



Differential neural responses to child and sexual stimuli in human fathers and non-fathers and their hormonal correlates



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Summary Despite the well-documented importance of paternal caregiving for positive child development, little is known about the neural changes that accompany the transition to fatherhood in humans, or about how changes in hormone levels affect paternal brain function. We compared fathers of children aged 1–2 with non-fathers in terms of hormone levels (oxytocin and testosterone), neural responses to child picture stimuli, and neural responses to visual sexual stimuli. Compared to non-fathers, fathers had significantly higher levels of plasma oxytocin and lower levels of plasma testosterone. In response to child picture stimuli, fathers showed stronger activation than non-fathers within regions important for face emotion processing (caudal middle frontal gyrus [MFG]), mentalizing (temporo-parietal junction [TPJ]) and reward processing (medial orbitofrontal cortex [mOFC]). On the other hand, non-fathers had significantly stronger neural responses to sexually provocative images in regions important for reward and approach-related motivation (dorsal caudate and nucleus accumbens). Testosterone levels were negatively correlated with responses to child stimuli in the MFG. Surprisingly, neither testosterone nor oxytocin levels predicted neural responses to sexual stimuli. Our results suggest that the decline in testosterone that accompanies the transition to fatherhood may be important for augmenting empathy toward children.

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1. Introduction

Considerable evidence now attests to the importance of hormone changes for the onset and maintenance of paternal caregiving (reviewed in [Rilling, 2013](#)). In particular, studies indicate that both oxytocin (OT) and testosterone (T) levels are altered when men become fathers ([Gettler et al., 2011](#); [Gordon et al., 2010](#)), and that these changes are important for paternal nurturance ([Feldman et al., 2011](#); [Gettler et al., 2011](#); [Gordon et al., 2010](#); [Mascaro et al., 2013](#)). However, it remains unclear how parenting-induced changes in OT and T influence brain function to support engaged fathering. Three plausible hypotheses have been offered.

One hypothesis is that these hormonal changes augment empathic responding to children in ways that promote positive child outcomes, and there is considerable indirect evidence to support the idea that a reduction in T and increase in OT may serve such a function in new fathers. For instance, exogenous testosterone impairs the ability to read emotional facial expressions ([van Honk et al., 2011](#)). In addition, men with higher testosterone levels report less sympathy in response to unknown newborn infant cries ([Fleming et al., 2002](#)), exhibit less affectionate touch toward their infant ([Weisman et al., 2014](#)), and are less involved in parental care ([Alvergne et al., 2009](#); [Gettler et al., 2011](#); [Mascaro et al., 2013](#)), which may reflect decreased empathic responding to children's needs. Oxytocin is also involved in empathy and emotion processing more generally ([Bartz et al., 2011](#)), and perhaps with paternal empathy more specifically. For example, baseline plasma oxytocin levels predict infant-father synchrony, social engagement, and interaction styles of fathers with infants aged 4–6 months and 7 weeks ([Feldman et al., 2011](#); [Gordon et al., 2010](#)). Furthermore, intranasal OT treatment caused fathers to touch their infants more and to engage in more social reciprocity with them ([Weisman et al., 2012b](#)), and altered the physical proximity and movement of fathers toward their infants during a play session ([Weisman et al., 2013a](#)). Intranasal OT also enhanced sensitivity and decreased hostility of fathers during play with their toddlers ([Naber et al., 2010, 2013](#)), and augmented the cortisol responses to a stressful stillface paradigm in fathers observed to have synchronous relationships with their infant, a finding interpreted as suggesting that OT enhanced the salience of infant social cues in available fathers ([Weisman et al., 2013b](#)).

If T or OT modulate empathy, they likely act on neural systems known to mediate empathic responding. Consistently, both the perception (audio and visual) and contemplation of the suffering of another elicits activation in the anterior insula (AI), particularly on the right side ([Lamm et al., 2010](#)), thought to represent a simulated mapping of the observed individual's body state onto one's own ([Singer et al., 2009](#)). The anterior insula is also consistently activated in response to infant cry stimuli ([Mascaro et al., 2013](#); [Rilling, 2013](#)), suggesting that AI activity may be important for paternal empathy. In addition to the anterior insula, more basic motor simulation supports the ability to read emotional facial expressions ([Carr et al., 2003](#); [Jabbi and Keysers, 2008](#)), so it is possible that changes in OT or T alter a father's simulation of children's emotional facial expressions. This hypothesis predicts that T will be negatively correlated with

responses to child stimuli in the AI and putative mirror system pathways, whereas OT will be positively correlated with these responses.

A second hypothesis is that hormone changes in new fathers may support paternal nurturance by enhancing the reward value of child stimuli in ways that motivate caregiving. The ventromedial prefrontal cortex (vmPFC)/OFC is broadly implicated in reward ([Rolls, 2000](#)), and in parental reward more specifically ([Parsons et al., 2013](#)), and the medial portion of the OFC is thought to trigger innate and specific responses to children's faces ([Kringelbach et al., 2008](#)). In addition to the OFC, rodent models of maternal behavior point to the importance of the mesolimbic dopamine (DA) system in the appetitive drive to nurture offspring, with DA-producing cell bodies in the ventral tegmental area (VTA) projecting to the nucleus accumbens (NA) to motivate proactive care of infants ([Numan and Stolzenberg, 2009](#)). Oxytocin acts at the VTA to facilitate DA release in NA ([Numan and Stolzenberg, 2009](#)), which facilitates maternal behavior in rats presumably by enhancing parental motivation and the reward value of offspring. Recent research showing the effects of intranasal OT administration on the VTA response to social stimuli in nulliparous women supports the idea that OT interacts with dopamine to enhance social reward processing in humans ([Groppe et al., 2013](#)), and it may be that increases in OT in new fathers function similarly in the VTA to enhance the reward value of child stimuli ([Mascaro et al., 2013](#)).

A third hypothesis for understanding hormone changes in new fathers is derived from Life History Theory (LHT), which posits a trade-off between mating and parenting effort and proposes that the hormonal changes that accompany fatherhood bias men's efforts and resources away from mating and toward parenting ([Kaplan and Gangestad, 2005](#); [Wingfield et al., 1990](#)). A large body of evidence supports the role of testosterone in mediating this trade-off. For example, experimental elevation of T increased mating effort and decreased parenting effort in socially monogamous birds ([Hunt et al., 1999](#)). In mammals, there is evidence that male parental behavior is more flexible with respect to hormonal changes. For example, male cotton-top tamarins increase T in response to their ovulating partner, but maintain high levels of parenting ([Ziegler et al., 2004](#)). Despite this added complexity, there is evidence that T supports mating effort at the expense of parenting effort among human males. As outlined above, men with higher testosterone levels tend to be less involved in parental caregiving. Furthermore, low levels of testosterone are associated with reduced libido among men ([Wang et al., 2000](#)). Within married couples, testosterone levels are negatively correlated with relationship quality and amount of time spent with one's partner ([Gray et al., 2002](#)) and high levels predict divorce ([Booth and Dabbs, 1993](#)) as well as polygyny ([Alvergne et al., 2009](#)). While there is less data to support the role of oxytocin in mediating LHT trade-offs, a recent study showed that self-administration of intranasal OT decreases approach behavior toward an unknown, attractive woman in partnered (but not single) males ([Scheele et al., 2012](#)). Taken together, these data suggest that changes in testosterone and oxytocin may alter neural responses to sexually provocative stimuli of unknown women in fathers compared to non-fathers in ways that decrease sexual pursuits that could conflict with parenting.

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