



# The neurobiology of human allomaternal care; implications for fathering, coparenting, and children's social development



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## A B S T R A C T

Allomothering, the caregiving to offspring by adults other than the biological mother including fathers and other group members, has characterized human societies throughout hominin evolution. Allomothering is common across the animal kingdom and carries long-term fitness benefits to offspring. Guided by our biobehavioral synchrony conceptual frame, we present research from our lab and others addressing the behavioral, hormonal, and neural systems that underpin human allomaternal care by fathers and studies on the coparental bond. Several important aspects of human allomothering are discussed: (i) father-child synchrony, (ii) longitudinal effects of fathering and coparenting on child outcomes (iii) cultural variability in paternal care, (iv) the role of oxytocin, vasopressin, prolactin, and testosterone in the formation and maintenance of human fathering, (v) evolutionary changes in fathers' brains within the parent-offspring interface and their contribution to children's long-term social adaptation, and (vi) the neural correlates of human coparenting. Based on our findings we propose that in the course of hominin evolution fathers' neuroendocrine systems, brain functionality and integrity, and behavioral responses to infant cues have undergone profound natural selection to accommodate the great variability in the paternal role across time and place, culminating in the contemporary cooperative, highly involved coparent observed in modern societies of the developed world.

## 1. Introduction

Throughout most of human history and across cultures, women have been the primary caregivers to their newborns, responsible for their daily nurturing, caregiving, and development. Over the past several decades, significant socio-cultural and economic changes in modern and developed countries of the Western world have led to reorganization of the human family that dramatically increased fathers' involvement in direct childrearing and caregiving activities [80,109,143,144]. Such changes have shifted both scientific and popular views from the matricentric thinking that was deeply rooted in our culture toward a view that parenting in humans is a far more complex, flexible, and cooperative process than the mother-infant bond. Such matricentric thinking limited our ability to fully understand the evolutionary context of human caregiving and the factors that contribute to children's development [128,129]. Overall, it has been suggested that

since human newborns are altricial, requiring an extended period of intense investment, and are dependent on others for protection and nourishing, human evolution has created selective pressure for active paternal care and cooperative breeding systems to assist mothers and create a social environment that facilitates the feeding and protection of children, thus maximizing their chances of survival [67–69,112,161].

The term allomothering was coined in 1975 by the evolutionary biologist Edward O. Wilson, by pairing the Greek word “allo-” (“other than”) with “mothering” to describe the care of offspring by any group member other than the biological mother, including fathers, family members (e.g. grandmothers and older siblings), and other women and men in the group. Unlike other Great apes, human mothers rely heavily on caregiving and provisioning provided mostly by female allomothers and biological fathers, while human babies, beginning at birth, are typically surrounded with and carried by group members other than the biological mother [87,93–95,127,153,154,176]. Thus, the cooperative

*Abbreviation:* AI, anterior insula; ASD, autism spectrum disorder; AVP, vasopressin; CT, cortisol; dACC, dorsal anterior cingulate cortex; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; fMRI, functional magnetic resonance imaging; GP, globus pallidus; IFG, inferior frontal gyrus; IL-6, interleukin-6; IPL, inferior parietal lobule; IOFC, lateral orbitofrontal cortex; mPFC, medial prefrontal cortex; NAcc, nucleus accumbens; OT, oxytocin; PAG, periaqueductal area gray; PPI, psychophysiological interaction; PRL, prolactin; STG, superior temporal gyrus; STS, superior temporal sulcus; T, testosterone; TP, temporal pole; TPJ, temporoparietal junction; vACC, ventral anterior cingulate cortex; vmPFC, ventromedial prefrontal cortex; VS, ventral striatum; VTA, ventral tegmental area

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nature of human childrearing, while diversely expressed and influenced by cultural and ecological factors, is evident universally [31,87,105]. This alternative and supplementary allomaternal caregiving system provides support for mothers throughout the long period of the child's dependence and assists children in acquiring the social skills required to become members of their social group [90,106,146]. Allomothering improves offspring's well-being and survival [162], influences maternal fertility [32,88] and caregiving behavior [17], and reduces rates of infant abandonment [14]. It is argued that unless mothers were able to trust and cooperate with other group members, including male partners, to provide adequate and shared care and provisioning for their slow-maturing young, humans could not have achieved the enhanced reproductive success nor afford the shorter birth intervals compared to other apes, and thus our species could not have competed with other hominins [37,86,127].

While paternal care is common among fish, birds, insects, and worms [29], it is relatively rare in mammals, observed in only 3–5% of mammalian species where males engage in both indirect care (e.g. provisioning, guarding, transport and defense) and direct care (e.g. carrying and grooming) to varying degrees [103]. Direct paternal care is displayed mostly by socially monogamous species [119] and in these species paternal care is facultative, that is, enhancing infant survival in the context of maternal care [65]. However, under specific conditions, in many mammalian species that are non-allomaternal in nature, prolonged exposure of males to cues from helpless infants may elicit behavioral plasticity in terms of males' willingness to respond to infant signals and to exhibit paternal behavior [69,148,153,154]. In some primates species males remain with the female they mated with to protect female and young against predation and infanticide [139,142]. It has recently been suggested that since primates' offspring are particularly vulnerable to infanticidal males, biparental care has evolved to shorten lactation period, thereby reducing infanticide risk by strange males and increasing reproductive rates [135]. However, in a few monogamous New World monkeys, such as titi monkeys or South American monkeys, the fathers, rather than the mothers is the primary caregiver figure [178].

Paternal care in humans is not obligatory and is highly variable among and within societies and across cultures; it varies according to local ecological setting, mating systems, social environment and even to social status [64,91–94,149,172]. Cross-cultural analysis showed higher paternal care in hunter gatherer groups compared to other agricultural modern societies, but great variability in patterns of paternal care also exist within hunter gatherer societies, for instance, low levels of male caregiving is observed among the South African! Kung as compared to highest levels of paternal involvement is found among Central African Aka pygmies.

The fact that paternal care is displayed by human fathers has led to an increased interest in the neurobiology of this behavior and its effects on offspring. From an evolutionary perspective, theories on paternal investment suggest that stable coparenting within the family and male investment in one female and her offspring are common in societies where direct male caregiving behaviors and provisioning operate as a flexible consolidation of mating access and male parental effort, mainly by improving their reproductive success due to females' shortened interbirth intervals [68,97,98,112,117,120,121,145]. Yet, in humans, a woman's reliance on her male partner as a potential and essential helper is a risky evolutionary strategy [85,92], and cross-cultural analyses show a reciprocal “trade-off” in relationships between paternal care and alloparenting (allocare provided by group members other than the biological mother and father); when other members are involved in childrearing, mainly the grandmothers, male parenting effort and the coparental bond between the man and the woman becomes less stable and less crucial [79]. Such trade-off in relationships highlights the father's importance in societies and during historical periods when couples lived apart from the extended family network [146,158].

Following Tinbergen's four questions on behaviors [167], research

in our lab over the past two decades has attempted to describe the mechanisms underpinning human parental care in order to provide insights into the functional significance of both maternal and paternal behavior. We assumed that if males have played an essential, albeit flexible and variable role in human parenting across human evolution by reducing Homo females' reproductive costs [66], their physiological systems have evolved by selective pressures to respond to committed fathering and to provide adequate and sensitive care to their infants.

Our research began with detailed developmental observation of fathering as compared to mothering and of the coparental bond in new families. Over the years, we complemented these behavioral studies with imaging research on the parental brain and neuroendocrine assessments of mothers, fathers, and children, addressing the role of oxytocin (OT), vasopressin (AVP), prolactin (PRL), and testosterone (T) in the formation and maintenance human affiliative bonds and parental care. Finally, in several longitudinal studies of mothers, fathers, and primary-caregiving fathers raising their infants with no maternal involvement since birth we assessed the cross-generational transmission of human sociality; from functionality and connectivity in fathers' brains in infancy to children's social skills and neurohormonal functions that supports sociality across the first six years. These studies provide empirical support for our conceptual frame on biobehavioral synchrony [43,45–48].

In this article we review major findings from our work over the past 20 years, as well as from other labs on allomaternal care by human fathers. We focus on mammalian-general and human-specific components of paternal care, identifying the neurobiological mechanisms that support fathering and addressing the long-term effects of fathering and coparenting on child development and family formation (Fig. 1).

## 2. Human paternal behavior

In all mammals, including humans, the birth of an offspring triggers a set of species-specific parental behaviors that are aimed to care for the young and assure survival and optimal growth by immediately responding to the child's physical and emotional needs and providing nurturing, security, and comfort during times of distress [25,38]. Mammalian maternal and paternal behaviors are underpinned by specific neuroendocrine processes and neural networks. Maternal behavior is genetically programmed and triggered by female biological processes (e.g. pregnancy, parturition, and lactation), and involves licking, grooming, and the species-typical forms of touch-and-contact. Paternal behavior, on the other hand, is rare among mammals, is mainly observed in socially monogamous species [118], and is more influenced by social experiences and the early social environment as compared to maternal behavior. Notwithstanding genetic differences among species, direct paternal care is often characterized by activities that involve physical stimulation, carrying pups in space, retrieval of pups to the nest, keeping pups from warm, huddling, and bringing food in carnivores. Male parenting often direct infants to the social world (e.g. scent marking, mutual greeting and wrestling) and such behaviors increase when offspring are exposed to stressors. Thus, increased paternal attention and responsiveness toward pups is observed during neonatal separation, fear, and other threatening paradigms [20,24,111,124,141,157].

Our behavioral research has focused on three important aspects of fatherhood: father-child synchrony, direct and indirect contributions of paternal behavior to child outcomes, and cultural variability, highlighting the human male's caregiving not only as supplementary to that of the female but as an essential contributor to children's development. In relation to behavioral synchrony we examined the degree of synchrony as well as its specific pattern in mothers and fathers. Mother-infant and father-infant pairs showed similar levels of synchrony, defined as adaptation of the human-specific parental behavior with the infant's state and social signals, yet, the specific format of synchrony differed among parents. Mother-infant interactions were organized in

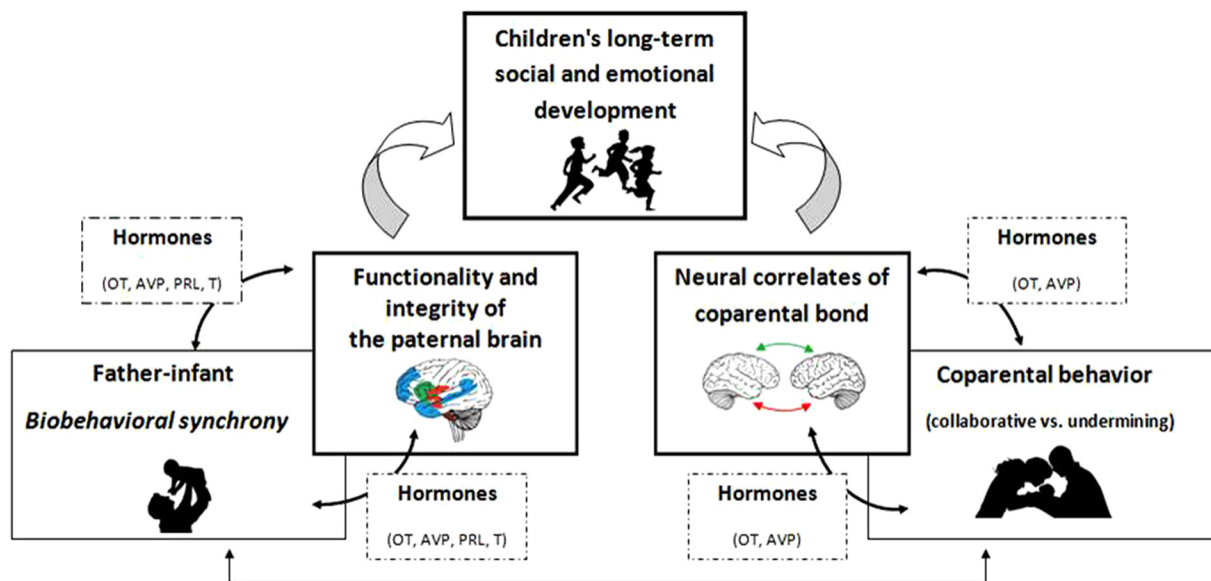


Fig. 1. Mechanisms that support human allomaternal care by fathers, the coparental bond, and the cross-generational transmission of human sociality from plasticity of the parental brain in the postpartum to the development of children's social competencies and well-being.

cyclic oscillations between states of low and medium arousal with a gradual increase toward positive affect. Such interactions employed a face-to-face position and utilized behaviors such as mutual gazing, co-vocalizations, and affectionate touch. Father-infant interactions, on the other hand, contained quick and sudden peaks of positive arousal that appeared more frequently as play progressed, focused on the environment and not on each other, and contained stimulatory contact. Moreover, while mother-infant synchrony was positively linked to the partners' social orientation and inversely linked to maternal depression and child's negative emotionality, father-infant synchrony was associated with the intensity of positive arousal and the father's secure attachment [41]. Such findings are consistent with attachment theory and with models suggesting that synchronous interactions with father promote children's exploration and curiosity [81] and contribute to the infant's capacity to engage in rapidly intense experiences while maintaining a sense of secure base [18]. We suggest that the rhythmic exchange an infant creates with each parent, the “rhythm of safety” with mother and the “rhythm of exploration” with father are both critical for the child's cognitive, social, and emotional growth. These findings also highlight the human father's evolutionary ability to interact with offspring in a well-matched “dance” to the same extent as mother. Consistently, we found that the range of father's sharing of household and childcare responsibilities partakes (e.g., bathing, doctor's visits, playing, feeding, etc.) predicted father's interactive sensitivity toward the infant [40].

In studies comparing toddlers' symbolic competence and socialized behavior to mothers and fathers, both mother-child and father-child synchrony in infancy and the parent's support of the child's symbolic play predicted the complexity of symbolic play in the toddler stage [42]. Yet, while children's self-regulated compliance was related to both maternal and paternal sensitivity, toddlers showed more compliance to father compared to mother, suggesting that children mobilize more regulatory efforts during interactions with their fathers or that fathers find ways to elicit more socialized behavior from toddlers [49]. In a longitudinal study on mothers, fathers, and their firstborn child followed from infancy to adolescence, we found that reciprocal interactions with both mother and father were individually stable over time, so that children who experienced greater reciprocity with the parent in infancy also received more reciprocal interactions during childhood and adolescence. Mother-child and father-child reciprocity were inter-related and each contributed to children's social competence in

preschool and to a more dialogical relationship with their best friend in adolescence, charting a line from parental to filial attachment [44,56]. However, mother and father contributed to children's social development in unique ways. While reciprocity with mother contributed to children's social competencies with peers in preschool and better dialogical skills during positive exchanges with best friend in adolescence, reciprocity with father reduced toddlers' aggression and enabled a better conflict negotiation in adolescence, highlights the father's unique impact on the modulation of aggression [57]. Such findings concur with numerous studies from other labs, which showed that father involvement and sensitive paternal behaviors serves as a protective factor against aggression and externalizing symptoms and promote social adaptation in children and adolescents [7,61,107,136,140].

In another series of studies we compared parent-child interactions and preschoolers' self-regulatory skills in high-functioning children with ASD compared to typically-developing controls. Mothers and fathers in both groups were equally aware of their children's distress signals during stressful paradigms; however, mothers and fathers of children with ASD employed more regulatory behavior, for instance, providing physical comfort to the child, touching/hugging, cognitive reframing, and emotional reflection [137]. We also measured children's self-regulated compliance and the parental support during a delay gratification paradigm with mother and father and here we found differences related to parent gender. Mother exhibited more direct support than fathers toward both children with ASD and typically-developing children, which may relate to the mothers' role as primary caregiver [138]. These findings underscores the great effort of both mothers and fathers of children with ASD to buffer children's social distress and parents' careful attunement to their children's social difficulties by assisting them to modulate their emotions. These findings emphasize that children with ASD, despite their social difficulties, can experience both mother and father as ‘secure base’ agents.

Mammalian paternal behavior can be categorized into direct and indirect investment in offspring survival and development [103]. In humans, father can provide social, emotional, and practical support to the mother, thereby impacting the quality and quantity of maternal care and the family atmosphere. Accordingly, we found that greater father involvement in childcare predicted lower maternal intrusive behavior toward the infant [51]. In the context of chronic maternal depression, sensitive paternal behavior buffered the negative effects of maternal depression on family life [170].

Finally, guided by evolutionary theories of socialization [19,152], we followed mothers and fathers in Israeli and Palestinian families, observing parenting in societies marked by individualistic and collectivistic orientations. Whereas both parents contributed to children's social development, there were more culture-specific effects in the role and impact of fathering, compared to mothering [52,53]. For example, while paternal control, defined as intrusive, controlling, and directing father behavior, interfered with Israeli children's social adaptation, it facilitated greater competence among Palestinian children [50]. These findings demonstrate the differences between the evolutionary-conserved maternal role versus the highly variable and flexible human paternal role and led to our “differential pathways, shared process” hypothesis of natural diversity in mothering and fathering across large evolutionary distances and within species. Such hypothesis posits that while different pathways, ancient or emerging, universal or culture-specific, may underpin human mothering and fathering, the care of both parents contribute in quite similar ways to offspring development over time, suggesting that these pathways are supported by similar neural and hormonal pathways, consistent with the findings in rodent models [12].

### 3. The neuroendocrine basis of human fathering

In several studies we examined four hormones that have shown to play a critical role in the expression of fathering in both humans and other species and undergo reorganization at the transition to parenthood to support the paternal role: Oxytocin (OT), prolactin (PRL), vasopressin (AVP) and testosterone (T) [163,179,180]. We measured hormones in fathers in relation to observed paternal behavior and in several studies, compared hormones in mothers and fathers or in parents and non-parents.

We found that levels of OT, which has been traditionally considered a maternal hormone, increased during the transition to parenthood in both mothers and father to the same extent and showed individual stability and consistently high levels across the first six months of parenting [73]. These results are in line with other evidence showing that partnered fathers have higher plasma OT levels than non-partnered non-fathers [123]. In line with studies of bi-parental mammals on similarities and differences in maternal and paternal OT and their associations with parental behaviors, we found that OT in mothers correlated with the social affective repertoire, including affectionate contact with the infant, mutual gazing and vocalization, whereas in fathers it was linked to positive arousal and stimulatory contact with the infant, including proprioceptive touch, placing the infant on father's knees, father moving the infant around the room, and father touching the infant with objects to stimulate attention. In addition, maternal and paternal OT were inter-related across the first months of family life, which suggest that a biobehavioral synchrony process between partner shapes each other's neuropeptide response through the coparental attachment [73]. Taken together, these findings provide compelling evidence that OT facilitates paternal caregiving in human males and that it directs fathers to a specific set of parenting behavior.

In another study of mothers and fathers (from different families) found that OT functions as a biobehavioral feedback loop in both parents; when parents provide more touch and contact during interactions, their OT levels increase following a 15-minute parent-infant play. Similar to studies in rodents on high-and-low licking and grooming mothers [33]; we found that only mothers who provided high levels of affectionate contact showed OT increase following parent-infant interaction. Among fathers, only those who displayed high levels of stimulatory contact showed an OT increase [54].

Studies in our lab examined OT in fathers in relation to other parenting-related hormones, consistent with the hypothesis that OT provides a neuroendocrine template for the integration of multiple hormones during bond formation in humans [48]. In a study on the involvement of OT and PRL in human fathering, we found that both

hormones showed high individual stability across the first months of fatherhood. Yet, when comparing the association of each hormone to fathers' social behaviors, PRL was associated with father-infant exploratory play, including behaviors such as father presenting toys, handling toys, jointly manipulating toys, and directing infant attention to toys. In contrast, OT was linked to more socially-focused interactions, including behaviors such as father directing gaze toward the infant, father expressing positive affect, and father vocalizing [74]. Other studies found that PRL is associated with individual differences in father responsiveness [36], is increased in new and expectant fathers during pregnancy [164], and fathers' PRL is associated with greater responsiveness to infant cries [60].

Vasopressin (AVP), a structurally-similar neuropeptide-hormone to OT, plays a central and important role in mammalian fathering [104,156]. Measuring OT and AVP in human fathers, we found that fathers with high levels of AVP exhibited more stimulatory contact with their infants, compared to fathers with high levels of OT who engaged in more affectionate contact with their infants [9]. In addition, intranasal AVP increased expectant fathers' interest in baby-related avatars compared to control men [30], and individuals reporting more paternal warmth in childhood reported greater empathic concern following AVP administration [165]. These findings indicate that both PRL and AVP are associated with distinct aspects of paternal care not directly supported by OT; PRL – with father's facilitation of infant's exploratory behavior, and AVP with the cognitive-stimulatory aspects of father-infant interactions.

With regards to the relationship between OT and testosterone (T), several studies in our lab found complex OT – T associations and modulatory effect of T on the relations between OT and parenting. While paternal T was individually stable across the first six months of parenting and predicted lower levels of father-infant synchrony, maternal T was neither stable nor predictive of maternal behavior [75]. Intranasal OT administration enhanced salivary T production in fathers and these changes correlated with father-infant social behavior at five months [175], pointing to the complex associations of OT and T. Fathers' T levels were negatively associated with parent-infant social behaviors including less touch, gaze, positive affect, and vocalization [175], and with paternal caregiving, but were marginally positively related to testicular volume [122]. Infant crying decreased T in men when coupled with caregiving responses, but increased when caregiving responses was not possible, probably when the infant's cries were perceived as a threat and a danger signal [60,171]. Sarma et al. [159] examined the link between sociosexual experiences during adolescence and men's adult psychobiology as fathers. Authors found that environmental harshness/unpredictability and age of sexual activity in adolescence and young adulthood interacted to predict elevated T levels among fathers and less of a decline in T levels when men transitioned to fatherhood. Such findings are consistent with human and animal studies showing that T levels are inversely related to direct caregiving practices (e.g. feeding, holding, playing), postpartum investment in couple relationship, but are positively associated with protection and provisioning in males [69,70,78,122,131,160,171].

During the period of parent-child bonding, functioning of the affiliation, reward and stress management systems become more tightly linked to ensure successful bonding [45,155]. Therefore, in another study we measured OT, beta-endorphin, and interleukin-6 (IL-6), biomarkers of the affiliation, reward, and immune-stress management systems, respectively. It was found that the effects of IL-6 and beta endorphin on behavioral synchrony in mothers and fathers of firstborn infants were mediated by their impact on the parents' oxytocinergic system [169]. The higher levels of beta-endorphin, IL-6 and behavioral synchrony in new mothers and fathers reflect the parent's reward from the infant and the caregiving role and the preoccupations, and vigilance that increase in parents during the postpartum. Furthermore, stronger inter-correlations were found between the three biomarkers in parents compared to non-parents. The greater activation of affiliation (OT),



reward (beta endorphin), and stress-management (IL-6) systems and their tighter cross-talk during bond formation jointly support the emerging bond and increase family cohesion and adaptability. While very little is known about the involvement of the human immune system in OT-mediated attachment processes, results of the current study concur with previous studies [28,76,96] that describe the interplay between attachment and health as moderated by OT functionality. Such findings underscore the essential role of fathers' immune and stress-management systems in supporting their capacity to become healthy, strong, and competent helpers to the nursing mother as well as to providing direct paternal caregiving and investment in the infant's well-being and safety.

Few studies in our lab assessed the cross-generational transmission of OT as mediated by parental behavior, consistent with findings in animal models [26,27]. The first study found significant correlations between salivary OT in mothers and fathers and their infant's OT. This cross-generational link was moderated by parent-infant synchrony; when parent-infant synchrony was high, close links were found between parental and child's OT but such associations were not found when parent-infant synchrony was low [55]. In a series of OT administration studies, we administered OT to fathers of 5-month old infants and examined its hormonal, behavioral, and autonomic effects on father and infant. Following administration, fathers' salivary OT levels increased dramatically and fathers displayed greater amounts of the key parenting behavior that characterize father-infant attachment. Surprisingly, it was found that infants' salivary OT levels also increased significantly following administration to father, although infants were not in the room of administration and were not exposed to the active substance, and their social focus and social gaze also increased [173]. OT administration also modulated father's proximity to the infant and subtle motion characteristics, and infant's OT reactivity was positively linked with father's movement acceleration [174]. OT administration studies from other labs similarly found alterations in paternal behavior, for instance, increased sensitivity and responsiveness during interactions with their healthy child and a child with ASD [132,133]. Among preschoolers with ASD, baseline OT levels were lower than those of typically-developing children. However, after an extended period of proximity and play with mother and father (25 min), OT levels normalized, but returned to baseline 10 min after a 45-min parent-child session [58]. In a 3-year longitudinal study Feldman et al. [56] found that mothers' and fathers' OT levels, which remained stable across the 3-year period, correlated with low risk alleles on the oxytocin receptor gene (OXTR) and CD38 genes and predicted child's OT levels and the ability to interact with reciprocity and dialogue toward best friend. It was concluded that greater functionality of the OT system, observed in OT administration studies, genetic variability, or endogenous levels start a chain of synchronous biobehavioral processes between parent and infant. Such 'external regulatory' functions enable children to enter the social world of the family unit and create later attachments with non-kin members of society similar to that observed in other mammals [89].

#### 4. The neural basis of human allomaternal care by fathers: flexibility, connectivity, and correlates

Over the last decades, interest in the brain basis of human parenthood has significantly increased. Studies often utilized fMRI to examine parents' brain response to auditory, visual or multimodal infant stimuli, such as infant pictures, movies, or cries, typically comparing "own infant" condition to "unfamiliar infant". Most imaging studies examined mothers and only few studies tested fathers, with or without comparison to mothers' brain (For review see: [46,48,150]). The first study from our lab that compared mothers' and fathers' brain activations in response to own infant versus unfamiliar infant video clips found that mothers showed significantly greater limbic activations, particularly amygdala, compared to fathers, and activation in the limbic-reward-

motivational circuit correlated with maternal OT, including amygdala, NAcc, insula and vACC. Fathers, on the other hand, exhibited greater activations in socio-cognitive cortical areas, particularly in the mPFC, dlPFC, dACC and IPL, which correlated with paternal OT, while activations in the insula, STG and IFG were linked with paternal AVP [10].

To tease out parent's sex from their caregiving role (primary versus secondary caregiving role), Abraham et al. [1] recruited 89 first-time parents raising their infant within partnered relationship: primary-caregiving heterosexual mothers, secondary-caregiving heterosexual fathers and a unique group of primary-caregiving homosexual fathers living in a committed two-parent family and raising their infants without maternal involvement since birth. In each two-father family one father was the biological father and the other was the adoptive father, genetically unrelated to the infant. Since this is the first time in human history when men are able to raise children within a partnered relationship with no maternal involvement since birth, our study was the first to empirically investigate the parental brain in such novel family setting. Several interesting findings emerged. First, we found a remarkable similarity across parents (men and women, biological and adoptive parents) in the activation of a global "parental caregiving" network that underpins parental care across individuals. This global network consisted two sub-networks, the emotional processing and the mentalizing networks that activate when parents were exposed to their infant's stimuli. Although mothers' and fathers' brain response to infant stimuli showed more commonalities than differences, consistent with findings in other mammals [12,38,110], two important differences emerged. Primary-caregiving mothers showed greater amygdala activation than secondary-caregiving fathers, which was linked to maternal OT and mother-infant synchrony. The amygdala, a component of the emotional processing network, is involved in motivational saliency and relevance, automatic vigilance processes, and reward learning [6]. In comparison, secondary-caregiving fathers displayed higher STS activation, associated with father OT and father-infant synchrony. The STS is a key structure in the mentalizing network, plays a vital role in social cognition, prediction making, updating regarding others' behaviors and affords a third-person perspective and future social planning [8,63]. Of interest, primary-caregiving fathers, both biological and adoptive parents, exhibited higher amygdala activation, similar to mothers, alongside greater STS activation comparable to secondary-caregiving fathers, and stronger functional connectivity between amygdala and STS was found in their brains while watching video clips of their own parent-infant interaction. Amygdala-STs connectivity has been associated with better social-cue detection and was observed in individuals with more complex social networks [16]. While significant stronger connectivity was found in primary-caregiving fathers compared to the other parent groups, in all fathers the amount of time each father spent in direct childcare was related to the degree of amygdala-STs connectivity.

Our findings on primary-caregiving fathers provide the first neurobiological evidence in support of evolutionary theories of human sex differences in reproductive strategies and parental care [22,29,65,168] and highlight the phylogenetically ancient role of maternal care, underpinned by ancient brain circuits, as opposed to the facultative human paternal care, supported by later-evolving higher brain circuits involved in social understanding, theory of mind, and cognitive empathy. Overall, and consistent with animal studies [13,104,110,113], it appears that direct childcare experiences shape the paternal brain and increase functional integration of social networks, particularly when father is the primary caregiving adult.

These studies have led the authors to assume that while only human mothers experience pregnancy, birth, and lactation, and these biological processes trigger maternal care via amygdala sensitization and the priming of OT during parturition, alternative and complementary "allomothering" pathways have been selected throughout hominin evolution. Such pathways can flexibly operate in all group members and come with practice, attunement, and social experiences [67,90].

Imaging studies of human fathers from other labs reveal important

findings on the neural basis of fathering. Consistent with our findings, studies showed that infant stimuli activated the “parental caregiving network” in fathers' brain and demonstrated associations between fathers' brain activations in the subcortical motivation/reward circuitry and paternal caregiving behaviors and T levels [108,122]. An MRI study found that fathers exhibited increases in gray matter volume in brain regions involved in motivation, reward, and mentalizing during the first few months postpartum [100]. Wittfoth-Schardt et al. [177] showed that OT administration to fathers attenuated functional brain responses to infant pictures and connectivity in subcortical regions implicated in vigilance, reward, and emotional processing, emphasizing the role of OT in facilitating approach behaviors while reducing social avoidance and aversion. Li et al. [114] found widespread brain activations to both own and unknown infant cries in neural systems involved in empathy and approach motivation in first-time fathers which were similar to those found in mothers in previous studies [115,116]. Furthermore, infant age was inversely correlated with father's neural responses, and father age was negatively correlated with dACC and the AI activation, suggesting that, older fathers may find baby cries less distressing or aversive compared with younger fathers. Overall, studies demonstrate both similarities in the brain response of fathers and mothers to their infant cues as well as father-specific activations and connectivity patterns that support the development of the allomaternal role.

##### 5. The cross-generation transmissions of human sociality: From parent brain to child social-emotional development and mental health

In three longitudinal studies [2–4], we followed the sample of primary-caregiving mothers and fathers from the time their children were infants until they were six years old to elucidate how mechanism underpinning the parental brain response in infancy support the development of children's social competencies over time. In two of the follow-up studies, we used Network Cohesion Indices (NCI, [147]) in the parental brain as predictors of children's social competencies at the preschool (3–4 years) and school-entry (6–7 years) stages. Network cohesion indices probe the dynamic of coordination both within a defined network (Intra-NCI) and between networks (Inter-NCI). We were particularly interested in network indices as fathering is associated with enhanced functional and structural connectivity and neural plasticity [110]. Therefore, we expected that the parent's complex social functions which are critical for offspring survival (e.g. social motivation, empathy/embody-simulation, theory of mind) would emerge from interactions within and between distributed brain network rather than from the activity of single regions, and such integrity indices would play a role in shaping offspring social outcomes.

We defined three network of the parental brain – (a) core limbic, which integrated structures related to the subcortical mammalian caregiving networks including the amygdala, hypothalamus, VTA, NAcc, PAG, GP, (b) embodied-simulation/empathy, which integrates structures of the empathy and mirror networks including the AI, ACC, IFG, and is a network that enables parents to draw on information from her or his own experiences to interpret the infant's emotional and bodily states by representing them in the parent's brain, grounding experience in the here-and-now [35,99], and (c) mentalization, including the dmPFC, vmPFC, STS, TP, and TPJ. At four years, we measure preschoolers' self-regulatory skill using the LabTab [71] and self-regulated socialization using a toy pick-up paradigm, involving a compliance situation where the parent asks the child pick up toys following joint play. These paradigms were micro-coded for negative and positive emotional expression and for the child's use of simple and complex self-regulation and socialization strategies. Parents' and children's salivary samples were collected for OT and cortisol (CT) analysis three times during the visit. At six years, child behavior problems were reported, including internalizing and externalizing problems and somatic

complaints.

Findings from these studies [2–4] revealed how changes in the parental brain in the postpartum impact children's long-term outcomes. Network integrity measures in the parental brain, assessing the functionally-coupled relationships among spatially-separated brain regions, while watching video clips of their own parent-infant interaction, predicted children outcomes in network-specific ways. Importantly, no differences were found in intra- and inter-connectivity among primary-caregiving mothers and fathers in any of the three networks. Furthermore, consistent with animal models [21,23], we found increased functional connectivity within and between networks in primary-caregiving mothers and fathers when exposed to their own infant's stimuli compared to unfamiliar infant's stimuli. Such increased coherence in the parent's brain to attachment stimuli may constitute a survival advantage for offspring [3].

As to long-term predictions, integrity of the core limbic network predicted children's expression of positive emotions and use of simple self-regulatory strategies, such as proximity seeking to parent, physical and verbal self-soothing, during tasks that presented children with high negative (fear) or positive (joy) situation. This likely describes a mammalian-general mechanism that traces the transmission from optimal parenting to social behavior in juveniles. Integrity of the parent's mentalizing network predicted children's self-regulated socialization which has been associated with theory-of-mind development. Integrity of the parent's embodied simulation/empathy network predicted children's use of more complex emotion regulation tactics, such as symbolization and attention diversion, to manage moments of heightened emotional arousal. This link from integrity of the parent's embodied simulation/empathy network and children's mature self-regulation was mediated by parent-infant synchrony in infancy, the first experience that sensitizes infants to the dyadic ‘here-and-now’. Path from parent's core limbic and embodied simulation inter-connectivity to preschooler's OT levels was moderated by parental OT in infancy [2]. We also found that the degree of connectivity between the embodied-simulation/empathy network and the mentalizing network in the parent's brain was longitudinally linked with lower child CT production in preschool, while between network connectivity of the embodied-simulation/empathy and mentalizing networks in the parent's brain in infancy was longitudinally associated with lower internalizing problems six years later, as mediated by the child's regulatory behavior in preschool [3].

In another study of the same sample, we focused on neural pathways that underpin human interoception, the perception of one's own bodily signals, leading from parent's brain functionality to the child's somatic problems, including nausea, headaches, nightmares, dizziness, chronic pains, fatigue and exhaustion, skin disorders, vomiting and stomach problems. We found that increased activation in the parent's AI was associated with lower somatic problems in the child at age six, while greater parents' amygdala activity predicted higher children OT levels. Parents' OT levels moderated the link between preschoolers' OT levels and somatic complaints at six years [4]. Consistent with these findings, Kim et al. [101] found that father's positive perceptions on being a parent was positively correlated with elevated activations in the caudate in response to own infant cry sounds at the first month postpartum and these activations longitudinally predicted children's socio-emotional competences at 18–24 months.

Overall, these findings provide the first compelling evidence for the non-genomic cross-generation transmission of human sociality from parent to child and suggest that neural processes implicated in simulation, mentalizing, and interoception in the parent's brain tune the infant's brain for social life possibly through mechanisms of brain-to-brain synchrony [47,83,84,102] during synchronous parent-infant interactions in the first months of life. These findings led to the conclusion that the human parental brain of both women and men, biological and adoptive parents marks an evolutionary platform for the complex and unique architecture of the human social brain that supports the offspring ability to enter the social group and parent the next generation.

## 6. Neurobehavioral perspective on the mechanisms underlying human coparenting

Many primates raise their young through the collaborative efforts of several females with or without male assistance and much flexibility exists in level of kinship among caregivers or the degree of coparental involvement even within a single species [90]. This suggests that while the adult-adult coparental bond is critical for childrearing and survival, the nature of this bond between adults who jointly raise infants is highly variable and flexible across species and contexts. Since human infants require the longest period of dependence to reach maturity, combined with various environmental factors such as food availability and frequency of predator interactions, the male-female sexual bond evolved to extend much beyond copulation into a long-lasting cooperation that increases infant protection, enhances feeding, and provides the necessary context for the acquisition of social skills [67,69]. In humans, the coparental bond is defined as a relationship of solidarity, coordinated action, and commitment to the child's well-being among the adults [39,125] and adaptive coparenting is considered a central contributor to infant survival since the dawn of humanity [94]. Still, there is a much cultural, ethnic and individual variations within and across societies in the extent of cooperative coparenting, and such variability depends on multiple factors, such as paternity certainty, exposure to infant cues and the amount of allomaternal care provided by other females from the group (e.g. grandmothers) [105].

Recent models describe the coparental bond as distinct from the marital relationship [126] and highlight the importance of a mutually-supportive coparenting for the development of children's mental health and social competencies [166]. In a series of studies we explored the behavioral, hormonal, and neural networks underlying coparenting, focusing on two types of coparenting described in the literature: collaborative coparenting and undermining coparenting.

In the first behavioral study, a microanalytic approach was used to examine coparental-child interaction, that is, a triadic interaction between two parents and their infant, assessing both the parent-child interaction and the relationship among the parents in supporting each other's parenting. Results revealed that when maternal coparenting was collaborative, that is, mothers supported father's involvement with the infant, fathers expressed more positive parental behaviors, such as vocalizations, positive affect, and high positive arousal than mothers. On the other hand, maternal positive parenting was independent from the father's coparental approach and was expressed under both undermining and collaborative coparenting from the father [72].

Mothers' and fathers' hostility levels toward each other measured during a conflict discussion decreased when they were exposed unconsciously to their own infant stimuli, that is, a picture of their infant appeared on a screen while they were discussing a typical conflict [130]. In an fMRI study, Atzil et al. [10] found online synchrony in cortical activations implicated in empathy and theory-of-mind, including the insula, IFG, IPL and LPFC, between mothers' and fathers' brains in response to their own infant stimuli. These findings are consistent with evolutionary theories on parenting [65] and show that the coupling between maternal and paternal physiology and behavior enable parents to synchronize their efforts in order to provide optimal care and protection for their children.

Finally, in a recent fMRI longitudinal study, we followed couples across the first six years of family formation, including opposite-sex and same-sex couples. Parents' brain responses to coparental stimuli (video clips of their partners interacting with the infants) were measured in infancy and parental OT and AVP were assayed. Coparental behavior was measured at three time points during the first six years of family formation: in infancy in a triadic interaction between the two parents and their infant, in preschool during a coparental discussion coded for collaborative and undermining behaviors, and at six years using self-reports. Results revealed that coparental behaviors were individually stable across time and measurement methods. Across family types the

coparental bond was underpinned by both the ventral striatum (VS) and caudate, striatal nodes implicated in motivational goal-directed social behavior. Whole brain PPI analysis indicated that both nodes were functionally coupled with the vmPFC, dlPFC and IOFC in support of the human coparental bond and this connectivity was stronger as collaborative coparental behavior increased. However, only the caudate showed distinct functional connectivity patterns that were linked with two stable coparental behavioral styles. Stronger caudate-vmPFC connectivity, which has been associated with cooperation [151], reward regulation [82], flexible goal-directed behavior, consideration of multiple outcomes to guide behavior [34], and delayed gratification [15], correlated with more collaborative coparenting and was associated with OT. Stronger caudate-dACC connectivity, which has been implicated in competition and conflict [11], was linked with an increase in undermining coparenting and was related to AVP, a hormone implicated in aggression, competition and the guarding of relationship exclusively in mammals [134]. Finally, dyadic path model showed that parental caudate-vmPFC connectivity in infancy predicted lower child externalizing symptoms at six years as mediated by collaborative coparenting in preschool [5]. Such findings provide the first neurobiological evidence that distinct neural pathways in the parent's brain in response to the other coparent and the endocrine systems and behavioral mechanisms related to those, serve an important regulatory role in children's development and may confer evolutionary advantages for the child, the family, and the whole group.

## 7. Conclusions and implications

It has been suggested that the nuclear family, consisting of primary caregiving mother, secondary caregiving father, and children, does not represent a universal format for optimal child development and many other childrearing formats may be found in the animal kingdom and across cultural communities [93,94]. Allomaternal assistance has been commonly practiced across a wide range of traditional human societies with high variability in the male's parental role [87]. Yet, over the past few centuries and across most modern Western societies children were raised by their biological mother and father, with the supplementary assistance from other women (wet nurses, nannies, female relatives, etc.), and the marital and coparental bonds were typically overlapping [109,143].

Lately, new types of families have been assembled due to political and socio-cultural changes in modern societies, and due to technological advantages that redefine the family unit in flexible ways. Men have become more involved in childcare, parents may or may not live in the same household, extended families become common again where parents are embedded in greater social networks, and more and more children are being raised in families headed by cohabiting-, step-, single- or same sex parents. Such family reorganization opened a renaissance in allomaternal care across human societies.

While there are remarkable variations throughout human history and across cultures in the way fathers and adult members other than the biological mother participate in childcare, the social and cooperative nature of childrearing has influenced children's psychological, social, and emotional well-being and increased infant survival [69]. Hence, it is plausible that throughout evolution, males' sensory and emotional exposure to their offspring have led to changes in both structural and functional neural circuits and the hormonal substrates related to them due to the human brain's enhanced plasticity. Based on our behavioral and imaging studies, and integrated with cumulative behavioral evidence in humans and animal models, we assume that humans' highly facultative paternal commitment may be built on an ancient alloparenting evolutionary substrate that supports a role of both male and female as direct caregivers with the ability to nurture the young, and that such caregiving neural system is based on human infants' innate abilities to elicit care and tune adults to adequate caregiving [62,68,77].

We suggest that not only the interpersonal bond between a mother and her infant, but also the bond between a father and his child, alongside a widespread social cooperation with other alloparents, facilitated the development of our flexible and adaptive social brain. Such highly plastic social brain supported the human ability to form complex cooperative social affiliations with others both within and outside the family and transformed humans into the uniquely collaborative hyper-social species they have evolved to become.

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