Review

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The adaptive human parental brain: implications for children's social development

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Although interest in the neurobiology of parent–infant bonding is a century old, neuroimaging of the human parental brain is recent. After summarizing current comparative research into the neurobiology of parenting, here I chart a global 'parental caregiving' network that integrates conserved structures supporting mammalian caregiving with later-evolving networks and implicates parenting in the evolution of higher order social functions aimed at maximizing infant survival. The response of the parental brain to bonding-related behavior and hormones, particularly oxytocin, and increased postpartum brain plasticity demonstrate adaptation to infant stimuli, childrearing experiences, and cultural contexts. Mechanisms of biobehavioral synchrony by which the parental brain shapes, and is shaped by, infant physiology and behavior emphasize the brain basis of caregiving for the cross-generation transmission of human sociality.

The brain basis of human parenting: an emerging field of inquiry

Parenting is the process most critically implicated in the survival and continuity of life on Earth. It is also the only social behavior observed across species and taxa, appearing in multiple forms from limited to extended, and provided to offspring variously by mothers only, mothers and fathers, father alone in some non-mammalian species, or collaboratively by parents and conspecifics. Thus, parenting likely contains both more evolutionarily conserved components than all other social phenomena on the one hand and the greatest plasticity on the other [1–3]. Moreover, parenting is the social phenomenon most profoundly affecting brain development of the young, necessitating flexibility and adaptation to diverse ecological conditions, and is reciprocally shaped by inputs from infant, partner, and colony [4–10]. Therefore, parenting provides a prototypical target for comparative research. Although interest in the neurobiology of parenting dates back to the early 20th century [11–13] and gained momentum once Lorenz had described social bonding in 1935 [14–17], the brain basis of human parental care is a recent area of inquiry, with most imaging studies appearing over the past 5 years, thus calling for an integrative perspective on the human parental brain.

Whereas several recent reviews ([1,18,19], but see also [20]) discussed the neurobiology of parenting from the animal research perspective, this review is human centered, focusing on the interface between conserved and human-specific components and addressing long-term effects of parental care on infant social development in light of human infants' protracted dependence and the extreme immaturity at birth of the human brain [21]. Three questions are addressed: (i) What is currently known about the brain networks that appear to support human parental care, their modulation by parenting-related hormones, and their sensitivity to multiple parenting determinants? (ii) What real-world implications do these hold for infant development? And (iii) can research

Glossary

Alloparental caregiving: caregiving to offspring by adults other than the biological parents, frequently observed across the animal kingdom and common in several human societies [110].
Biobehavioral synchrony: the online coordination of physiological and behavioral processes among affiliated members during social contact. Parent–infant biobehavioral synchrony is a mechanism that supports children's physiological and social growth and must be experienced during an early sensitive period (Box 2, main text). Disruptions to synchrony due to conditions such as maternal postpartum depression carry long-term effects on infant development [51].
Embodied simulation (mirror) network: includes the pre-SMA, IPL, and IFG. The 'mirror' network responds to both action performance and action observation, and enables one to simulate others' goals and actions in one's own brain [106].
Emotion regulation/executive network: marks the latest-evolving cortical structures, including the dlPFC, mOFC, MFG, and frontopolar cortex. It enables top-down control over attentional, emotional, and cognitive processes, and allows individuals to engage in multitasking, inhibit emotion, select actions, and hierarchically organize activity according to long-term goals [105].
Empathy network: includes the AI, dorsal anterior cingulate cortex, and SMA [101]. It supports the capacity to resonate with others' pain and emotions by forming shared circuits of first- and third-person experience [99,101], and to anchor feelings in the present moment [102].
Mentalizing network: includes the STS/STG, TPJ, precuneus, PCC, and vmPFC. It allows individuals to infer others' mental states by predicting relations between external events and internal states (i.e., theory of mind) [104].
Social brain: structures in the mirror, mentalizing, and empathy networks jointly define the human 'social brain'.

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on the parental brain shed further light on global topics in human sociality, including higher order social functions and the social brain? I hypothesize that the parental brain marks a peak expression of human evolution that integrates survival-related ancient functions with networks supporting the exquisite complexity and multifinality of the human brain, opening an important window into human-specific social functions such as the capacity to resonate with others' mental states (empathy) or to coordinate facial signals to enhance attachment (social synchrony).

The parental brain: animal models

Animal studies have mainly tested the parental brain in female rodents; therefore, less is known about fathers, nonhuman primates, or species forming an exclusive maternal–infant bond [6]. This research has described the critical role of the medial pre-optic area (MPOA) in the hypothalamus for initiation of maternal behavior. Primed by pregnancy hormones, particularly oxytocin and prolactin, the MPOA acts, via its projections to the mesolimbic dopamine circuits [especially the nucleus accumbens (NAcc) and ventral tegmental area (VTA)], to increase maternal reward from infant interaction, thus sensitizing a limbic network of maternal care [22–24]. In parallel, oxytocin acts directly on the VTA to facilitate dopamine release in NAcc [22], enhancing the mother's motivation to care for her young. The amygdala, similarly receiving projections from MPOA, increases maternal vigilance for infant signals [25,26], and oxytocin-primed synaptic plasticity of the amygdala-accessory olfactory bulb pathway supports formation of social memories by augmenting the salience of bonding-related cues [27].

The initiation of maternal behavior involves a two-stage process in female rodents that first suppresses their typical aversion to infant cues and then increases maternal motivation via MPOA–dopamine connections [6,25]. Studies in rodents describe the initiation and maintenance of maternal behavior as two distinct phases, the first hormone primed and automatic, the second more memory based and shaped by inputs from infant and nest [6,24]. Furthermore, parenting in rodents is accompanied by increased brain plasticity and research highlights the postpartum period as the time of highest plasticity in the adult brain [28]. Importantly, oxytocin functions as a modulator within this amygdala–hypothalamus–dopaminergic caregiving circuit and the increase in oxytocin during childbirth sensitizes this system in terms of activity, connectivity, and susceptibility to reorganization based on social experiences [29–31]. Findings in rodents [30] and primates [32] indicate that the oxytocin system of the infant's brain is organized through the mother's species-typical postpartum behavior and tactile contact. Yet, rodent studies have directed little attention to cortical processes, and have highlighted maternal care as being subcortical, hormonally controlled, and modulated by olfactory cues.

The human parental brain

Evolutionary conserved components

Several conserved aspects of parental care are observed in humans. Both the amygdala and reward circuitry are key components of the human parental brain and support parental vigilance and/or anxiety for infant safety as well as reward from the attachment relation [33]. Similarly, studies have pointed to increased brain plasticity in humans, which provides an opportunity for reorganization of the parent's brain [34]. Finally, the modulatory role of oxytocin in the subcortical network that supports mammalian caregiving also underpins multiple socio-affective functions in humans, including empathy, group cohesion, and social understanding [35]. Thus, the ancient system sensitized by pregnancy and triggered by the birth hormone is also implicated in a host of higher order sociocognitive functions throughout human life [36]. However, one important difference between the mammalian maternal care circuit and the human parental caregiving network is the connectivity of these subcortical structures to multiple insula-cingulate and frontotemporoparietal networks, which are integrated into the human parental care network along the subcortical areas described in rodents.

The exclusive human parental–infant bond

The exclusive human parental–infant bond represents a key departure from rodent models. Whereas rodent mothers promiscuously care for any infant in their surroundings, human bonding is person specific [37]. This exclusive bond requires representational and associative processes involving continuous network reorganization based on past experiences over a lengthy sensitive period, where specific pathways are built over time from reciprocal exchanges of parent and infant cues [38]. To some extent, such elaborate associative processes are human specific: it has been shown that the increase in size of associative cortex compared with sensory-motor areas represents the main departure of the human brain from that of chimpanzees, our closest relative [39]. Although exclusive bonding is also found in herding animals, such as sheep, bonding of lamb and ewe is mediated by olfactory cues [5]. With the evolution of large neocortex mammals, olfactory-centered bonding gave way to affiliative bonds based on multimodal signals, memory, and associative processes [40]. The exclusive human parent–infant bond involves brain plasticity required for the fine-tuning of the parent brain to inputs from each child via a process termed 'biobehavioral synchrony' [37,41], which is the co-wiring of parent's and infant's brains and behavior into a synchronous unit that supports the infant's brain growth and buttresses social competencies (see Glossary). Oxytocin has a critical role in neural plasticity at both the molecular and network assembly levels due to its unique mode of release from both oxytocin-producing hypothalamic sites and dendrites, which enable a long half-life, activity at locations distant from receptors, and experience-dependent network reorganization leading to autoregulated release in response to attachment cues [42–45]. In humans, oxytocin functionality is transferred from parent to child via repeated experiences of social synchrony during parent-infant interactions, that is, the matching of parent's and infant's behavior in the gaze, touch, affect, and vocal modalities, an experience that ushers the development of children's social competencies [46–49].