Clinical Child and Family Psychology Review (2022) 25:93–109
https://doi.org/10.1007/s10567-022-00381-9

The Neural Basis of Human Fatherhood: A Unique Biocultural Perspective on Plasticity of Brain and Behavior

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Accepted: 19 January 2022 / Published online: 5 February 2022

Abstract
With the growing involvement of fathers in childrearing and the application of neuroscientific tools to research on parenting, there is a need to understand how a father's brain and neurohormonal systems accommodate the transition to parenthood and how such neurobiological changes impact children's mental health, sociality, and family functioning. In this paper, we present a theoretical model on the human father's brain and the neural adaptations that take place when fathers assume an involved role. The neurobiology of fatherhood shows great variability across individuals, societies, and cultures and is shaped to a great extent by bottom-up caregiving experiences and the amount of childrearing responsibilities. Mechanisms of mother-father coparental brain coordination and hormonal correlates of paternal behavior are detailed. Adaptations in the father's brain during pregnancy and across the postpartum year carry long-term implications for children's emotion regulation, stress management, and symptom formation. We propose a new conceptual model of *HEAL*thy Father Brain that describes how a father's brain serves as a source of resilience in the context of family adversity and its capacity to "heal", protect, and foster social brain maturation and functionality in family members via paternal sensitivity, attunement, and support, which, in turn, promote child development and healthy family functioning. Father's brain provides a unique model on neural plasticity as sustained by committed acts of caregiving, thereby affording a novel perspective on the brain basis of human affiliation.

Keywords Paternal brain · Father-child relationship · Paternal care · Child development · Fatherhood

Who rides there so late through the night dark and drear?
The father it is, with his infant so dear;
He holdeth the boy tightly clasp'd in his arm,
He holdeth him safely, he keepeth him warm.
(From "Erlkönig" by Johann Wolfgang von Goethe).

Introduction

Research on the neurobiology of fatherhood has contributed some novel insights into the story of humanity as it unfolds; how biology, environment, social experience, and cultural norms intersect and jointly shape the adaptive brain and sustain the neuroendocrine architecture that underpins the human mind (Geary, 2000). Particularly interesting is how neurobiological changes in the father's brain and hormonal systems mirror current sociocultural changes and how they translate into long-term child developmental achievements and family functioning. An exciting question is whether and how such neurobiological changes may provide protective buffers under conditions of family adversity on the one hand, and might be served as biomarkers of social adversity, psychopathology, and dysfunctional parenting among high-risk fathers on the other.

Centuries of civilization have placed the *Father*, [from the Latin *pater*—a man who has sired a child (Merriam-Webster Dictionary, 2002)], in the role of a provider, moral and ethical authority, disciplinarian, sex-role model, and benevolent

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elder (Lamb, 2010). Across time and cultures, heroic myths have depicted the father-child relationship within the context of societal issues and themes such as pride, rivalry, faith, and punishment (e.g., the Greek myths of "*Oedipus*" and "*Daedalus And Icarus*", the biblical story of the "*Binding of Isaac*", and the Hindu myth of "*Yayati and Yadu*") and these functioned to shape socialization, usher the formation of moral laws and assist the preservation of social order.

Since the turn of the nineteenth century, mothers, at least in Western societies, were considered the most influential force in shaping children's physical and mental lives (Dye & Smith, 1986). The popularity of post-Freudian and attachment theories during the 1950-the 60s of the twentieth century constructed a mother-centric view of child development and deemphasized the father's *direct* contribution to healthy development or the formation of psychopathology (Badinter, 1981). For example, Winnicott (1960) thought that the central component of the father's role was to "*help mother feels well in her body and happy in her mind*" (p.114), and suggested that fathers play an important role in child well-being by buffering the hate generated in the mother–child relationship, allowing the "loving" aspects of the mother-infant bond to develop. Similarly, Margaret Mahler (1955) saw the father as the "*uncontaminated mother substitute*" during the separation-individuation process, and *"the knight in shining armor"* (p.6) who played a vital role in protecting the child from the regressive maternal forces during the rapprochement stage, while John Bowlby (1951), in his ethological-based attachment theory, suggested that the father's prominent role was to support the mother, emotionally and instrumentally, and this, in turn, contributed to children's healthy development.

The social movement of involved fatherhood along with the gradual re-organization of the traditional family in the Western world starting from the 1970s have stimulated research on fathers and encouraged scholars to advocate the importance of fatherhood and detail its influences on children's development, both directly, through father-child interaction, and indirectly via their impact (positive and negative) on the family's social and emotional climate. This resulted in a growing line of research, first on the effects of father absence and next on the impact of father involvement and coparenting on child development culminating in studies that empirically observed father-child interactions (Lamb, 2010). In addition, research in non-human mammals began to identify evolutionary mechanisms that underpin variations in paternal care, ranging from infanticide to complete avoidance to nurturing care (Clutton-Brock, 1991).

Lately, a growing body of ethnographic and observational research has begun to challenge the ethnocentric view on the "typical" Western family by studying fatherhood across a wide range of ethnic and social groups, including low-income and minority groups, as well as in traditional societies in the developing world (Cabrera et al., 2008; Hewlett, 1993). These studies highlighted the importance of *Allomothering*- the care of offspring by group members "*other than*" the biological mother, including fathers, and their key role in enhancing the survival and thriving of human infants (Feldman et al., 2019; Gettler, 2014; Rosenbaum et al., 2021).

Although interest in the neurobiology of parent-infant bonding is almost a century old, only recently has it been possible to characterize the neurobiological mechanisms that regulate parental behavior in humans (Feldman, 2015, 2016). Mammalian maternal care is obligatory for offspring survival, and mammalian mothers undergo significant changes in physiology, morphology, and behavior to become mothers and successfully rear their offspring. Paternal care is observed in only 3–5% of mammalian species. Still, in these few species, the onset of fatherhood is often accompanied by pronounced neuroplasticity and behavioral responses to the young (Feldman et al., 2019; Horrel et al., 2020).

Despite significant progress in research on the neurobiology of human parent–child bonding over the last two decades, research on the neurobiology of fatherhood faces unique challenges and carries exciting opportunities. Most studies still focus on the mother and mainly describe functions and processes based on cross-sectional studies on biological mothers and their infants from "traditional" nuclear families. As such, the mechanisms underlying neuroplasticity in fathers and their functional significance are not well understood. Moreover, most studies of the neurobiology of fatherhood focus on healthy partnered fathers from middle-class families who assume a secondary caregiving role, and do not explore potential neurobiological processes implicated in risk and resilience in the context of high-risk fatherhood or among fathers that do not accept parental responsibility. As societal roles of male caregivers change, untangling the neural mechanisms that sustain human fatherhood, their neural correlates, and their long-term effects on child development is a critical next step toward advancing our understanding of human attachment within a broader interpersonal context as well as the impact of the family environment on children's mental and physical health. Since much less is known about the neurobiology of "*Other than the mother*" care (Kenkel et al., 2017), including paternal care, examining sex differences and commonalities in the neural and neuroendocrinology of human caregiving may add to the larger knowledge base of human development and describe how multiple caregivers join their forces at critical developmental nodes to optimize infants' well-being and chances of survival. Studying the neurobiology of fatherhood provides a unique window into neural plasticity within the parent–offspring interface, the context where Darwin (1859) initially proposed structural and functional adaptations take place.

In this paper, we provide a theoretical model on the neurobiology of human fatherhood. Given the size and scope of this literature, this paper is by no means a comprehensive review and addresses mainly findings from our work at the Center for Developmental Social Neuroscience over the past 20 years and selected recent findings from other research groups. We begin by identifying similarities, differences, and complementarity between maternal and paternal caregiving behaviors, and the father's contribution to child cognitive and social-emotional development across cultures and societies. We then discuss the neurobiological and neuroendocrine underpinnings of human paternal caregiving, describe the father's brain as comprising several interconnected neural networks that support paternal caregiving, and address hormonal and behavioral correlates of the father's brain. Next, we propose a new model of *HEAL*thy Father Brain (see Fig. 1) as a conceptual framework to further understand how the neurobiology of fatherhood can enhance resilience and promote family cohesion and long-term child development. Lastly, we outline some important unresolved topics in human fathering research and discuss persistent challenges and critical new directions. We highlight how future cross-cultural and prospective longitudinal pregnancy/birth cohort studies of healthy and high-risk samples can illuminate some of these critical gaps and describe opportunities for prevention and early-life interventions that can 'break the cycle' of adversity in vulnerable children and families.

Paternal Caregiving, Child Development, and Cultural Variability

Paternal caregiving research has highlighted aspects related to paternal behavior, father-child relationship, longitudinal outcomes, and cultural variability.

Paternal Behavior and Father-Child Relationship

To describe the unique patterns of father-infant synchrony, the parent's careful adaptation of caregiving behavior to the infant's social signals, we visited the homes of one hundred Israeli middle-class families and videotaped free play

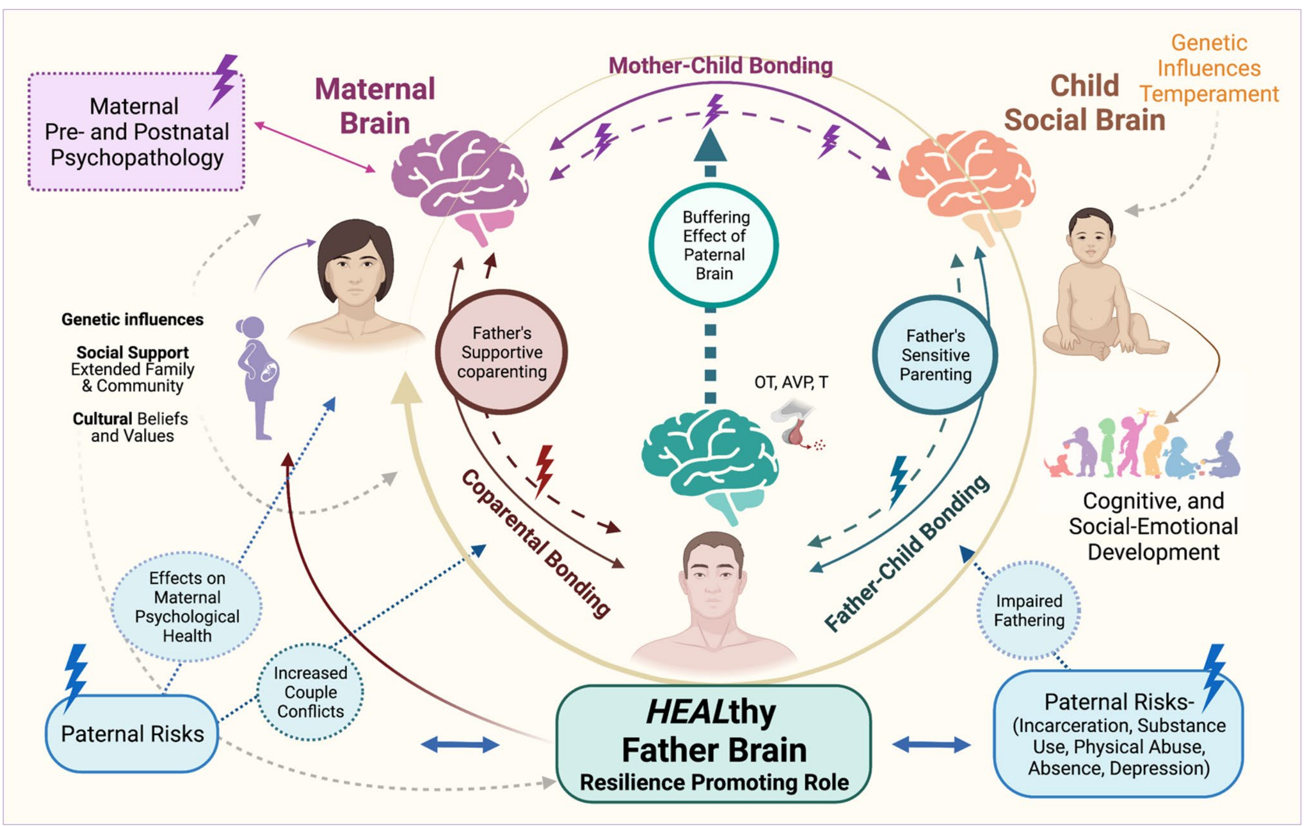

Fig. 1 *HEAL*thy Father Brain. A suggested model of how the neurobiology of fatherhood fosters resilience; how it promotes adaptive family functioning and long-term child cognitive, social-emotional development and well-being, how it may "heal", protect, or tune family members' social brains in the context of high-risk familial conditions via father-mother supportive coparenting and father-child well-attuned interaction, and how the network integrity in the father's brain becomes compromised in the context of paternal risk factors, which in turn interrupts optimal family processes

interactions between infants and each parent in the natural habitat. We found that mother-infant and father-infant pairs engaged in similar levels of synchrony, yet the overall structure of synchrony presented a parent-specific pattern. Mother-infant interactions cycled between medium and low arousal and involved mutual gazing, co-vocalizations, and affectionate touch. Father-infant interactions, on the other hand, contained quick peaks of positive arousal, focused on the environment, and involved more stimulatory contact and play. These two types of synchronous experiences chart the "rhythm of safety" versus the "rhythm of exploration" and infants require these two forms of synchrony to grow and adapt (Feldman, 2003). These findings are in line with studies indicating that maternal sensitivity is expressed by emotional warmth and support, whereas paternal sensitivity is expressed through physical stimulation and playful interactions (Volling et al., 2002).

Overall, a focus on highly arousing play is more typical of the paternal style. Compared to mother–child interaction, play is more characteristic of the father-child relationship in Western cultures (Cabrera et al., 2017); Fathers tend to play more often while engaging in caregiving tasks than mothers. Their play interactions tend to be more physical, spontaneous, playful, led by the child, focused on exploring the social world, and include more limit-setting, teaching skills, and conflict resolution (Caldera & Lindsey, 2006; John et al., 2013).

However, regarding sensitive caregiving, fathers appear to be as sensitive as mothers in their overall acknowledgment and response to the child's signals and specific vulnerabilities. In a series of studies (Hirschler-Gutternberg et al., 2015; Ostfeld-Etzion et al., 2015, 2016), we compared parent–child interactions and preschool children's self-regulatory skills in high-functioning children with Autism Spectrum Disorder (ASD) compared to typically developing controls (TD). Mothers and fathers in both groups were equally aware of their children's distress signals during stressful paradigms. However, both mothers and fathers of children with ASD utilized more co-regulatory behavior during moments of high arousal, for instance, providing more physical comfort to the child, touching/hugging, cognitive reframing, and emotional reflection. Mothers exhibited more direct support during a delay gratification paradigm compared to fathers in both the ASD and control groups, which may relate to the mother's role as the primary caregiver. These findings underscore the great effort mothers and fathers to children with ASD recruit to buffer their children's social distress and demonstrate the parents' careful attunement to their children's social difficulties and their effort to carefully modulate the child's emotions.

From an attachment perspective, studies have shown that not only were children attached to both mother and father but that the nature of their attachment to each parent was similar (Verissimo et al., 2011) and that similar proportions of children were securely attached to their fathers and mothers (Lickenbrock & Braungart-Rieker, 2015). Moreover, the intergenerational transmission of attachment showed the same pattern for fathers and mothers (Verhage et al., 2016). A recent study (Abraham et al., 2021a, 2021b) found similar patterns of intergenerational continuity of maternal and paternal parenting styles, in terms of care and overprotection, across three generations of American families at high and low risk for major depression (MDD).

Fathers' Influences on Children's Cognitive and Social-Emotional Development and Mental Health

In testing the long-term effect of parent-infant synchrony, we found in an Israeli sample that mother-infant and father-infant synchrony were each predictive of child's symbolic complexity in preschool (Feldman, 2007). Furthermore, both maternal and paternal sensitivity are linked with children's self-regulated compliance, an orientation that supports the child's (Feldman & Klein, 2003). In another longitudinal study from infancy to adolescence, we found that reciprocal interactions with both mother and father supported children's social skills with peers in preschool and relationships with best friends in adolescence, charting links from parental to filial attachment (Feldman, 2016). However, while reciprocity with the mother predicted children's social competencies with peers and dialog with a best friend, reciprocity with the father reduced preschoolers' aggression and enabled adolescents to manage conflicts with respect, underscoring the father's unique impact on the modulation of aggression (Feldman et al., 2013). Similarly, involved Pacific Islands fathers who showed more attentiveness and help in schoolwork had children with fewer behavioral problems upon school entry, even after controlling for relevant maternal covariates (Tautolo et al., 2015). These findings are supported by a meta-analysis of father involvement in families from a diverse ethnic background in the USA, which showed that both active (e.g., playing, conversation) and passive (e.g., financial support, presence) father involvement led to lower emotional and behavioral problems in their children (Harris, 2015), and accord with numerous studies showing that father involvement and paternal sensitivity serve as protective factors against aggression and promote social adaptation in children and adolescents (Dumont & Paquette, 2013; Opondo et al., 2016).

While the quality of attachment to mother and father was similar, such security may be associated with different developmental outcomes. For example, Portuguese children who developed a secure attachment with their father, but not with their mother, tended to have more friends after controlling for maternal attachment (Verissimo et al., 2011;

Verschueren & Marcoen, 2005). USA boys securely attached to their father exhibited less internalizing behavior and had better peer competence (Marcus & Mirle, 1990), and secure father-child attachment predicted enhanced self-efficacy in Chinese children (Pan et al., 2016). Overall, authors have suggested that a secure attachment to the father may help the child better understand how to develop friendship relations in more complex social networks. These findings are in line with several studies in the USA and China, which documented that the quality of father-child relationship reduces preschoolers' aggression, promotes better abilities in dealing with peers, enhances social competence and popularity, and enables adolescents to manage conflicts with friends (Baker et al., 2011; Zhang, 2013).

Cross-cultural observations of fathering have revealed differences in paternal behavior related to child outcomes in culture-specific ways. We followed 141 low-risk Israeli and Palestinian families. We found that in both middle eastern cultures, the way mothers and fathers resolved conflicts and exerted discipline contributed to children's social adaptation. Yet, more culture-specific effects were found for fathering, which led to the hypothesis of "differential pathways, shared process" of fathering across cultures. For instance, "intrusive-controlling" fathering in the Israeli group interfered with children's social development, whereas greater paternal control functioned in the opposite way in the Palestinian society and enhanced preschoolers' social competencies (Feldman & Masalha, 2010).

A few studies investigated the contribution of paternal caregiving and involvement to children's well-being and development among low-income minority families. In a large study of 11,473 preschool-aged children and their parents across a diverse group of Caribbean countries, researchers found that mothers were more likely to engage in cognitive and social interactions with children compared to fathers. However, both parents' engagement predicted their children's literacy and social skills (Yildirim & Roopnarine, 2017). In another longitudinal study that aimed to characterize father involvement in a low resource South Asian context, Maselko and colleagues (2019) investigated the associations between father involvement and child development in 996 families across the first year of life. They found associations between father involvement, both overall engagement and more specific involvement, such as during play or soothing, at three months with child's social-emotional development at six months, and several domains of development at twelve months, including motor skills and cognitive functions. Furthermore, in another large sample of rural low-income Latinos families, Pancsofar and Vernon-Feagans (2006) found that during a shared task, father's, but not mother's vocabulary, predicted more advanced language development at 15 and 36 months of age. Other researchers found that reading habits among Latino fathers were directly associated with their children's academic achievement (Goldenberg et al., 2005; Ortiz, 2004), and that Latino fathers who were attuned and sensitive to their toddlers during play were nearly five times more likely to have children within the normal range on a cognitive measure as compared to fathers who were low in sensitivity (Shannon et al., 2002; Shears, & Robinson, 2005).

While mounting research has been dedicated to identifying maternal risk factors for adverse childhood outcomes, far less attention has been given to the effect of paternal risk factors on fetal and child development. In a study that included 36,731 birth records collected in New York, USA, from 2004 to 2015, the authors (Meng & Groth, 2018) found that paternal risk factors of age (older age), race/ethnicity (other than non-Hispanic white), and educational level (high school or less) were significantly associated with adverse birth outcomes (e.g., preterm birth, low or high birth weight and small for gestational age) even after adjustment for maternal demographic, medical, and lifestyle factors, supporting the unique association between fathers and neonatal health.

The potential impact of paternal psychopathology, mainly depression, on child development has been the focus of increasing research in the past decade. For example, in a birth cohort study of 1089 American families, paternal depression, when a child was three years old, was associated with increased odds of child neglect at age five, even after accounting for the strong effects of maternal parenting risks (Lee et al., 2012). In another national prospective study of American children and their families, after analyzing data on 4109 two-parent families, Paulson and colleagues (2009) reported that 14% of mothers and 10% of fathers showed elevated levels of depressive symptoms at nine months. Maternal and paternal depression at nine months was negatively associated with the quality of parent-to-child reading interactions. However, only for fathers was earlier depression associated with later reading to child and child's expressive vocabulary development at 24 months. Another study found that paternal depression was associated with a less engaged, less positive style of father–infant interaction, which in turn predicted increased behavioral problems in young children (Barker et al., 2017).

A few key sociodemographic and economic factors, such as a father's younger age, presence or absence in the home, employment status, and job prestige and insecurity, were linked with risk for physical child abuse and neglect (Guterman & Lee, 2005). Fathers' fewer economic resources were associated with greater child abuse potential, inconsistent fathering, and poorer quality of home environment (Miller & Azar, 2019).

In addition, several psychosocial factors related to the father's experiences and behaviors in the family context also appear to play an important role in shaping families' risk for physical child abuse and neglect, including father's substance or alcohol abuse, history of childhood maltreatment in this own family of origin, quality of direct child-caring activities, and the degree of coparenting relationship (supportive or undermining) (Scott et al., 2021).

The independent and additive contribution of fathers' cognitive deficits, biases, and distortions with maltreatment risk indicators was tested in a sample of 61 disadvantaged resident fathers of children aged two–six years living in rural areas in the USA (Miller & Azar, 2019). They found that overall cognitive deficits factors in fathers were associated with more inconsistent parenting and with maladaptive injury prevention beliefs. Specific risk factors of unrealistic expectations for children and poorer executive functioning were related to more maladaptive injury prevention beliefs. Findings highlight the importance of a father's cognition in children's risk of physical abuse, neglect, and unintentional injuries.

Research on the protective role of father-child relationships and father involvement pales in comparison to studies on fathers' role in child maltreatment (Scaife, 2008). In our studies, we found that the protective role of paternal care may become more important when the mother is depressed. In the context of maternal depression and low mother-infant synchrony, sensitive and reciprocal fathering can mitigate the adverse effects of maternal depression on the family process, which was less cohesive with less harmonious and collaborative style when the mother was depressed and father uninvolved but improved when the father showed greater involvement even if the mother was chronically depressed (Vakrat et al., 2018a). Similarly, sensitive fathers reduced in half the increased prevalence of child psychiatric disorder in families where the mother was depressed (Vakrat et al., 2018b). Findings underscore the father's resilience-promoting role in cases of maternal psychopathology and emphasize the role of reciprocal and sensitive paternal behavior in promoting child resilience (Feldman, 2021).

In summary, integrating this body of work on father-child relationship and attachment, father involvement, and paternal protective and risk factors and their long-term consequences for children's development across cultural communities, findings demonstrate the high variability of paternal care and elucidate both diversities and commonalities in father's role and involvement, depending on the local ecological setting, childrearing philosophies, mating systems, social environment, and status. There are some similarities, differences, and mainly complementarity between mothers' and fathers' responsiveness to their children and their contribution to child development, determined not only by biology but also by cultural beliefs and values (Cabrera et al., 2014). While there are wide variations in the ways in which fathers interact with children within societies and across cultures, research suggests that the physical presence of a father, as well as the close emotional tie between father and child, contribute to children's overall development and well-being. At the same time, a host of biological, familial, and environmental-cultural factors may mediate and/or moderate these associations. Still, it is important to remember that most existing studies on paternal caregiving still come from Western societies. Further work is needed on paternal caregiving across cultures and sub-cultures.

Plasticity of the Paternal Brain: Effects of Paternal Caregiving and Coparenting on Neural Structure and Function

Imaging studies of the parental brain have typically exposed parents to their own infant stimuli, including cries, pictures, or videos, in comparison with unfamiliar age- and race-matched infants, tapping the "exclusive" component in attachment relationships. Within this line of work, studies of the maternal brain are still more abundant than those tapping the paternal brain.

In reviewing fMRI studies (Feldman, 2015, 2020; Numan, 2020) of parents' brain responses to infant stimuli, several overall conclusions emerged. First, strikingly, Western middle-class mothers, fathers, and non-parents activated the same structures to infant stimuli, which assemble into a *global human parental caregiving* network. Studies presenting infant cues to adults elicited activations in motivation/reward circuit, including the ventral tegmental area (VTA), nucleus accumbens (NAcc), orbitofrontal cortex (OFC), as well in neural systems involved in social understanding, such as the medial prefrontal cortex (mPFC) and superior temporal gyrus (STG), and emotional recognition and empathy: anterior insula (AI), inferior frontal gyrus (IFG), anterior cingulate cortex (ACC) (Abraham & Feldman, 2018a; Rilling &Young, 2014). Second, the affiliative bonding and the cooperative nature of childrearing by human adults and its reward, regulation, and approach-related motivation are ignited by two ancient neuroendocrine systems that support neural plasticity—the oxytocinergic (OT) and dopamine (DA) systems, which play an important role across animal evolution to ensure survival and increase adaptation (Feldman, 2017, 2020; Hrdy, 2011).

Lately, neuroimaging studies on human fathers have brought unprecedented information about the paternal brain, its flexible adaptations to caregiving experiences, and its role in the development of father-child bonding. fMRI studies comparing primary caregiver mothers' and secondary caregiver fathers' brain responses to infant stimuli, particularly infant cry, reported that mothers showed greater amygdala activation, a key region in the ancient limbic circuit. In contrast, fathers exhibited greater activations in socio-cognitive cortical areas, including the IFG, inferior parietal lobule

(IPL), supplementary motor area (SMA), and superior temporal sulcus (STS) (for review, see Glasper et al., 2019; Rilling & Mascaro, 2017). In another study measuring brain function in 39 first-time fathers in the USA as they listened to their own infant cry, fathers showed widespread activations in circuits involved in empathy and approach motivation, and stronger activations were associated with younger infant age. Interestingly, older fathers found the infant cry as less aversive and exhibited attenuated response in the dorsal ACC (dACC) and AI, suggesting that older fathers are better able to avoid the distress associated with empathic over-arousal in response to infant cry (Li et al., 2018). Freeman and Young (2013) examined the neural responses of 20 new fathers in the USA to infant cries while either passively listening or actively attempting to console the infant. Compared to passive listening, active response deactivated brain regions involved in anxiety and stress, including the amygdala and hippocampus, and activated brain circuits implicated in empathy and approach motivation, including the dACC, VTN, Substantia nigra (SN). Fathers who reported greater frustration in the inconsolable condition had less activation in the ventral pallidum, an important region supporting parental caregiving and rich in OT receptors in humans. The authors suggest that the frustration during the active responding task, which in extreme cases can lead to infant abuse, may involve a combination of low approach motivation and low emotion regulation.

Another mechanism of neural plasticity was observed in gray-matter-volume changes in new mothers and fathers across the first postpartum months. In a longitudinal MRI study of 35 white American mothers and fathers, gray matter increased in both parents in the amygdala and hypothalamus, areas of the "mammalian caregiving network", as well as in PFC. Fathers, but not mothers, showed gray matter increase in the striatum, subgenual-cortex, and STS. Interestingly, while mothers' brains showed only gray-matter increases, fathers also exhibited gray matter decreases in the OFC, posterior cingulate, fusiform gyrus, and the insula. These findings suggest that fathers reduce levels of ambiguity and stress during the first months of parenting to initiate them into the paternal role (Kim et al., 2014).

Recent models in social neuroscience have proposed that social neuroscience should move from studying the functionality of a single brain to detailing how two brains communicate during live social interactions (Bilek et al., 2015; Levy et al., 2021). Within this line, several recent studies showed how attachment relationships provide a useful context for the study of brain-to-brain synchrony (Djalovski et al., 2021; Endevelt-Shapira et al., 2021). Few imaging studies investigated the mechanisms underpinning brain coordination among coparents and those involved in father-child brain-to-brain synchrony. In an fMRI study, we found inter-subject synchronization among 30 Israeli mothers and fathers while couples watched their own infant videos (Atzil et al., 2012) in cortical regions implicated in empathy and mentalizing, such as the pre-motor and motor cortices, IPL, IFG, and insula. A recent hyperscanning fNIRS study on 24 Singaporean heterosexual couples reported that the presence of a coparenting spousal partner (vs. sitting in different rooms at different times) was associated with greater coparental synchrony in attentional and cognitive control circuits, including the dorsal and ventral-parietal pathways, while listening to infant vocalization (Azhari et al., 2020). Such neural synchrony among parents may assist the formation of shared and efficient caregiving in maximizing infant survival, and this may have played an important role in the evolution of the human family.

Finally, as for father-child neural synchronization, Azhari and colleagues (2021) found a unique inter-subject neural synchronization in the bilateral mPFC in 29 father-preschooler dyads during co-viewing of narrative visual scenes compared to control dyads (randomly paired signals), which was modulated by father's age. Dyads with older fathers exhibited diminished synchrony, and older fathers were also observed to display greater activation in the frontal right cluster compared to their younger fathers. The authors speculate that a father's age may confer parents with a greater sense of security in their parenting role without the need to excessively synchronize with their child's social cues throughout the interaction. However, more research on the effects of a father's age on parenting brain mechanisms is needed.

In another hyperscanning fNIRS study, 66 German fathers and their six-year-old children showed increased brain-to-brain synchrony in bilateral dlPFC and left temporoparietal junction (TPJ) during a collaborative problem-solving task, which was associated with the father's positive attitude toward parental role (Nguyen et al., 2021). These hyperscanning studies begin to uncover a range of important discoveries about which brain regions are active during early social interaction and illustrate the importance of studying the family system in ecologically valid contexts and focusing on multiple subsystems such as interactions between fathers and children and between coparents.

Research in mammals has suggested that mammalian males may begin to acquire paternal phenotypes before the infant is born (Storey & Ziegler, 2016). Imaging the brains of 72 Japanese males, including expectant fathers and childless men, to infant interaction videos showed that while all men exhibited activations in regions of the *global human parental caregiving* network, only expectant fathers showed changes in AI, IFG, and amygdala. These changes were associated with gestational age and the men's perception of parenting (Diaz-Rojas et al., 2021). A recent prenatal fMRI study reported greater activations in regions that support mentalization, including STS and dmPFC, during a "Theory of Mind" task in a sample of 39 expected fathers in the USA, which were associated with fathers' parenting believes about attuned parenting at three months postpartum (Cardenas et al., 2021). A longitudinal fMRI study of processing threat to infants examined the neural basis for protective parenting before and after the birth of Dutch fathers' first child. The authors found increased neural responses in bilateral amygdala and other cortical regions, such as the insula, superior frontal gyrus (SFG), and ACC, possibly indicating preparation for action, when expectant fathers imagined that the threatened infant was their own rather than someone else's. After the birth of their baby, no differences between brain responses to one's own and someone else's infant were found. Still, fathers who reported more protective behavior postnatally had greater frontal pole activity when they imagined that their own infant was in a similar danger to that presented in the movie (Van 't Veer et al., 2019), suggesting that protective mechanisms present during pregnancy may broaden to include other unfamiliar children after the experience of having an infant. Those studies on fathers-to-be highlight that the transition to parenthood is a window of growth and change for men and may offer a more nuanced understanding of the prenatal factors that shape children's development.

Among the key questions regarding the paternal brain relate to the neural processes that support the human father's adaptation to the caregiving role and experiences. It was unclear how a father's brain would organize when fathers raise infants without maternal involvement but also without the biological priming by the hormones of pregnancy. To tease out sex from primary/secondary caregiving role, we (Abraham et al., 2014) recruited three groups of first-time Israeli middle-class parents: 20 mothers (primary caregivers), 21 heterosexual fathers (secondary caregivers), and 48 primary caregiver homosexual biological and adoptive fathers raising infants within a partnered relationship without maternal involvement since birth. Parents underwent fMRI observing own versus unfamiliar parent-infant interaction videos. In all parents, own infant cues activated multiple parental brain areas, including structures in the limbic-subcortical circuits and cortical networks implicated in empathy, embodied simulation, mentalizing, and emotion regulation. Similarities between mothers and fathers, primary- and secondary caregivers, and biological and adoptive parents were found in most brain structures, supporting previous findings indicating that these regions consolidate into a *global human parental caregiving* network in all adults that assume an active parental role. However, two areas exhibited marked gender differences. Mothers showed fourfold amygdala activations compared to secondary caregiving fathers, and fathers had higher activation of the STS. The surprising findings emerged for primary caregiver fathers, who showed high amygdala activations similar to mothers, alongside high STS activation comparable to secondary caregiving fathers. Testing the mechanisms underpinning this amygdala hyper-activation, it was found that only among primary caregiver fathers was there functional connectivity between the amygdala and STS. Moreover, in all fathers, the degree of connectivity between amygdala and STS correlated with the time father spent alone with the infant and the range of childrearing activities. Recently, in an MRI study, Long et al. (2021) examined the volume of the hypothalamus, an important subcortical brain region for mammalian bonding, in 50 German fathers of five–six-year-old children and 45 non-fathers. While no differences in hypothalamus volume were found between fathers and non-fathers, hypothalamus volume was positively associated with fathers' enjoyment during interactions with their child and their beliefs about the importance of a father's engagement and involvement.

Interestingly, the father's brain activation is also sensitive to baby-related interventions. In a recent fMRI randomized controlled trial (RCT) study, Riem and colleagues (2021) examined the effect of baby carrier intervention (caring the infant in a carrier for at least six hours per week, for three weeks) on neural responses to infant crying in 63 first-time Dutch fathers. While all fathers showed reactivity to infant cry in the *global human parental caregiving* network, only those who used the infant carrier exhibited increased amygdala activity to infant crying, compared to the control group (who used a baby seat). This effect was most pronounced in fathers with adverse childhood experiences.

In sum, the abovementioned findings point to the existence of a human *global parental caregiving* network that is mainly consistent across parents—males and females alike, and activates in a relatively similar fashion in both biological and adoptive parents. This network is characterized by great plasticity, and its malleability is a function of the parent's caregiving role, early-life adversities, and current social experiences, expectations, and beliefs. It appears that a father's brain adapts, via co-wiring the maternal and paternal pathways, to the survival demands of infant care, and a father's brain may thus provide a novel model on the plasticity of the "affiliative brain" that evolves through involvement, commitment and effort and is not triggered by hormones of pregnancy (Feldman, 2017; Feldman et al., 2019; Rilling & Mascaro, 2017).

Overall, findings on the parent's brain response to infant cues underscore both commonality and specificity in males and females, suggesting that distinct neurobiological pathways may underpin human maternal and paternal caregiving and that both may be sensitive to the interplay between biology and social experience. Compared to mothers, fathers tend to exhibit more limited structural changes during the transition to parenthood and show less neural activation in the limbic "mammalian caregiving" regions such as the amygdala. In contrast, fathers tend to display greater activations in cortical regions involved in social understanding and mentalization. These findings may reflect the phylogenetically ancient role of maternal care, biologically embedded in reward, vigilance, and motivation processes, and the facultatively expressed paternal care, deriving more from social and cultural processes.

Hormones and Behavior as Correlates of the Paternal Brain

Three hormones were found to play a critical role in the expression of paternal caregiving in humans and other species, and these neuroendocrine systems undergo reorganization at the transition to parenthood: oxytocin (OT), vasopressin (AVP), and testosterone (T) (Wynne-Edwards, 2001). Interestingly, although OT has been repeatedly implicated in processes of mother-infant bonding, including birth and lactation, in several samples, we have shown that at the transition to parenthood, both plasma and salivary OT levels increased to the same extent in mothers and involved fathers (Feldman, 2016). In another study of 160 middle-class Israeli cohabitating mothers and fathers, we found that OT correlated with the parent-specific type of synchrony; with affectionate contact, mutual gazing, and co-vocalizing in mothers, and with exploratory play and stimulatory contact in fathers (Gordon et al., 2010). These findings are consistent with work by other labs. For example, higher plasma OT levels were found among 88 American partnered fathers compared to 55 non-partnered non-fathers (Mascaro et al., 2014a, 2014b). In another study, 45 American fathers engaged in more playful proprioceptive touch with their six-month-old infants showed higher OT, both extracted and unextracted levels. However, paternal affectionate touch was associated only with unextracted OT levels, while fathers who did not engage in any physical contact had the lowest OT extracted and unextracted levels (Morris et al., 2021).

Arginine vasopressin (AVP), a structurally similar neuropeptide to OT (Feldman et al., 2016), plays a central role in mammalian fathering (Story et al., 2020). In a study of 119 Israeli mothers and fathers, AVP correlated with greater father exploratory play and joint attention, while OT was linked with fathers' affectionate contact with the infant (Apter-Levi et al., 2014). Furthermore, following AVP, but not OT intranasal administration, 46 Dutch fathers-to-be invested more time watching the baby-related avatars than non-fathers (Cohen-Bendahan et al., 2015).

A decline in testosterone (T) was observed in fathers from the USA, Europe, and the Philippines during pregnancy and the transition to parenthood (Gettler et al., 2011; Perini et al., 2012; Saxbe et al., 2017). T levels correlated with more positive paternal behavior in samples of Jamaican, Canadian, and USA fathers, supporting theories on the trade-off between mating and parenting (Gray et al., 2017; Kuo et al., 2018). Interestingly, in a study of 80 Israeli couples, we found that while paternal plasma T was associated with lower father-infant synchrony at six months, only when T levels were high was there a negative association between paternal OT and affectionate touch. In contrast, among mothers, only under high T levels, there was a positive association between OT and maternal touch (Gordon et al., 2017).

Findings on the complex bidirectional effects of hormones in the context of parental caregiving and family relationships are in line with two recent studies (Gettler et al., 2019, 2021). In the first study, the authors examined mothers' and fathers' OT and T in a small-scale fishing farming society in the Republic of the Congo. They found that fathers who were viewed as better providers had lower OT and higher T levels but also had more marital conflict compared to those with reduced T and higher OT. On the other hand, mothers in conflicted marriages showed the opposite profiles of lower T and higher OT. Mothers also had higher OT and lowered T if fathers were uninvolved in direct child caregiving activities but showed an opposing pattern for the two hormones if fathers were involved in childrearing and care. In the second longitudinal study of 211 USA men, the authors found cross-over interaction (OT x T) in predicting fathers' later postpartum involvement and father-child bonding. Fathers whose T levels declined while holding the infant on the day of birth reported spending more time playing with their infants three months later, but only if their OT levels increased, compared to fathers who experienced an increase in both hormones.

Moreover, intranasal OT administration was found to impact hormonal response in fathers and infants. OT administered to fathers markedly increased both father's and infant's salivary OT levels (Weisman et al., 2012); decreased father's cortisol (CT) (Weisman et al., 2013), and altered T levels and fluctuations (Weisman et al., 2014), all as a function of an increase in paternal and infant social behavior, including touch, gaze, and exploratory behavior.

These findings highlight the flexibility of human parental neuroendocrine systems as related to fathers' roles and functions in the family setting and appear to present a similar picture across cultures.

Given the evidence that OT, AVP, and T influence human paternal behavior, studies have also investigated whether these hormones modulate activation in the neural circuits implicated in fathering. We found that father's OT was associated with STS activation and father-infant synchrony (Abraham et al., 2014) and negatively correlated with areas in the *emotion regulation* network, including dlPFC and dACC in Israeli fathers in response to own infant's video clips (Atzil et al., 2012). These findings also mirror the gray matter findings, highlighting the associations between paternal OT and neural pathways underlying social-cognitive processes. While amygdala activation was much higher in mothers, compared to fathers, and positively correlated with OT, it was linked with AVP in fathers (Atzil et al., 2012), underscoring links between these two ancient neuropeptides of the OT-family and the ancient limbic system that underpins parental care in mammals and other taxa (Feldman, 2017).

In a double-blind, placebo-controlled MRI study, Li and colleagues (2017) explored the effect of intranasal OT administration on the functionality of the father's brain. The researchers randomized 30 USA fathers to receive either intranasal OT or placebo or AVP or placebo before the scan while viewing their children. Intranasal OT, but not AVP, increased activation in the caudate and the dACC, suggesting the OT augments activity in brain circuits implicated in reward and motivation as well as empathy and attention.

Furthermore, USA fathers' T levels were linked with lower activations in the VTA and middle frontal gyrus (MFG), key components of the mesolimbic reward-motivation system, and emotion processing, respectively, in response to viewing pictures of one's own child (Mascaro et al., 2014a, 2014b). T was also found to play a role in expectant fathers' brain response to infant cry. In a recent study, Khoddam and colleagues (2020) measured neural, behavioral, and psychological responses of 34 expectant fathers to infant cry. They found that higher prenatal T predicted greater activation in the supramarginal gyrus (SMG), implicated in social cognition, and the precuneus, involved in arousal and reward learning.

Very few studies have addressed the effects of fathers' childhood adversity and psychopathology on their brains and hormonal systems. In an MRI study of 121 new and expectant fathers in the Netherlands, negative childhood caregiving experiences were associated with fathers' difficulties to regulate behavioral responses to infant crying. However, stronger structural connectivity between the amygdala and PFC, which supports effective downregulation and inhibitory control, buffered the effects of father's childhood maltreatment exposure and excessive handgrip force during infant crying (Alyousefi-van Dijk et al., 2020). Authors speculate that maltreated fathers with high tract integrity in the PFC-amygdala connection might be protected against the effects of childhood maltreatment on emotional hyperreactivity and impaired behavior, pinpointing a resilience component in the intergenerational transmission of maltreatment. In another study, Verhees and colleagues (2021) examined associations between childhood maltreatment experiences, CT and T concentrations, and the ability to modulate handgrip force when exposed to infant crying in 152 expectant and new Dutch fathers. Fathers who experienced more maltreatment during childhood used more excessive handgrip force during infant cry sounds. Still, no links were found between father's CT and T levels and experienced childhood maltreatment or handgrip strength modulation. These findings confirm that fathers' adverse childhood experiences reduce their ability to regulate their behavioral responses during infant cries. Only one study examined fathers' hormones in the context of paternal depression. In a study of 149 American couples (Saxbe et al., 2017), mothers and fathers reported on postpartum depressive symptoms at two, nine, and fifteen months postpartum, and paternal T levels were assessed at nine months. Fathers with lower T reported more depressive symptoms at two and nine months postpartum. However, whereas higher paternal T was found to protect against paternal depression, it contributed to maternal distress and suboptimal family outcomes (e.g., partner aggression) at 15 months postpartum.

Overall, studies on human fathers show that hormonal changes are associated with father-specific neural and behavioral markers of human parenting and that these changes parallel the amount of active paternal behavior and father's well-being.

*HEAL*thy Father Brain: Resilience, Risks and Long-Term Implications for Children's Cognitive, Affective and Social Processes

We propose a conceptual model for the *HEAL*thy Father Brain (Fig. 1) as a "situated" organ that adapts, via bottom-up processing and behavior-based inputs, to the changing demands of family and social life and culture-specific living conditions. Our model highlights the role of the healthy father's brain and its plasticity as a resilience buffer under a host of high-risk family conditions, in particular under conditions of early-life maternal inadequate care, by supporting the partner's caregiving and increasing mental health and well-being, reducing family distress, and promoting positive father-child relationship, all of which in turn, may "*heal*", protect and shape family members' social brains and have positive long-term consequences for children's health and development. Our model also includes potential paternal risk factors (e.g., absence, physical abuse, substance use, depression), that may be associated with structural and functional abnormalities in the father brain, resulting in impaired caregiving and disruptions of father-child and coparenting bonds- all of which increase the risk of adverse psychological outcome in children.

While evidence supports the hypothesis that the human parental brain marks an evolutionary apex and promotes the infant's ultimate ability to parent the next generation, to date, very few studies examined the longitudinal associations between parents' brain responses to infant cues and children's later social-emotional developmental outcomes. In our longitudinal study of 68 Israeli biological and adoptive primary caregiver mothers and fathers, we employed network integrity indices in the parental brain in infancy as predictors of children's social-emotional and neurohormonal development across the first six years of life. Network integrity-the degree to which structures cohere into a network-like functioning, serves as a marker of neural plasticity (Lambert et al., 2011) and was measured for three global networks: *Core limbic* (e.g., amygdala, PAG, VTA, striatum), *Embodied simulation* (e.g., AI, ACC, IFG) supporting empathy and interoception, and *Mentalizing* (e.g., STS, vmPFC, dmPFC) related to theory of mind. No differences emerged in network integrity between primary caregiver mothers and fathers, and in both, exposure to own infant stimuli, compared to an unfamiliar infant, led to an increase within- and between- network connectivity (Abraham et al., 2018). Thus, increased coherence within the *global human parental caregiving* network charts a neural marker of attachment that is comparable in primary caregiver mother's and father's brain, and in line with research in biparental rodents showing that active paternal care led to closer integration of networks implicated in nurturance, learning, and motivation in the father's brain (Lambert et al., 2011).

We focused on two key competencies that enable preschool children to socially participate in interactions with peers and non-kin adults—self-regulation and socialization (An & Kochanska, 2020; Eisenberg et al., 2018). Preschool children participated in two self-regulation procedures of positive and negative emotions, the 'Bubbles' and 'Masks', respectively, adapted from the laboratory temperament assessment battery (Lab-TAB) (Goldsmith & Rothbart, 1999), and in the 'Toy Pick-up' paradigm—a compliance situation (Kochanska & Aksan, 1995). We found direct links between the parents' brains in infancy and children's later self-regulation abilities at three and four years old. Greater network connectivity in fathers' and mothers' *Core limbic* network predicted children's more positive emotions (e.g., positive affect, positive vocalizations, and laughter) and use of simple regulatory mechanisms, such as proximity seeking, mimicking, physical and verbal self-soothing. The integrity of the fathers' and mothers' *Mentalizing* network predicted children's self-regulated socialization, including children's enthusiastic compliance to task, displaying positive affect, and continuing to work without adult monitoring, which was associated with empathic and moral development. The integrity of the fathers' and mothers' *Embodied simulation* network predicted children's use of mature self-regulation tactics, such as symbolization, functional play, and attention diversion, to manage negative emotions, and predicted lower children's CT levels throughout the home visit (Abraham et al., 2018). Parent-infant synchrony partially mediated this longitudinal association (Abraham et al., 2016). Finally, connectivity between fathers' and mothers' *Core limbic* and *Embodied simulation* networks was longitudinally associated with the development of children's OT response at preschool. Connectivity between the *Embodied simulation* and *Mentalizing* networks predicted children's lower internalizing problems (e.g., depressive tendencies, anxiety symptoms, and somatic complaints) at six years, as fully mediated by the children's regulatory behavior at preschool (Abraham et al., 2019).

In a recent study (Abraham et al., 2021a, 2021b), we were interested in exploring the role of parent-infant synchrony and parental OT, two core components of the Neurobiology of Affiliation (Feldman, 2021), during infancy as moderators of the links between child's temperamental traits and salivary cortisol (CT) and secretory Immunoglobulin A (s-IgA) concentrations, biomarkers of stress and immune systems, respectively, in 94 Israeli mothers, primary and secondary fathers and their children. We found that preschoolers with low self-regulation had higher s-IgA levels compared to those with better regulatory skills, but only in the context of low parental synchrony in infancy. Similarly, preschoolers with high negative emotionality had higher CT levels than those with low negative emotionality, but only in the context of low parental OT in infancy. Findings highlight the role of early markers of the neurobiology of mothering and fathering as a protective buffer against the link between a child's self-regulation difficulties and the stress-immune axis in childhood.

We were also interested in characterizing the neurobehavioral mechanisms underlying human coparenting (Abraham et al., 2017). We measured the brains' responses to coparental stimuli (videos of their partners interacting with the infants), parental OT and AVP were assayed, and coparental behavior was measured at three-time points across the first six years of family formation in Israeli same-sex and opposite-sex families. We found that both the ventral striatum (VS) and caudate, striatal nodes implicated in motivational goal-directed social behavior, activated while fathers and mothers viewed video clips of their partner interacting with their infant. However, only the caudate showed distinct functional connectivity patterns and was positively associated with two coparental behavioral styles, the collaborative and the undermining. Stronger caudate-vmPFC connectivity was positively associated with more collaborative coparenting and was positively related to salivary parental OT. Stronger caudate-dACC connectivity, on the other hand, was linked with an increase in undermining coparenting and was related to salivary parental AVP. A dyadic path model showed that parents' caudate-vmPFC connectivity in infancy predicted lower child externalizing behaviors, reflecting less conflict with others and violation of social norms, at six years as mediated by collaborative coparenting in preschool. Such findings provide the first neurobiological evidence that distinct neural pathways in the father's brain in response to the other coparent and the endocrine systems and behavioral mechanisms related to those serve an important regulatory role in a child's development and may confer evolutionary advantages for the child and the family.

In sum, findings from our longitudinal studies on the parental brain indicate that the reorganization that takes place in the father's brain during the first year of a child's life is an essential feature of the family attachment relationships depending on the degree of father involvement in childcare and bears significant consequences for children's emotion regulation, stress management, symptom formation and family functioning.

Recently, using a 3-generation longitudinal design with richly characterized biological, clinical, psychological, and social functioning data over 40 years, Abraham and colleagues (2022) applied a graph theoretical analysis to examine the social cognition-related neural pathways by which familial risk for major depressive disorder (MDD), namely maternal and paternal history of MDD, led to future depression and interpersonal impairments in the third generation. Authors identified abnormalities in the organization of the social cognition network during resting-state fMRI (rs-fMRI) in 108 American offspring at high familial risk for MDD relative to offspring at low familial risk. Path-analysis models indicated that familial risk impacted offspring's brain function and clinical and interpersonal outcomes in two ways. First, absence of a maternal and paternal history of MDD (low familial risk) was indirectly associated with offspring's lower likelihood of experiencing first and recurrent MDD episodes and with lower depressive symptoms eight years later, via higher nodal influence of the right posterior superior temporal gyrus (pSTG) on connections within the *Social cognition* network. Second, low familial risk was indirectly associated with better interpersonal functioning, eight years later, via increased nodal influence of right IFG on those network connections. Moreover, in the same high-risk cohort, Abraham and colleagues (2020) imaged 44 mother- and father–child dyads and investigated white matter connections between basal ganglia seeds and selected regions in the temporal cortex, all of which implicate in mental representation of others, social communication, and bonding, using diffusion tensor imaging (DTI) tractography. Authors found dyadic concordance in cortico-basal ganglia white matter connections, which was diminished when the parent had a history of MDD, while better early-life maternal and paternal care predicted greater neural concordance. Findings emphasize the long-term role of maternal and paternal psychopathology and quality of early caregiving and attachment in shaping children's brain architecture and neural concordance between parent and child in circuits implicated in social cognition.

Overall, while there are remarkable variations throughout human history and across cultures in the way fathers participate in childcare, and paternal care in humans is not obligatory, it is now clear that fathers count. The social and cooperative nature of human childrearing, including paternal involvement and care, has influenced children's psychological, social, and emotional well-being, and increased infant survival (Abraham & Feldman, 2018a; Rosenbaum & Gettler, 2018). We argue that the highly plastic father's brain in humans has evolved by selective pressure to respond to committed fathering, namely, to support the partner throughout the long period of child dependence and to provide attuned and shared care for the infant. Such involved fathering improves offspring's survival, and under conditions of early-life maternal inadequate care buffers against the long-term effects of maternal separation or neglect. In the absence of potential paternal risk factors, through mechanisms of *brain-to-brain* synchronization (Abraham & Feldman, 2018b; Hasson & Frith, 2016) during (collaborative) father-partner interaction and during (well-attuned) father-child interactions, males' healthy *social brain* may "heal", protect and tune the family members' *social brains*, probably resulting in mitigating early maternal adverse effects on child cognitive and emotional development and in supporting child's social function and mental health (Feldman, 2021).

The Father's Brain- Future directions, Unresolving Topics, and Open Questions

Fathering represents a unique form of plasticity of the human social brain. Recent neuroimaging studies on human fathers provide insight into the neural adaptation that fathers experience during pregnancy and after the birth of their children. Still, fathering is context-bound, representation-guided, and behavior-based, and it is less bound by pregnancy hormones and can assume diverse forms and these have been observed across eras and cultures. Thus, caution is needed in order to not generalize findings from one setting, culture, or social group to another. Future models should incorporate models that highlight the "crosstalk" between environmental, contextual, and neurobiological factors that will offer a promising cross-cultural perspective in the neurobiological research of fatherhood. Our understanding of the neurobehavioral basis of parenting for human fathers is still limited, mainly in comparison to the well-established field of research that examines the neural adaptation to motherhood, and many topics remain to be explored.

Several topics may be particularly important for future research. First, researchers should further examine fathers' brain responses to multiple infant social cues by which they attract and engage their fathers, such as laughter, voices, movements, and speech within the ecological niche. Second, future studies on the father brain should continue expanding the lens from focusing on activation of discrete brain substrates to investigating the dynamics in brain networks.

Third, since neuroimaging studies on human parents are correlational, it is still unknown whether functionality in the father's brain leads to the expression of parenting behavior or vice versa, that specific neural pathways in the father's brain are built over time from continuous reciprocal father-infant social exchanges. Therefore, intervention studies are needed to establish causal links between a father's brain morphology and function, hormones, caregiving behavior, and child's developmental outcomes. Fourth, to date, there is limited knowledge on how a father's age, childhood experiences, cultural background, and conditions such as extended family or group living, work hours, nature of employment, stable versus nomadic habitat, permanent absence, and conservative versus egalitarian worldviews shape the father's brain architecture. Fifth, an exciting question for future research is how a father's brain responds to children as they grow older, varies with the child's gender, temperament, and supports later maturation and the child's growing independence. Sixth, another avenue for future research is the neurobiology of fatherhood in the context of children's intellectual or developmental disabilities. In the same vein, it is important to test father's brain response when maternal (or the other partner's) ability to parent is compromised (e.g., maternal postpartum depression or hospitalization). Seventh, we need more longitudinal research to investigate the specific changes that take place in the father's brain during the transition to fatherhood. Studies that prospectively follow fathers from pregnancy to the postnatal period may provide valuable insights on the links between neural, hormonal, and psychological changes during pregnancy and the father's emotional bond with the child. Eighth, very few studies examined neural response in high-risk fathers. Future neuroimaging work may provide insights into the ways by which high-risk conditions, such as homelessness, social-economic disadvantages, war, immigration, paternal psychopathology, and incarceration, shape fathers' brains and behavior. Further research on the re-organization of a father's brain, its long-term effects, and its resilience-promoting role in the context of early-life adversity is needed. Much further research should focus on characterizing the neural, neuroendocrine, and epigenetic mechanisms that underpin the intergenerational transmission of parental behavior, parenting practices, and other social behaviors from fathers to sons and daughters (Abraham et al., 2021a, 2021b). Ninth, mapping the neurochemistry of the father's brain in response to infant cues and further exploring the density and distribution of relevant neuropeptide receptors, such as OXTR and AVPR1a in the father's brain, as well as measuring brain-to-brain coupling between fathers and children during interactions, will deepen our understanding of the embedded nature of the human social brain (Endevelt-Shapira et al., 2021).

Of note, however, it is important to remember that neuroscience research on the parental brain, hormones, and behavior cannot focus on one caregiver, whether mother or father, without including contextual variables and multiple caregivers. Such limited research may lead to inaccurate findings and misleading conclusions that may not represent the complete experiences of parent and child in their social ecology.

Finally, instead of exclusively focusing on the mother–child dyad for prevention and intervention, as has often been the case in high-risk parenting, translating existing studies and focusing future effort on the coordination of mothers' and fathers' brain mechanisms and behavioral expression to relationship-based interventions is critically important. We need to devise father-child and coparenting programs that can mitigate some of the long-term adverse effects of family adversity, increase father involvement and caregiving, and improve youth's social-emotional development and family well-being. Future research should examine how fixable the father brain is to early interventions that increase body contact, proximity, and synchrony between father and infant for high-risk families.

In sum, given the direct and indirect effects of fathering on children's development across multiple domains, even when fathers do not live with their children, it is imperative that scholars, practitioners, and policymakers should consider the complexity of human childrearing, recognize the diversity of family life and the changing patterns of fathering across history, cultures, and societies, and give a more prominent place to father-derived risk and protective factors as they play a role in children's physical and mental health.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies conducted by the authors of this paper involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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