The role of caregiver touch in early neurodevelopment and parent-infant interactional synchrony

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ABSTRACT

Though rarely included in studies of parent-infant interactions, affectionate touch plays a unique and vital role in infant development. Previous studies in human and rodent models have established that early and consistent affectionate touch from a caregiver confers wide-ranging and holistic benefits for infant psychosocial and neurophysiological development. We begin by providing a brief review of how affectionate touch tunes the development of infant somatosensory, autonomic (stress regulation) and immune systems. Affective touch also plays a foundational role in the establishment of social affiliative bonds and early psychosocial behavior. These touch-related bonding effects are known to be mediated primarily by the oxytocin system, but touch also activates mesocorticolimbic dopamine and endogenous opioid systems which aid the development of social cognitive processes such as social learning and reward processing. We conclude by proposing a unique role for affectionate touch as an essential pathway to establishing and maintaining parent-infant interactional synchrony at behavioural, physiological and neural levels. The limitations of the current understanding of affectionate touch in infant development point to fruitful avenues for future research.

(173 words)

INTRODUCTION

Early interactions with a parent provide the foundation for infant cognitive and socioemotional development (Raby et al., 2015; Mermelshtine and Barnes, 2016). Affectionate touch, which includes stroking and holding, is a unique and essential feature of an infant's interpersonal landscape (Hertenstein, 2002). The experience of affectionate touch is mediated by distinct class of mechanoreceptors, known as C-tactile afferents (CTs) (Olson et al., 2016). Light pressure and gentle stroking, especially at skin temperature, results in vigorous CT firing and is perceived as being most enjoyable or rewarding (Löken et al., 2009; Ackerley et al., 2014; Pawling et al., 2017). Importantly, children prefer CT-targeted touch throughout development, and when parents are asked to stroke their babies, they naturally do so at a velocity that optimally activates CTs (Croy et al., 2016, 2019). During face-to-face interactions, parent use of affectionate touch decreases an infant's arousal and increases positive emotionality (Peláez-Nogueras et al., 1997; Fairhurst et al., 2014). The impact of affectionate touch is far from transient; early interventions involving touch such as kangaroo care, or KMC, lead to positive physiological and psychological outcomes such as promoting mother-infant bonding and breast-feeding success, while the deprivation of touch is associated with a range of developmental deficits (Feldman et al., 2002a; Field, 2010b; Moore et al., 2016).

While affectionate touch remains conspicuously understudied, advances have been made in recent years through both human neuroimaging studies and animal models of maternal care, such as rodent licking and grooming (LG) behavior (Ardiel and Rankin, 2010; Botero et al., 2020). A complete understanding of the role of touch remains elusive, in part because of its dependence on the higher-level social and cultural dimensions of the human person (Ellingsen et al., 2016; Feldman, 2016). However, studies have linked affectionate caregiver touch to infant development across five interrelated domains: the somatosensory

system, the autonomic system, immune function, affiliative bonding, and social cognition (Figure 1).

Domain	Somatosensory tuning	Autonomic regulation	Immune function	Affiliative bonding	Social cognition
Implicated regions and systems
Effects of touch in rodents	Increased connectivity within S1, refined cortical and callosal connections	Blunted fear and stress responses, epigenetic alterations to HPA axis	Altered microbiome, decreased hippocampal inflammation	Upregulated oxytocin, greater social behaviour	Altered limbic structure and function, regulation of dopamine and opioid systems
Related effects in humans	Greater hemispheric maturation and functional connectivity	Lower stress reactivity, heightened vagal activity	Decreased risk of infection, activation of natural killer cells	Upregulated oxytocin, increased breastfeeding, mother-infant bonding	Maturation of social brain, regulation of dopamine release and opioid receptor distribution
Possible developmental outcomes	Improved sensory processing and cognitive function	Adaptive regulation of stress and arousal	Protection from mental and physical illness	Development of social behaviour and secure attachment	Regulation of reward-seeking behaviour and enhanced learning

Figure 1. Physiological and psychosocial benefits of early-life caregiver touch.

PHYSIOLOGICAL BENEFITS OF CAREGIVER TOUCH

A. Somatosensory tuning

Caregiver touch in infancy may aid the maturation of the somatosensory system through experience-dependent plasticity. Most tactile information, including the location and intensity of pleasant touch, is processed in the somatosensory cortex (S1) while the valence and ‘pleasantness’ of touch is detected by the posterior insular cortex (Lindgren et al., 2012; Gordon et al., 2013; Case et al., 2016; Morrison, 2016). The somatosensory processing pathway is highly organized, both serially between regions and somatotopically within regions (Ruben et al., 2001; Björnsdotter et al., 2009; Seelke et al., 2012). While its initial formation is based on genetic factors and sensory feedback from spontaneous movements (Milh et al., 2007; Antón-Bolaños et al., 2019), the system is subsequently refined through experience-dependent mechanisms of structural plasticity (Feldman and Brecht, 2005). In

rodents, S1 matures soon after birth, and early-life contact is responsible for the refinement of both its intrinsic connectivity and its cortical and callosal projections (Seelke et al., 2016; Khazipov and Milh, 2018).

Affectionate touch may refine the somatosensory system in humans as well. The fundamental shift from spontaneous to evoked somatosensory activity occurs in the third trimester (Fabrizi et al., 2011), and after birth, the intensity and valence of touch experiences continue to shape somatosensory development (Maitre et al., 2017). In infants, gentle stroking preferentially activates both S1 and the posterior insular cortex; these regions are slightly different from those activated in adults, which may reflect an experience-dependent shift in the localization of affectionate touch processing (Jönsson et al., 2018; Pirazzoli et al., 2019; Tuulari et al., 2019). Lower-level processes of sensation and perception lay the foundation for development of higher-level cognitive functions, therefore early experiences of touch also contribute toward the maturation of neural circuitry for complex cognitive and social function. In fact, infants whose mothers use skin-to-skin touch show greater frontal alpha EEG asymmetry, a pattern of neural activity that reflects emotional processing and cognitive maturation (Hardin et al., 2020). Similarly, pre-term babies who receive caregiver skin contact show faster hemispheric maturation and improved functional connectivity (Scher et al., 2009; Schneider et al., 2012). In fact, an intervention of skin-to-skin contact paired with contingent vocalisations is currently under investigation for its effects on neonatal neurocognitive development (Neel et al., 2019). Conversely, institutionalized children – who often receive inconsistent and low-contact care – tend to exhibit sensory dysregulation, including heightened sensory reactivity, higher rates of sensory processing disorders, and some degree of touch aversion (Dozier et al., 2002; Wilbarger et al., 2010).

B. Autonomic regulation

Early-life touch changes the function of the hypothalamic-pituitary-adrenal (HPA) axis, which mediates the mammalian stress response. Rats raised with more parental licking and grooming (LG) show blunted responses to stress and attenuated fear of novelty, due to epigenetic alterations in the expression of hormone receptors in the hippocampus and amygdala (Liu et al., 1997; Caldji et al., 1998; Kundakovic and Champagne, 2015). These effects are specific to touch, as the experimental addition of gentle stroking in the absence of the dam can activate the same molecular pathway (Jutapakdeegul et al., 2003). Consistent with these findings, affectionate touch is linked to lower HPA activity in human and non-human primates, particularly during critical periods of development (Smotherman et al., 1979; Acolet et al., 1993). This effect is especially pronounced in the mother-child bond, and maternal touch – both during free play and KMC – decreases an infant's physiological stress reactivity (Feldman et al., 2010b; Hardin et al., 2020). Interestingly, rodents that experience less LG in infancy exhibit greater hippocampal-dependent learning in stressful situations (Champagne et al., 2008), which may indicate that a lack of affectionate touch primes the developing infant to survive in a context of deprivation and threat. However, an enhanced memory for stressful events may be maladaptive in secure and low-threat environments.

Secondly, caregiver touch enhances parasympathetic function. Throughout infancy, both maternal and paternal touch triggers cardiac deceleration, but only when it involves stroking at speeds that optimally activate CTs (Aguirre et al., 2019; Manzotti et al., 2019; Van Puyvelde et al., 2019). Similarly, neonatal skin-to-skin contact promotes heart rate stabilization and arousal regulation, as well as greater and more rapid weight gain (Feldman et al., 2002b; Cong et al., 2012; Samra et al., 2013). According to Field & Diego (2008), the effects of touch may be mediated by activity of the vagus nerve, which is responsible for digestive and heart rate regulation (Yuan and Silberstein, 2016). In fact, there is evidence that

stimulation of pressure receptors in the skin increases vagal activity, and that infant vagal activity increases during mother-child interactions (Field and Diego, 2008). Thus, an absence of caregiver touch could lead to adverse mental and physical outcomes through decreased vagal tone, which dysregulates the HPA axis (Porges, 2001; Thayer and Sternberg, 2006). In line with this explanation, the infants of depressed mothers – who use less affectionate touch – fail to show an increase in vagal tone over time and often exhibit developmental delays (Field et al., 1995; Herrera et al., 2004; Aoyagi and Tsuchiya, 2019; Mantis et al., 2019).

C. Immune function

Early experiences of caregiver touch may modulate immune function. Inflammatory cascades have been linked to the pathogenesis or prognosis of an increasing number of common chronic conditions, including both physical (e.g. asthma, cardiovascular disease) and mental (e.g. depression) illnesses (Bennett et al., 2018).

A lack of early life-care can lead to immune dysregulation. In rats, early isolation alters gut microbiota and raises levels of inflammatory molecules in the hippocampus, indicators of immune dysfunction that are linked to anxiety-like behaviors (Dunphy-Doherty et al., 2018). Children with history of institutionalization experience a higher risk of intestinal and respiratory infections, as well as skin disorders (Rutter et al., 1998). While the deprivation of touch has yet to be studied in human immune development, childhood adversity is linked to elevated inflammation, T-cell proliferation, and impoverished cellular immune function (Fagundes et al., 2013), and greatly increases risk of physical and mental illness (Anda et al., 2006).

Several studies link caregiver touch to positive immunological outcomes. The use of Kangaroo Mother Care (KMC) decreases a neonate's risk of severe infections, as well as a variety of other illnesses (Charpak et al., 2001; Boundy et al., 2016). The use of massage increases an infant's proportion of active natural killer cells, although other immunological

markers are unaffected (Ang et al., 2012). One explanation is that touch enhances infant immune function through the transfer of microbiota from the mother's skin (Groer et al., 2015). However, the improvements could be mediated by CT activity itself, as massage leads to positive immunological outcomes in a range of populations (Field, 2010b).

PSYCHOSOCIAL BENEFITS OF CAREGIVER TOUCH

A. Affiliative bonding

Touch shapes the physiological development of the oxytocin system, which is involved in reproductive and social behaviors (Insel, 1992). In rats, CT-optimal touch selectively activates oxytocin neurons in the hypothalamus, and maternal LG induces region-specific increases in oxytocin receptor expression (Francis et al., 2001; Okabe et al., 2015). Similarly, in humans, both pleasant social touch and KMC raise infant levels of oxytocin, likely through CT activity (Field, 2010b; Walker et al., 2017; Hardin et al., 2020). In general, maternal engagement is associated with different patterns of oxytocin receptor methylation in infants (Krol et al., 2019), which modulates the development of the infant social behaviour, including social play, social learning, and social motivation (Gordon et al., 2011; Markova, 2018; Xu et al., 2019).

Moreover, affectionate touch is bidirectionally related to parent-infant bonding. Mothers who exhibit high levels of affectionate touch show increased oxytocin during interactions with their infant (Feldman et al., 2010a). Oxytocin increases parental responsiveness, as well as maternal milk production and consequent breastfeeding (Feldman and Eidelman, 2003; Vittner et al., 2018). In fact, mothers who perform KMC demonstrate heightened sensitivity towards their infant, as well as increased chances of a successful and long first breastfeeding (Tessier et al., 1998; Karimi et al., 2019). Conversely, depressed mothers show blunted oxytocin release, fewer face-to-face interactions, and reduced breastfeeding (Lovejoy et al., 2000; Field, 2010a; Stuebe et al., 2013). Both responsiveness

and breastfeeding foster the development of the mother-child bond, which in turn is a strong antecedent of the child's socio-emotional and cognitive development (Stams et al., 2002).

The parent-infant bond, in turn, appears to promote the effectiveness of affectionate touch.

For instance, nine-month-old infants show greater parasympathetic responses to CT-targeted (stroking at 3 cm/s) in the presence of their parents (Aguirre et al., 2019). Furthermore, when six to eight-month-old infants are gently stroked, they prefer to watch their mother receive synchronous touch over asynchronous touch, but do not show such a preference when gazing at strangers (Maister et al., 2020).

B. Social cognition: Social learning and reward processing

A growing body of evidence links caregiver touch to social cognition and function. In young rodents and infant macaque monkeys, early handling and stroking is positively associated with later social learning (Lévy et al., 2003; van Hasselt et al., 2012; Simpson et al., 2019). Children who receive more frequent maternal touch during play show a greater social orientation, or relative interest in faces compared with other objects (Reece et al., 2016). Finally, gentle caregiver stroking – but not other forms of touch – enables 4-month-old infants to recognize faces with an averted gaze, though they typically attend only to faces with a direct gaze (Della Longa et al., 2019). These changes may be mediated by the maturation of the social brain, as frequent maternal touch is associated with greater activity and connectivity of cortical regions implicated in social processing (Brauer et al., 2016).

Rats that experience less LG show suppressed synaptic plasticity and intrinsic excitability in the dorsal hippocampus, and heightened plasticity and excitability in the ventral hippocampus, changes related to anxiety-like behaviors (Nguyen et al., 2015). Conversely, early tactile stimulation in rodents triggers dendritic changes that increase the connectivity of the prefrontal cortex and amygdala, differences which are linked to heightened performance on learning tasks (Richards et al., 2012). Though comparable studies

have not yet been conducted in humans, in general, parent-infant synchronous interactions have been identified as a key factor in the formation of reward circuitry (Feldman, 2017).

Early experiences of touch also regulate motivational salience through changes to the mesocorticolimbic dopamine and endogenous opioid systems. Maternal LG triggers a lasting increase in the number of dopaminergic neurons in the ventral tegmental area (VTA), particularly in nuclei connected to reward-related areas such as the ventral striatum and the amygdala (Peña et al., 2014). Furthermore, developmentally isolated rats show region-specific changes in dopamine turnover, while rats that received more handling or grooming show heightened dopamine release in response to natural stimuli and blunted sensitivity to stress or psychostimulants (Heidbreder et al., 2000; Brake et al., 2004). Several studies in humans parallel these findings: pleasant touch triggers dopamine release, while less early-life care is associated with greater dopamine release in response to stress (Pruessner et al., 2004; Field et al., 2005). With regard to the opioid system, neonatal handling of rodents increases the expression of μ opioid receptors (MOR) in reward-related areas (Kiosterakis et al., 2009). Similarly, pleasant social touch increases the availability of MOR in human adults in the thalamus, striatum, and frontal, cingulate, and insular cortices (Nummenmaa et al., 2016). Therefore, affectionate touch appears to promote the development of neural circuits involved in social forms of learning, as well as motivation and reward processing.

A ROLE FOR TOUCH IN PARENT-INFANT INTERACTIONAL SYNCHRONY

Finally, affectionate touch may provide a unique and essential path to achieving synchrony during parent-infant interactions. Synchrony is the interpersonal coordination of behavioral and neurophysiological rhythms, a normative early-life experience that advances sensory processing, potentiates learning, regulates emotions and arousal, and promotes a stable attachment bond between the infant and her caregiver (Harrist and Waugh, 2002; Beebe et al., 2010; Wass et al., 2020). To facilitate synchrony, parents are primed to express

a range of behaviors from the time of their infant's birth, including infant directed speech, gaze, positive affect, and touch (Feldman, 2012). Most developmental research has focused on the vocal, visual, and affective modalities, because synchrony between humans can be established in the absence of physical contact (Feldman et al., 2011). However, several recent studies point to the importance of touch for achieving and maintaining parent-infant synchrony.

Touch in parent-infant communicative rhythms. Touch may convey information that is necessary for the coordination of communicative rhythms between parent and infant. Previous research has found that mothers typically direct communicative behaviours toward their infants while the child is quiet but wakeful ((Bell, 2020). As caregiver touch tends to provoke a state of calm alertness (Harrison et al., 2000), parents may use touch to ensure that their infants are available and ready to engage in patterns of communication. Continuous interpersonal touch may be more important during interactions with mothers, whose communicative patterns are usually more regular than the short arousing bursts typically used by fathers (Feldman, 2003).

On the part of the infant, experiences of affectionate touch appear to support the development of bodily self-awareness, which in turn permits bodily attunement with their mothers (Montirosso and McGlone, 2020). Touch may perform this role by facilitating the coordination of sensory processing across modalities: in a recent study, infants detected and showed a preference for synchronous visuo-tactile stimuli over asynchronous stimuli while experiencing CT-targeted gentle stroking, but not during other touch (Della Longa et al., 2020). As interactional synchrony requires awareness of self and other, and takes place through coupled auditory, tactile, and visual signaling, affectionate touch may be a critical precursor to the infant's detection of and participation in communicative rhythms.

Touch in parent-infant physiological rhythms. A number of physiological oscillatory mechanisms, including heart rate and respiration, are coupled during synchronous interactions (Feldman, 2007). Among communicative modalities, affectionate touch is well positioned to promote parent-infant coupling of internal physiology through its effects on vagal activity and pulsatile oxytocin release (Feldman, 2017; Markova et al., 2019). Maternal touch increases the activity of an infant's vagus nerve, which in turn modulates parasympathetic rhythms such as heart rate (Field and Diego, 2008; Yuan and Silberstein, 2016). Touch is also a cue for dendritic oxytocin release, which takes place in rhythmic bursts; the time-sensitivity of oxytocin release enables the temporal coordination of endocrine activity (Ludwig and Leng, 2006; Feldman, 2015). As infants are not yet capable of maintaining homeostatic balance on their own, the joint physiological regulation achieved through affectionate touch appears to be a steppingstone to the child's later self-regulation (Bazhenova et al., 2001; Davis et al., 2017).

Touch in parent-infant neural synchrony. Touch may mediate the interpersonal coordination of neural activity. Specifically, parental social ostensive cues (typically gaze and speech, but also touch) are hypothesized to reset the phase of ongoing neural oscillations in an infant's neocortex (Wass et al, 2020). This entrains the infant to the ongoing pattern of communication, and also aligns the oscillatory phases of parent and infant neural activity for optimal mutual receptivity. In this way, interpersonal social behaviors such as touch could trigger the synchronization of neural activity with concomitant benefits for communication and learning. A range of evidence supports this proposal along the visual and auditory modalities; both direct gaze and infant-directed speech generate unique patterns of cortical activity in infants (Zhang et al., 2011; Urakawa et al., 2015), and direct gaze produces temporally fine-grained neural entrainment between an adult and infant (Leong et al., 2017). Maternal vocal and facial expression of positive emotion also increases parent-infant neural

coupling more than negative affect (Santamaria et al., 2020). More broadly, mothers and their infants exhibit neural coupling during synchronous interactions, particularly in areas of the frontal cortex (Reindl et al., 2018; Nguyen et al., 2020). In adults, interpersonal touch such as hand holding enhances neural synchrony (Goldstein et al., 2018). While touch has yet to be isolated in studies of parent-infant neural synchrony, it appears probable that, like the ostensive cues of gaze and speech, touch leads to the phase reset and entrainment of neural oscillations.

CONCLUSION AND FUTURE DIRECTIONS

Experiences of affectionate touch, mediated by the CT system, are an essential component of parent-infant interactions. Affectionate touch appears to promote an infant's somatosensory system development, autonomic regulation, parent-infant bonding and social development, reward processing and learning, and immune function.

Touch may be particularly important for synchronous interactions, which involve the temporal coordination of behavior and physiology. Up until now, very little research on parent-infant synchrony has included assessments of touch, affectionate or otherwise. However, advances in naturalistic methods for parent-infant dyadic brain imaging (Georgieva et al., 2020; Noreika et al., 2020) now permit the fine-grained examination of complex social behavior involving multiple sensory modalities and their neural substrates (Neale et al., 2018). Therefore, the incorporation of affectionate touch as a key mechanism influencing bio-behavioral synchrony could provide a fruitful avenue for future research on parent-infant interactions.

Future research should also seek to clarify the relationship between affectionate touch and relevant parent and infant characteristics. More broadly, parent-infant interactions involving touch may vary based on the personality and temperament of the partners (Mammen et al., 2016; Beebe and Lachmann, 2017). A wide range of developmental

disorders, perhaps especially autism, have been bidirectionally linked to differences in touch interactions in infancy (Feldman et al., 2004; Cascio, 2010; Mammen et al., 2015; Van der Klerk et al., 2019). These individual differences in early social sensory behavior could inform the development of sociometric markers for neuropsychiatric disorders in development (Leong and Schilbach, 2019). Finally, mothers touch their male and female infants differently, and a number of sex differences have been found in infant somatosensory processing, including in responsivity to skin-to-skin contact (Velandia et al., 2012; Fausto-Sterling et al., 2015; Walker et al., 2018). Therefore, measures of cognition, personality and temperament, developmental status, and sex and gender should be incorporated in future studies of caregiver touch and its role in parent-infant interactional synchrony.

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