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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 cingulated 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; lOFC, lateral orbitofrontal cortex; mPFC, medial prefrontal cortex; NAcc, nucleaus 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 cingulated 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 agriculturalor 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 alloparening (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