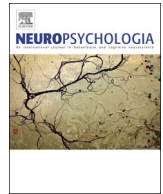




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Empathy networks in the parental brain and their long-term effects on children's stress reactivity and behavior adaptation

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ABSTRACT

Parental empathy is a key component of sensitive parenting that supports children's social adaptation throughout life. Consistent with a two dissociable network perspective on empathy, we measured within- and between-network integrity of two empathy-related networks in the parental brain as predictors of children's social outcomes across the first six years of life. We focused on two empathy networks; *embodied simulation*, which supports parents' capacity to resonate with infant state and emotions and implicates cingulo-insular structures, and *mentalizing*, which underpins parents' theory-of-mind and mental attributions via prefrontal-temporo-parietal circuit. We followed 87 first-time parents across the first six years of family formation, including heterosexual and homosexual parents. In infancy, parents' brain response to own versus unfamiliar infant stimuli was imaged; in preschool, children's cortisol production and emotion regulation were assessed; and at six years, children's behavior problems were reported. Parents' intra- and inter- network integrity increased when viewing their own infant compared to unfamiliar infant, suggesting that attachment stimuli increase network coherence in the parental brain. Functional connectivity within the parent's *embodied simulation* network in infancy predicted lower child cortisol production while inter-network connectivity among the *embodied simulation* and *mentalizing* networks was associated with more advanced child emotion regulation skills in preschool and lower internalizing problems at six years. Children's emotion regulation capacities mediated the link between inter-network integrity in the parental brain and internalizing symptoms. Our findings, the first to demonstrate that integrity of empathy-related networks in the parental brain shape children's long-term stress reactivity and emotional adaptation, highlight the brain component of the parental empathy attribute, suggest that increased coherence within the "parental caregiving network" marks a key feature of parent-infant attachment, and contribute to discussion on biobehavioral mechanisms underpinning the cross-generation transmission of human stress reactivity and sociality.

What does the baby see when he or she looks at the mother's face? I am suggesting, that ordinarily, what the baby sees is himself or herself. In other words the mother is looking at the baby and what she looks like is related to what she sees there.

(Winnicott, 1971, p.112).

1. Introduction

Theoretical perspectives consider the parent's empathic capacity - defined as the parental ability to share the child's feelings, thoughts,

motives, and wishes - as a central component of sensitive parenting and as a cornerstone of children's social adaptation, including evolutionary theories (Hrdy, 1999), psychoanalytic theories of affect (Kohut, 1971; Winnicott, 1965), developmental theories (Feshbach, 1990), social learning theory (Iannotti, 1978), and attachment theory (Bowlby, 1973). Empirical studies within these conceptual frameworks have shown that the parent's empathic capacity plays a key role in children's socialization, affect regulation, symbolic competence, cognitive functioning, and the child's ultimate ability to internalize a moral code and empathize with others (Feldman, 2007a; Strayer and Roberts, 2004; Feshbach, 1990; Landry et al., 2006; Psychogiou et al., 2008; Eisenberg

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and McNally, 1993). The parent's empathic orientation enables children to feel secure, recognize their own thoughts and feelings, show compassion toward others, and become competent members of social groups (Feldman, 2016; Fonagy et al., 2007).

Evolutionary models suggest that the capacity for empathy evolved within the mammalian parent-offspring bond to provide care that exceeds feeding and includes nurturing and comfort, thus maximizing offspring survival and reproduction (MacLean, 1985; De Waal, 2008; Gonzalez-Liencreces et al., 2013). Across mammalian evolution the "parental caregiving system" extended to include other group members and the "empathic" capacity to other social relationships (Bell and Richard, 2000; Hrdy, 2009; De Waal, 2007; Feldman, 2015a, 2017). In mammals, the parent's ability to detect motivationally salient and survival-related cues to recognize offspring's distress is underpinned by the ancient limbic system (Feldman, 2015a; Lindquist et al., 2012; Shahrokh et al., 2010; Dulac et al., 2014), which enables parents to rapidly respond to infant physiological and emotional signals. Yet, across human evolution, there was a progressive increase in length of infant dependency and in the complexity of social networks that grew to include both biological and non-biological helpers (Clutton-brock, 2002). The parent's automatic response to infant distress became insufficient, and abilities such as affect sharing, biobehavioral synchrony, self-other awareness, mental flexibility, and perspective-taking, supported by paralimbic and cortical networks, evolved to increase offspring's adaptation (Decety, 2015; De Waal, 1996; Feldman, 2015b).

Research in human neuroscience supports a two-system model of empathy; an *emotional* and a *cognitive* system that implicate dissociate brain networks (Shamay-Tsoory, 2011). The emotional system not only supports affective sharing, but also serves a more fundamental *embodied simulation* function. Embodied simulation is a phylogenetically-early, bottom-up process that enables vicarious sharing of the bodily states of others and is supported by an assemblage of brain structures, including the anterior insula (AI), anterior cingulate cortex (ACC), and inferior frontal gyrus (IFG). The embodied simulation network enables parents to respond to infant pain and emotions by representing them in the self (Fan et al., 2011; Feldman, 2015a), ground emotional experiences in the present moment on the basis of interoceptive representations (Craig, 2009; Gallese, 2014), and afford perceptual-motor coupling of infant action to better understand infant communications (Rizzolatti and Craighero, 2004). Cognitive empathy is a more advanced top-down *mentalizing* system that supports inferences on others' mental states (Shamay-Tsoory, 2011) and imaginative transposing of self into the thoughts and feelings of others (Decety and Jackson, 2006). It includes structures such as the dorsomedial prefrontal cortex (dmPFC), ventromedial prefrontal cortex (vmPFC), temporal parietal junction (TPJ), temporal pole, superior temporal sulcus (STS), and frontopolar cortex, and enables parents to understand the infant's non-verbal intentions from actions, represent infant state, and plan future caregiving (Feldman, 2017; Frith and Frith, 2006, 2012; Decety and Cacioppo, 2012). Importantly, parental empathy, like empathy in general, requires self-other differentiation to allow parents to distinguish their own thoughts and feelings from those of the infant's (Feshbach, 1990).

The aforementioned empathy-related networks - *embodied simulation* and *mentalizing* - have been consistently found to activate in paradigms that elicit empathy (Raz et al., 2014). Since empathy is a multidimensional construct ranging from emotional contagion to cognitive perspective-taking, it is assumed that sensitive parenting requires the integration of both networks into the "parental caregiving network". Indeed, fMRI studies of the human parental brain have repeatedly shown activation of embodied-simulation and mentalizing structures when parents are exposed to auditory, visual, or multimodal stimuli of their infants compared to unfamiliar infants (Abraham et al., 2014, 2016; Atzil et al., 2011, 2012; Feldman, 2015a, 2017; Swain, 2011, Swain et al., 2014), suggesting that activation of these two networks in the parental context index attachment-specific responses. This is consistent with research in humans and animals indicating that

social closeness or distance, that is, familiarity, kinship, and group membership, modulate the degree of empathy (Singer, 2006; Engert et al., 2014; Wang et al., 2016; Gonzalez-Liencreces et al., 2013; Decety, 2015; Melloni et al., 2014). Yet, despite the centrality of empathy to parenting, no our knowledge, has tested the degree to which these empathy-related brain structures cohere into dissociable networks when parents view their own, as compared to unfamiliar infants. It is also unknown whether intra- and inter-connectivity of the two networks in the parental brain bear long-term consequences for children's development. In the current study we examined within and between network integrity of the two empathy-related networks in the parental brain as predictors of children's development across the first six years of life focusing on three outcomes: stress reactivity as measured by cortisol production, emotion regulation strategies, and externalizing and internalizing symptoms.

Cortisol (CT), the end product of the hypothalamic pituitary adrenal (HPA) axis, marks the body's central response to stress and plays a key role in establishing homeostasis after threat is removed (Ponzi et al., 2016). The HPA system has well-known effects on growth, reproduction, physiological homeostasis, and socio-emotional response, including empathy (Schneiderman et al., 2014; Rubin et al., 2005; Anderson and Galinsky, 2006). Individual differences in HPA activity are associated with children's internalizing and externalizing problems (Cicchetti and Dawson, 2002). Higher basal CT may reflect a failure to effectively regulate physiological and emotional arousal and is linked with low empathy (Reinhard et al., 2012), internalizing problems (Smider et al., 2002; El-Sheikh et al., 2008; Goodyer et al., 2001; Lopez-Duran et al., 2009), aggressive behavior (Dettling et al., 1999), and depressive symptoms in children, adolescents, and adults (Bhagwagar et al., 2005; Ruttle et al., 2011; Dietrich et al., 2013), as well as with increased attention to threat (Vasey et al., 1996), conduct disorder, and anxiety (McBurnett et al., 1991).

The parent-child relationship is among the central contributors to the consolidation of children's CT response (Gunnar and Donzella, 2002; Repetti et al., 2002; Gunnar et al., 2015; Hostinar et al., 2014a, 2014b; Jessop and Turner-Cobb, 2008). Sensitive parenting, including parental empathic responses to child emotional signals, attenuates children's CT response to social stressors (Feldman et al., 2010a, 2010b; Weisman et al., 2013; Ahnert et al., 2004; Albers et al., 2008; Blair et al., 2008; Berry et al., 2016; Hostinar et al., 2014a, 2014b). In contrast, insensitive parenting alters the development of children's stress response and threat-detection neurobiological circuits (Hostinar et al., 2014a, 2014b), and correlates with higher CT production (Marceau et al., 2015a, 2015b; Ahnert et al., 2004; Berry et al., 2016; Enlow et al., 2014) and inflexible response (Apter-Levi et al., 2016). However, to date, imaging studies have not explored the relationship between the parental brain and children's CT reactivity.

Emotion regulation (ER), defined as the ability to manage states of increased positive and negative arousals to organize goal-directed behaviors (Rothbart and Posner, 1985; Cole et al., 2004; Eisenberg and Morris, 2002), is a key predictor of social-emotional and mental-health outcomes throughout life (Eisenberg, 2000; Moffitt et al., 2011). During the preschool years, children make important strides in ER abilities (Feldman, 2009; Zeman et al., 2006; Hirschler-Guttenberg et al., 2015). ER deficits have been linked with internalizing and externalizing symptoms (Eisenberg et al., 2009; Buckholdt, 2013; Morris et al., 2010; Aldao et al., 2010), low empathy and conscience (Feldman, 2015b; Kochanska et al., 2000), peer rejection, and antisocial behavior (Trentacosta and Shaw, 2009). Sensitive parenting that externally-regulate infant distress through empathic and supportive responses help children develop ER strategies for accurately labeling emotions, coping with distress and happiness, and communicating affect in socially-accepted ways by the preschool years (Batson, 2011; Feldman, 2003, 2007b). It has been shown that sensitive early parenting promotes both ER skills (Eisenberg et al., 1998; Morris et al., 2007) and lower behavior problems in the preschool years (Cicchetti and

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