COMMENTARY

Flexibility of the father's brain

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Females are responsible for the direct rearing of offspring in more than 95% of mammalian species (1). Humans are an intriguing exception to this pattern of paternal investment, and shifts in society and culture have led to increases in men's involvement in the care of infants. The modern-day family comes in a variety of structures, and more and more people are playing unconventional roles in childrearing. In PNAS, Abraham et al. (2) show that fathers' brains are malleable and can adapt to different parental roles.

This is the first investigation of the relationship between parenting behaviors, oxytocin, and neural activity in both mothers and fathers raising their firstborn infant in different parenting structures. The researchers investigated this relationship in heterosexual primary-caregiving mothers (PC-mothers), heterosexual secondary-caregiving fathers (SC-fathers), and primary-caregiving homosexual fathers who are raising the infant without the mother's involvement (PC-fathers). The set of results is fascinating and has widespread implications for the understanding the plasticity of the brain–body orchestration of parenting.

Abraham et al. first assess parenting behaviors, such as warmth, gaze, touch, and vocalizations and how these are coordinated with the infants' signals and changing states. This parent–infant synchrony was significantly higher in PC-mothers and PC-fathers than in SC-fathers, although oxytocin levels were similar across groups. Notably, there were no differences between biological and adoptive PC-fathers in the parenting behavior and oxytocin levels. Thus, genetically related and unrelated PC-fathers yield the similar caregiving and hormonal ties to fatherhood.

Pregnancy and childbirth are thought to help program the mother's brain for caregiving duties. It is well known that the neurohormone oxytocin plays a pivotal role in enabling the uterine contractions for childbirth and breast milk ejection during nursing. It also facilitates maternal behaviors required for caring for a child, including attachment, attunement, affection, motherease, and sensitivity (3, 4). Recent studies have suggested that oxytocin supports paternal behavior as well (4). Interestingly, in SC-fathers, oxytocin release correlates with stimulatory play involving object exploration and moving the infant around (5). These findings and those by Abraham et al. propose that the hands-on experience of parenting alone can bring about neuroendocrine responses to fathers' interactions with their infants.

Abraham et al. next uncover a "parental caregiving network" by using functional MRI while parents viewed videos of their parent–infant interactions in the natural habitat of their homes (Fig. 1). One component of this network is emotional, rich with oxytocin receptors, and involves structures key for processing distress, vigilance, and reward, including the amygdala and ventral tegmental area. Together, these regions respond instinctively and unconsciously to protect and nurture and provide the caregiver with immense gratification from seeing the child. The other component is for mentalizing and includes areas important for the cognitive processes underlying theory of mind, perspective taking, and empathy, such as the ventromedial prefrontal cortex (vmPFC) and superior temporal sulcus (STS) (6). This system is involved in a parent's ability to deduce, forecast, and plan an offspring's states and needs.

PC-mothers displayed the greatest activation of the emotional system, and this activation significantly related to parent–infant synchrony and oxytocin levels. SC-fathers, in contrast, exhibited more activation of the cortical system. Fascinatingly, PC-fathers showed amygdala activation similar to PC-mothers and STS activation similar to SC-fathers, with pronounced functional connectivity between the two regions. This suggests that when a baby is raised by PC-fathers, both systems are used for optimal childrearing.

For both PC-fathers and SC-fathers, the STS–amygdala overlap directly related to how much the men were involved in tending to the baby, and STS activation correlated with oxytocin levels and parent–infant synchrony. This provides evidence that exposure to the infants and caretaking activities can groom oxytocin and neural systems to carry out the degree of paternal involvement.

Oxytocin promotes caregiving behaviors through its targets in the body and the brain (3, 7). In the autonomic system, oxytocin facilitates social engagement via interactions with parasympathetic branch, including the vagus nerve, which slows heart rate to allow

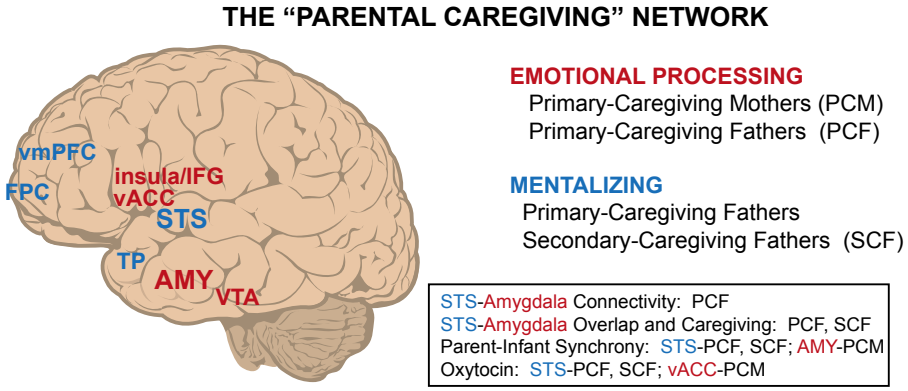

Fig. 1. The Caregiving Network by Abraham et al. (2) includes emotional and mentalizing components. The emotional network includes the amygdala (AMY),* ventral anterior cingulate cortex (vACC),* insula,* inferior frontal gyrus (IFG), and ventral tegmental area (VTA).* *Subcortical and paralimbic structures not located at the outer cortical surface. The mentalizing network includes superior temporal sulcus (STS), frontopolar cortex (FPC), ventromedial prefrontal cortex (vmPFC), and temporal poles (TP). Relationships between neural activation, oxytocin levels, and parent-infant synchrony varied in primary-caregiving mothers (PCM), primary-caregiving fathers (PCF), and secondary-caregiving fathers (SCF).

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calm states necessary for affiliation (8). In the brain, oxytocin lowers the amygdala response to emotional stimuli (9). The amygdala is responsible for initiating the stress response required for survival behaviors (10), including activation of the sympathetic fight-or-flight system, which allows for immediate responding to assure the safety and well-being of an infant.

Social bonds are represented in the heart, as well as the brain. The prairie vole is an ideal animal model for studying the neurophysiology social bonds, including parenting and alloparenting. Alloparenting in the male prairie vole involves both sympathetic acceleration of the heart and recruitment of the vagal brake (11). This uncommon dual activation of the sympathetic and parasympathetic systems occurs when the situation calls for both social engagement and stress arousal, thereby ensuring the well-being and safeguarding of infants. Other unique circumstances that recruit both systems include sexual activity (12) and emotional crying (13).

Social processing and vagal input can be regulated by "top-down" cortical influences including the vmPFC (14, 15), an integral component to Abraham et al.'s mentalizing network. In addition, the STS is key for empathizing (6). It would be very interesting to see how the dual activation of the emotional and mentalizing systems in PC-fathers relates to sympathetic and vagal influences of the heart during infant care and how this pattern compares to PC-mothers, SC-fathers, and SC-mothers. Along these lines, single parents may also recruit both networks due to the need to provide the complementary caregiving duties of partnered parents.

Oxytocin activity can be related with that of vasopressin, a neuropeptide that shares genetic and structural commonalities. Although the role of vasopressin in parenting has not been studied extensively in humans, in animal models, it seems to be closely related to social bonds in males and also to defensive behaviors to preserve the self and family members (12, 16). In humans, vasopressin is correlated with the activation of cortical structures from the mentalizing system in fathers (17). Moreover, in both mothers and fathers, vasopressin levels relate to stimulatory contact and object play, whereas oxytocin levels relate to affection and eye contact with infants (18). Relatedly, a drop in testosterone has been shown to facilitate tender fathering (19), and oxytocin-induced changes in testosterone levels relate to emotional, visual, tactile, and auditory synchrony with the infant (20).

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Oxytocin is also associated to the release of dopamine and endogenous opioids (3, 19), which may bring about some of the rewarding elements of parenting.

Follow-up work by this group and others may probe how other neurochemical cascades interact with oxytocin's in the orchestration of the various neural events related to motherhood and fatherhood. Future research could also probe this malleability in other family structures, including those with two mothers, unpartnered parents, or nonparents raising a child. To further delineate the different influences of nature and nurturing, subsequent studies may look at the brains of both men and women before and after they become parents.

Abraham et al. provide evidence that the father's brain is plastic and sensitive, tuning itself according to the caregiving role. Further, both the emotional and mentalizing components of the parental caregiving network are available to fathers, and they adjust according to the type of infant-rearing responsibilities. Accordingly, the neural and hormonal events that underlie parenting behaviors are not unique to mothers. This will undoubtedly become a landmark study that builds on the pioneering work on the neurobiology of fatherhood in humans and animal models (3, 4, 16).

These findings illustrate that there are innate neural and endocrine substrates that have likely evolved to adapt to divergent familial circumstances so that the child receives the most advantageous caretaking from the parents. Consequently, the brain has emotional and mentalizing components to parenting, and children raised by two fathers are recipients of the same caregiving network-mediated events as children raised by a mother and father. Sociocultural movements are leading to more variations in family compositions and caregiver roles. This study by Abraham et al. suggests that the brain is flexible enough to keep up with the times.

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