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Reviews and perspectives

The neural and hormonal bases of human parental care

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ABSTRACT

As parents in modern western societies face increasing pressures that strain their ability to provide quality childcare, it is important to consider the neural and hormonal bases of sensitive and nurturing parenting. The topic has been explored systematically in non-human animals, and these studies have yielded a rich source of hypotheses for human studies. Considerable evidence links oxytocin (OT) with sensitive caregiving in both men and women, and with stimulatory infant contact in men and affectionate infant contact in women. Testosterone, on the other hand, decreases in men who become involved fathers, and testosterone may interfere with aspects of paternal care. In neuroimaging studies, exposing parents to child stimuli activates neural systems involved in understanding others' facial expressions (the putative mirror neuron system), others' feelings (anterior insula and thalamocingulate regions) and others' thoughts (dorsomedial prefrontal cortex), as well as reward systems involved in approach-related motivation (ventral tegmental area, substantia nigra, ventral striatum and medial orbitofrontal cortex), and systems involved with emotion regulation (lateral prefrontal cortex). There is some evidence that this activity can be attenuated in mothers who do not breastfeed, and mothers with post-partum depression, perhaps due in part to lower levels of OT exposure. On the other hand, there is evidence suggesting that high levels of oxytocin (OT) may enhance activation in some of these systems. For example, OT may stimulate dopamine release in the ventral striatum, rendering child stimuli more rewarding. A few recent studies have gone beyond merely describing neural correlates to establishing the functional significance of activation patterns by linking them with observed maternal behavior outside the scanner. The results of these studies suggest that there may be an optimal range of activation within certain neural systems, neither too high nor too low, that supports appropriate parenting. There is also mounting evidence that the very structure of the human brain is altered by the cognitive challenges inherent in learning how to parent. Given that human mothers typically receive help with childrearing, it will be important to begin studying the neural and hormonal bases of alloparental care, with a particular emphasis on fathers due to their increasing involvement in childcare in modern western societies.

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1. Introduction

Considerable evidence suggests that sensitive parenting, defined as contingent, reciprocating responses to children, is associated with positive child outcomes, whereas insensitive parenting, as in neglect, abuse or as is sometimes found with post-partum depression, is associated with poor developmental outcomes (Barrett & Fleming, 2011; Belsky et al., 2006; Cassidy & Shaver, 2008; Feldman, 2007; Gaudin, 1999). These associations could be direct and causal, or they could be driven by genetic or environmental factors shared by parents and offspring. Cross-fostering experiments in animals support a causal link (Champagne & Meaney, 2001). Despite the importance of sensitive care for healthy child development, our modern lifestyles may challenge the ability of parents to provide sensitive and sufficient caregiving. Humans are an alloparental species (Hrdy, 2009), meaning that although mothers are usually the primary caregiver, they typihyphen-qj;cally receive help from fathers, grandmothers, sisters, brothers, older children, etc. Nevertheless, modern western parents often live with their children in isolated nuclear families, removed from kin who might otherwise provide assistance. Moreover, the proportion of American women participating in the labor force has increased from 34% in 1950 to 58.6% in 2010, as reported by the U.S. Department of Labor (2011; Toossi, 2002). Thus, American mothers face increasing demands on their time that limit their availability for childcare. Often, the only one available to compensate is the father, who also typically works outside the home. This situation can result in increased stress on working mothers and fathers, stress which could have negative consequences for the quality of care they provide. One common solution to relieve this stress is to hire professional alloparents who are unrelated to the child and whose empathic regard for the child may not match that of a relative. The situation is all the more stressful for single mothers or fathers who have no spousal support and for those living in poverty. Thus, there is an increased need for interventions that sustain parental sensitivity and motivation (Bakermans-Kranenburg, van, & Juffer, 2003; Gaylord, 2001; Kalinauskiene et al., 2009), both in strained mothers and fathers, but also in day care workers. This review will focus on the neural and hormonal systems that mediate sensitive parental care that these interventions may be able to target.

2. Review of neural and hormonal bases of parental care in nonhuman mammals

Parental care is by far the most obvious and pervasive example of altruism in the animal kingdom, and may well represent the original form of prosocial behavior from which all others are derived (Panskepp, 1998). Parenting is uncommon in fish and reptiles, and when it occurs, is often limited to egg guarding. In contrast, parental care is common in birds and mammals. In birds, biparental care is the norm, whereas uniparental care by females is the mammalian norm (Clutton-Brock, 1991). What neural and cognitive machinery is required for an animal to engage in this form of altruism? Some forms of parental behavior, such as placing food into the gaping mouth of a young bird, are largely innate. Parental motivation is required, but awareness of the mental state of the offspring is not. Reed warbler parents, for example, will feed parasitic cuckoo bird chicks many times their size simply because the gape area of their beak and their begging rate effectively mimic that of a brood of much smaller warbler chicks (Kilner, Noble, & Davies, 1999). Fixed action patterns like these are typically orchestrated by what Paul MacLean referred to as the reptilian brain complex, which is dominated by the basal ganglia (MacLean, 1990).

While it is difficult to infer the mental states of birds, it is clear that parental care becomes infused with emotion in mammals, which MacLean attributes to the limbic system (Konner, 2002; MacLean, 1990). Amazingly, hamsters still parent effectively after removal of their neocortex, as long as the limbic system is spared. However, further damage to the thalamocingulate pathway, a part of the limbic system, severely disrupts maternal behavior (MacLean, 1990). One component of this pathway, the dorsal anterior cingulate cortex (dACC), has been proposed to function as a neural alarm system, notifying the organism of the need to address a problem (Eisenberger & Lieberman, 2004). For example, physical pain reliably activates the dorsal anterior cingulate cortex, as does psychological pain associated with social rejection (Eisenberger & Lieberman, 2004; Panksepp, 2003). The dorsal anterior cingulate cortex is also one of the brain regions most consistently engaged in studies of empathy (Fan, Duncan, de Greck, & Northoff, 2011). In conjunction with the anterior insula, it allows one to feel what another is feeling (Craig, 2004; Singer & Lamm, 2009). It may be this capacity to resonate with the feelings of offspring, and to sound a neural alarm in response to their distress, that distinguishes mammalian from non-mammalian parenting.

2.1. Rodents

2.1.1. Maternal behavior

While the thalamocingulate pathway may therefore help a mammalian mother understand the needs of her offspring, a