic bond (Schneiderman et al., 2012).

Parent and Infant's Brain Respond to "Own" Partner

Based on research in animal models, a specific brain circuitry has been proposed for the development of parenting that includes hypothalamic–midbrain–limbic–paralimbic–cortical circuits. Areas rich in OT binding receptors play a critical role in parenting behavior, including the hypothalamus, medial preoptic area, the bed nucleus of the stria terminalis (BNST), substantia niagra, midbrain-pons, and superior colliculus (Leckman & Herman, 2002). Assessing the brain response of parents (fMRI) to their own versus standard infant cries and pictures in the first postpartum month and again at 3–4 months, we found that own infant cries elicited greater brain activations in this parenting networks, including the anterior cingulate, midbrain, hippocampus, basal ganglia, thalamus, and amygdala, as well as in temporal and parietal cortices, areas implicated in motivation, reward, emotional processing, habit formation, and empathy (Swain et al., 2007). Observations of parent-infant interactions were conducted at 3 months, and the parent's sensitivity, expressed in visual, vocal, tactile, and affective behaviors and their adaptation to infant cues, was coded. Greater activations in mothering-related regions to own-infant cry in the postpartum in these areas predicted greater maternal sensitivity at 3 months (Kim, Feldman, Leckman, Mayes, & Swain, 2011). In another study, we examined the brain response of synchronous mothers—those who coordinate their response with infant cues—and intrusive mothers—those who provide excessive stimulation—to videotaped vignettes of mother-infant interactions. We found that among synchronous mothers, greater activations were found in the nucleus accumbens, a central nucleus in the reward pathway, whereas intrusive mothers showed greater activation in the amygdala. Furthermore, among synchronous mothers activation in reward pathways were functionally connected to the cortical social brain circuitry, which enable the mother to read the nonverbal signals of her infant and plan for adequate parenting. Furthermore, activations of the nucleus accumbens in synchronous mothers was correlated with the level of maternal OT. Thus, mother-infant synchrony appears to be based on reward networks, affiliative hormones, and closer concordance between motivational reward and brain structures implicated in theory of mind and empathy (Atzil, Hendelr, & Feldman, 2012). Bond formation, therefore, may involve the coordination of parenting-related brain circuits with parenting behavior directed to the selective element in attachment, to "owness."

Parallel findings were observed in the infant's brain. Event-related potential response of 6-month-old infants to neutral, sad, happy, and angry facial expressions were assessed in two experiments. In the first, infants observed standard emotional faces; in the second, their own mother's emotional faces. Consistent with previous research, infants showed greater amplitudes of the Nc component to emotional compared to neutral faces, particularly to angry faces, suggesting greater allocation of attentional resources to the expression of emotions. The mother's emotional faces elicited greater activations than the unknown face, with greatest amplitudes observed to own mother's angry face. Infants of depressed mothers showed greater activations in response to maternal angry face and these were negatively related to mother–infant synchrony during interactions (Eidelman, Goldstein, Berger, & Feldman, 2010). Thus, attachment relationships may enhance the saliency, relevance, and meaning of emotions, and infants utilize the emotions and behaviors of attachment partners to perceive, encode, and learn the rules of emotional communication with social partners.

Summary

Since the 1920s, the term *synchrony* has been used to describe the process by which the physiology and behavior of mother and young during social contact are coordinated into an affiliative bond. The data presented here in the autonomic, hormonal, and brain systems point to the unique ways in which the physiology and behavior of human partners synchronize to form a selective and enduring biobehavioral attachment. Such an affiliative bond between parent and child provides an overall protective envelope that shapes the child's capacities for emotion regulation, stress management, empathy, symbol formation, and social adaptation and is observed during other periods of bond formation throughout life, such as falling in love and the transition to parenthood. Similar to other mammals, the pace, rhythms, sensory inputs, arousal contour, and interactive resonance experienced within early attachments during the critical period of gestation-to-weaning is likely to play a role in the individual's capacity to form friendships and engage in meaningful relationships throughout life.