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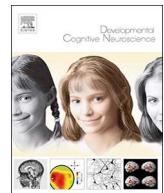
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Social touch and human development

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ABSTRACT

Social touch is a powerful force in human development, shaping social reward, attachment, cognitive, communication, and emotional regulation from infancy and throughout life. In this review, we consider the question of how social touch is defined from both bottom-up and top-down perspectives. In the former category, there is a clear role for the C-touch (CT) system, which constitutes a unique submodality that mediates affective touch and contrasts with discriminative touch. Top-down factors such as culture, personal relationships, setting, gender, and other contextual influences are also important in defining and interpreting social touch. The critical role of social touch throughout the lifespan is considered, with special attention to infancy and young childhood, a time during which social touch and its neural, behavioral, and physiological contingencies contribute to reinforcement-based learning and impact a variety of developmental trajectories. Finally, the role of social touch in an example of disordered development –autism spectrum disorder—is reviewed.

1. Affective versus discriminative touch

We've spent nearly two hundred years studying the wonders of the skin's rich and varied innervation, and the corresponding perceptual experiences of touching or being touched, of an itch or a pin prick, or the warmth of the sun. The exquisitely quantifiable phenomena of one of these sub-modalities, tactile acuity and discrimination, have been part of perceptual experimental psychology since its inception (Weber, 1834). While these discriminative dimensions of tactile experience, mediated by myelinated A-beta and A-delta fibers, are crucial for sensorimotor control and haptic exploration, they do not address questions such as, "What temperature of bath water feels the most relaxing?" or "Why does my partner rubbing my back sometimes feel comforting and other times feel maddening?" In other words, the fine-grained ability to discriminate physical properties of touch does not speak to some of the most salient somatosensory experiences in daily life: conveyance of affective and socially relevant information.

Recent evidence points to orthogonal somatosensory subsystems for discriminative and affective touch (McGlone et al., 2014), and a considerable body of work has emerged describing and quantifying the affective touch dimension (Ackerley et al., 2014; Löken et al., 2009; Olausson et al., 2002, 2010). Unlike the straightforward nature of discriminative touch, affective touch spans a range from orgasmically pleasant to excruciatingly unpleasant, and is further complicated by its

inextricable links to context, gender and sexuality, culture, and other individual, interpersonal, and societal factors (Ellingsen et al., 2016; Morrison et al., 2010). The work in this issue of Developmental Cognitive Neuroscience focuses on nonsexual, pleasant affective touch that is social in nature and its role in human development. In this review, we will consider both the neurobiology and higher-order interpersonal and social factors that define social touch within these constraints, and trace the influence of social touch on learning and development through the stages of the human lifespan.

2. Defining social touch: bottom-up

What makes touch "social?" One way of operationalizing social touch has been handily provided by the correspondence between properties of much naturalistic affiliative interpersonal touch and the unique tuning characteristics of low-threshold unmyelinated peripheral afferent fibers (C-touch, or CT fibers). These fibers respond preferentially to gentle, slow, caress-like stroking (Olausson et al., 2010; Vallbo et al., 1993; Wessberg et al., 2003) and at temperatures near those of human skin (Ackerley et al., 2014). Importantly, CT activation is linked with positive affect: psychophysical ratings of touch "pleasantness" (Essick et al., 1999, 2010) correspond closely to the firing frequency of these afferents (Löken et al., 2009), as do implicit measures of perceived pleasantness such as activation of the zygomaticus

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major muscles (needed for the upturning of the mouth seen in smiling) (Pawling et al., 2017). CT afferents are found only in hairy skin, but not the glabrous skin of the palm that is so central to discriminative touch (Georgopoulos, 1976). CT afferents project to the posterior insular cortex, rather than primary somatosensory (SI) cortex (Olausson et al., 2002) which is the primary target of myelinated fibers that carry the fine-grained signals used for discriminative touch and tactile manipulation of the environment. These properties further support a distinction of the CT system for affective touch from discriminative touch.

The parallels between the effects of CT-mediated touch and oxytocin release on physiological arousal, pleasant feeling, and prosocial interaction suggest CT fibers as a likely mediator of endogenous oxytocin (OT) release during affiliative and nurturing touch (Walker et al., 2017). Although OT has a central role in the neurobiology of close social relationships, it is only part of a complex system. An integrative view comes from the Brain Opioid Theory of Social Attachment (BOTSA), which highlights that while the oxytocin/vasopressin social neuropeptides are critical for mate selection, parental behavior, and other core social functions in mammals, they fail to account for the more complex dynamics observed in primate social behaviors (Henning et al., 2017). BOTSA extends the recognition that opioids are implicated in social reward and motivation to posit that OT, dopamine and serotonin play a more prominent role at the onset of bonding whereas the mu-opioid receptor (MOR) system underpins the maintenance of complex and enduring close social relationships, such as we see in humans (Pearce et al., 2017). Evidence for mediation of the rewarding nature of social touch by endogenous opioids includes increased MOR activity during social touch (Nummenmaa et al., 2016) and naloxone's effects on the perceived pleasantness of social touch (Case et al., 2016).

The fundamental distinction between the discriminative and affective touch systems can thus be summarized in this way: the type of touch mediated by the glabrous skin of the hand primarily conveys properties (i.e., shape, texture, etc.) of elements in the extrapersonal environment that are being actively explored with the hand. In contrast, the CT system mediates passively received touch from other people and overlaps heavily with neurobiological systems for affiliative reward and interoception. This overlap with interoceptive and affective neural circuits allows CT-mediated touch to serve as a bridge between the extrapersonal stimulation and the intra-personal world of the self (Ebisch et al., 2011; Jönsson et al., 2015).

CT afferents, which are so ideally suited for socially relevant touch that they have become known as a “social touch system” (Gordon et al., 2013; Olausson et al., 2010) are absent from the glabrous skin of the palm. However, the palm is clearly not excluded from social touch, given the central social functions of handshakes and hand-holding in multiple cultures across the world. Even CT-targeted touch, delivered by the glabrous skin, is pleasant to the giver as well as to the receiver (Gentsch et al., 2015). Similarly, pet owners exhibit reduced blood pressure and decreased stress while petting their animals (Jenkins, 1986). Active delivery of social touch to another human hand (i.e., “social haptic behavior”) has a neural profile distinct from haptic exploration of an inanimate object (Ebisch et al., 2014a,b), and is, as with receiving social touch, believed to trigger the release of oxytocin (OT) and endogenous opioids (Ellingsen et al., 2016). Further, active social touch in the context of providing comfort to a loved one in pain results in changes to physiological rhythms associated with empathy: EEG mu wave suppression (Peled-Avron et al., 2017) and inter-partner respiratory and cardiac coupling (Goldstein et al., 2017). Thus, the hedonic value and affiliative effects of social touch include, but are not limited to, tactile experience mediated by CT afferents. In line with this, researchers have recently developed a database to index a wide range of social touch events based on valence and arousal to facilitate a more comprehensive treatment of various kinds of social touch (Lee Masson and Op de Beeck et al., 2018).

The complex interplay between different afferent nerve classes that result from reciprocal social touch may be likened to that of a musical

chord comprising individual notes on a keyboard. When individual keys are struck, a pure tone ensues, but combinations of individual keys can produce chords that are somehow greater than the sum of their parts and, importantly, cannot be deconstructed back to the original notes that formed them. This is paralleled in how different somatosensory receptor types combine to produce “touch blend” percepts (Bentley, 1900), such as the perception of wetness resulting from coincident tactile and thermal receptor activation (Ackerley et al., 2012). The skin innervated by CTs is also innervated by myelinated fibers, and the concurrent activation of both types of fiber, integrated and associated repeatedly throughout development, may be ultimately what works together to achieve the percept of pleasant, affiliative touch.

3. Defining social touch: top-down

Having considered social touch from the bottom (peripheral afferents)-up, we now turn to top-down contextual factors that influence how social touch is defined. While the CT system may constitute a primary physiological platform for social touch, higher-order factors including the personal relationship and social context are key ingredients in the definition of social touch. While there are a wide range of contexts, stimulus types and modes of delivery that represent social or interpersonal touch (Gallace and Spence, 2010), we limit our focus to two main contextual factors: 1) the partner in the exchange (i.e., “who” is delivering the touch), and 2) the intent behind the tactile stimulation (“why” it is being delivered).

A clear criterion for social touch is that it is interpersonal, that is, it is shared between conspecifics who have some reciprocal relation to one another, whether that is an intimate, long-term relationship or a more transient or superficial one. Studies have ranged from neuroimaging of sexual partners during intimate touch (Kreuder et al., 2017), to quantifying the behavioral effects of casual touch between strangers in a brief encounter such as the effects of touch between a server and patron in a restaurant (Jones and Yarbrough, 1985). Even between people who have never met, touch can be used to communicate a variety of emotions (Hertenstein et al., 2009) and to impel compliance with requests (Patterson et al., 1986). Between intimate partners, social touch is incredibly powerful. A recent study demonstrated that hand holding by romantic partners resulted in increased brain-to-brain coupling that mediated relief from a painful stimulus (Goldstein et al., 2018)

Despite the evidence against a principal role for primary somatosensory cortex (SI) in affective touch, the perceived sex of an experimenter delivering a sensual caress during an fMRI scan modulated SI response, suggesting that SI may have more of a role in social touch than previously thought (Gazzola et al., 2012). This is further evidence that the complex perceptual experience of social touch is not limited to CT afferents, but involves multiple somatosensory submodalities acting in concert. It’s not clear whether SI response would extend to affective touch from a familiar person; more research in this area is needed to map out the convergence and divergence of neural circuits for different kinds of social touch. Interestingly, comfort with social touch can be topographically mapped as a function of the kind of relationship we have with the other person (Suvilehto et al., 2015).

Research on touch within romantic relationships supports the role of both social neuropeptides and neural reward systems as discussed above. Posterior insular responses to romantic caresses from a lover are modified by anticipation of the touch and sexual desire (Ebisch et al., 2014a,b). This kind of romantic touch between partners also engages reward regions of the brain; response from these regions such as ventral striatum and anterior cingulate cortex is boosted by administration of oxytocin (Kreuder et al., 2017). Interestingly, this facilitation by oxytocin correlates inversely with subclinical autism traits (Scheele et al., 2014). Studies such as these, which combine rigorous experimental design with the ecological validity of a partner or other socially significant person to the individual, are critical to understanding the role

of the lived experience of affiliative touch and its cumulative effects on social reward over the course of human relationships.

Contextual factors outside of identity of the two partners or their relationship to one another also influence the experience of and neural response to social touch. Somatosensory evoked potentials to interpersonal touch vary in amplitude depending on the emotional facial expression of the person delivering the touch (Ravaja et al., 2017). Further, multisensory interactions that impact the brain's response to social touch are not limited to the visual system, as unpleasant odors can reduce the perceived pleasantness and alter the response of insular and opercular cortices to affective touch (Croy et al., 2016a,b). Finally, touch can interact with much more complex and multiple aspects of the context of the encounter, as in the alleviation of induced existential concerns (i.e., fear of death) by touch from an experimenter (Koole et al., 2014). Interestingly, in this study, the effect of social touch on fear was specific to individuals with low self-esteem. This complex interaction of intra- and extrapersonal factors in the touch encounter highlights the intricacies of contextual factors in the experience of social touch.

Two lines of research – vicarious touch and remote or “mediated” touch - demonstrate that interpersonal touch does not necessarily need to be direct to be social. In vicarious touch paradigms, individuals watching interpersonal touch rate CT-targeted caresses as more pleasant than non-CT-targeted touch and exhibit responses in posterior insular cortex, as if experiencing the touch themselves (Morrison et al., 2011). Further, neural response to watching affective (interoceptive) and discriminative (exteroceptive) touch are distinguishable along the same lines as for actual touch, with response to viewed affective social touch in the posterior insula, and modulation in secondary somatosensory cortex with perceived intensity of viewed somatosensory stimuli (Ebisch et al., 2011). Recent work suggests that viewing dyadic interactions that include touch biases visual attention to the emotionally relevant aspects of the scene relative to those that don't include touch (Schirmer et al., 2018).

In mediated touch paradigms, two people in remote locations can exchange touch via a device. While technology has facilitated long-distance interaction in the auditory and visual realms, the development of applications for long-distance interpersonal touch is still in its infancy. However, early studies have laid the groundwork for the conveyance of simple ideas and emotions using remote interpersonal touch (Haans and IJsselsteijn, 2006), and these devices are likely to be of substantial value to the experimental study of social touch. Thus, interpersonal touch can be social even when only viewed between two other individuals, or delivered indirectly between individuals through a device.

Is the criterion of exchange of touch between socially relevant conspecifics sufficient to define social touch, or are other factors important? An additional potential criterion is communicative intent: does the touch convey a particular message such as comfort, playfulness, warning, sexual desire, etc., that makes it *relational*? Or can it be more functional in nature (such as a parent using one hand to support an infant in a sitting position)? While some forms of interpersonal touch may appear largely pragmatic on the surface, they often involve inherent social corollaries which are reinforced by repetition throughout development (Grandi, 2016). In the example of supported sitting, while the primary purpose of the physical contact is to augment the infant's still-developing trunk muscles to keep him/her upright, a secondary consequence is that the infant receives the implicit message that touch from a parent results in a greater feeling of security and safety. In the case of grooming, ostensibly a highly pragmatic and instrumental form of interpersonal touch, a deeper look into the evolution of primate social communication reveals that extended periods of grooming evolved to establish, reinforce, and signal social bonds and hierarchies (Dunbar, 2010). Thus, even a highly instrumental form of interpersonal touch such as grooming is deeply rooted in communicative intent both between grooming partners and to other members of the social group.

Given these associations between touch and implicit social or emotional corollaries, it seems that nearly all interpersonal touch between people in any kind of enduring relationship to one another is social. It may be, then, that the only interpersonal touch that could be considered non-social are rare instances of accidental and very brief contact between unfamiliar people, with no communicative intent, behavioral outcome, or learned association, such as an unheeded, accidental brush of the shoulder on a crowded subway. Thus broadly defined, the vast landscape of social touch and its broader impact depends not only on the interpersonal relationship and the context, but also critically on developmental stage. The same social touch experience may impact an infant very differently than an adolescent; the neural systems for interpreting the experience of social touch continue to develop and evolve over the lifespan. We now turn to examine how social touch changes with development.

4. Social touch over the human lifespan

Touch is the earliest sensory modality to develop (Maurer and Maurer, 1988; Montagu, 1986), serving as a “sensory scaffold on which we come to perceive our own bodies and our sense of self (Bremner and Spence, 2017).” In the first few months of postnatal life, touch is a key “active ingredient” in the development of secure attachment (Duhm, 2010; White, 2004) and the formation of family bonds (Gordon et al., 2010). Indeed, social touch from caregivers is so consistently paired with rewards (i.e., comfort, nourishment) that it is a strong candidate for a pivotal mediator of Hebbian learning in the developing “social brain.” Indeed, the reward value of social touch is so powerful that it rivals drugs of abuse and may be protective against substance use disorder (Zernig et al., 2013). In the following sections, we highlight evidence for the role of social touch in reward learning during development, and explore potential mechanisms for how interpersonal touch may influence neural and behavioral social development throughout the lifespan.

4.1. Pre- and perinatal

The ontogeny of social touch is even appreciable prenatally. Fetuses in the third trimester respond to maternal touch on the mother's abdomen with more tactile exploration of the uterine wall and less self-touch compared to those in the second trimester (Marx and Nagy, 2017). An intriguing hypothesis proposes that the rhythmic stimulation of lanugo hairs during fetal movement through the amniotic fluid stimulates CT fibers and induces a social priming effect in the fetus via oxytocin release (Bystrova, 2009). By extension, if these in utero tactile experiences are rewarding to the fetus, vestibular sensation associated with movement through the amniotic fluid may serve as a secondary reinforcer, contributing to the comfort neonates derive from rocking, bouncing, and swaying. In support of this idea of prenatal vestibular input and its sequelae in neonates, for both humans and mice, maternal carrying of distressed infants reduces crying, body movements, and heart rate over and above the (also significant) effect of maternal holding alone. Further, the calming effect produced a positive feedback cycle of decreased infant movement and increased ability for mothers to carry the pups (Esposito et al., 2013). This combination of tactile-vestibular-proprioceptive stimulation in the context of parental comfort in a positive feedback loop may be a powerful mediator of associative learning that predisposes the brain to respond to social rewards. In a study that measured the effects of tactile and kinesthetic stimulation in 12 premature infants, White and Labarba (1976) observed significant effects on a range of measures including birth weight, body temperature, respiration, and feeding behavior (White and Labarba, 1976). While comprehensive cross-cultural research is sparse, a study comparing Italian and West African mothers suggests that the relative use of tactile versus kinesthetic stimulation for soothing young infants may vary across cultures (Carra et al., 2014).

4.2. Infancy

There is highly converging evidence for the developmental importance of social touch in infancy, and early experiences with touch have extremely far-reaching sequelae throughout the developing brain. In prairie voles, a monogamous species of rodent with a highly affiliative social structure, rearing styles vary in the degree of physical contact between parent and pup. Offspring of low-contact parents show more aggression and less stress response to social isolation than that of high-contact parents (Perkeybile and Bales, 2015). Offspring of parents with high versus low contact styles also exhibit vastly different patterns of connectivity throughout the brain (Seelke et al., 2016). In rats, a sensitive period comprising the first postnatal week has been described, during which maternal licking and grooming exerts long-term epigenetically-mediated effects on cognition, social behavior, and stress reactivity (Bagot et al., 2012; Kaffman and Meaney, 2007). Male offspring reared by high contact dams are less responsive to stress, show more exploratory behaviors in a novel environment, and higher performance on cognitive tasks (Caldji et al., 2000). These far-reaching, epigenetically-mediated effects on development have been studied more broadly in the context of critical windows in the social and physical environment in humans as well (Szyf, 2012).

In humans, 65% of face to face interactions between mothers and infants involve touch communication, which is associated with immediate reductions in both behavioral (Stack and Muir, 1990) and physiological (Feldman et al., 2010b) response to stress. Further, the quality of the touch also matters, with gentle stroking touch generating more smiling in infants than static touch (Jean et al., 2009; Stack and Muir, 1990), and infants as young as 9 months demonstrating decreased heart rate and increased engagement in response to pleasant, CT-targeted touch (Fairhurst et al., 2014). Indeed, there is apparent observational evidence that when parents stroke their infants, that they spontaneously adopt a speed of touch consistent with CT stimulation (Croy et al., 2016a,b).

The benefits of touch in infancy are also apparent over longer time scales. Skin-to-skin contact has analgesic effects in healthy neonates and promotes weight gain, shorter hospital stays (Field et al., 1986) and stronger neural responses (Maitre et al., 2017) in preterm infants. Parental touch is linked to increased oxytocin levels in parents (Feldman et al., 2010a) and has effects on later social-emotional behavioral issues in children that are associated with maternal prenatal anxiety (Pickles et al., 2017). Between 6 and 10 months, the anterior prefrontal cortex begins to respond to gentle touch that is not CT-targeted (delivered to the palm) (Kida and Shinohara, 2013). In addition to its clear role in the development of affective attachment, caregiver touch paired with concurrent speech, plays an important role in infants' ability to detect word boundaries, contributing to receptive communication development. This study suggested that the earliest vocabulary words are often those frequently linked with caregiver touches (Seidl et al., 2015).

While most of the extant research addresses infants as recipients of social touch, those as young as 5 months also use touch to communicate their emotional state to their mothers (Moszkowski and Stack, 2007). Further underscoring the critical role of parental touch, 6-month-old infants of mothers with depression show more self-touch than controls, interpreted as a compensatory behavior for reduced positive touch from their mothers (Herrera et al., 2004). fMRI studies in nursing dams suggests that suckling stimulation engages neural reward systems to a degree that outpaces cocaine administration (Febo, 2011; Ferris et al., 2005), and that this effect is likely mediated by oxytocin (Febo et al., 2005). Thus, even during the first few months of life, there is a reciprocity and an active component of social touch experience that shapes social, communication, and cognitive development in the months and years to come.

Although the feature of affective touch that is most often considered when predicting outcomes is touch frequency (i.e. Brauer et al., 2016),

future research may want to adopt more nuanced measures to explain greater variance in these outcomes. For example, theoretical accounts of the purpose of affiliative touch propose that this serves to promote social relationship development (Morrison et al., 2010) and/or to reduce negative affect (Dunbar, 2010). Here then it will not necessarily be that simply more social touch will have beneficial effects on development, rather that functional social touch in response to a need state will lead to better outcomes. The development of a synchronous relationship between an infant and caregiver has been shown to be an important predictor of later social development (Jaffe et al., 2001). This process involves the infant and caregiver entering into a natural exchange of engagement and disengagement (Tronick, 1989), and here children have been shown to be adept at making social bids when desired and disengaging attention when sated. Parent-infant synchrony has been shown to be an important precursor to attachment formation (Feldman et al., 1999b) attachment security (Jaffe et al., 2001), self-regulation capacities (Feldman et al., 1999a), symbolic competence (Feldman and Greenbaum, 1997), and cognitive skills (Feldman et al., 1996).

Disruption in this early social-sensory input during infancy has severe developmental consequences throughout the lifespan. Infants who are deprived of touch delivered by caregivers, or who avoid it, are at higher risk for sensory processing problems (Lin et al., 2005; Wilbarger et al., 2010) such as over-sensitivity. Avoidance of social touch in infancy is also a predictor of autism spectrum disorder in older children (Baranek, 1999; Mammen et al., 2015). In this case, avoidance of social touch indicates that it is not perceived as pleasant or reinforcing by the infant, which may have significant cascading effects on the development of the social brain. More broadly, altered touch perception in early life, comprising two separate mechanosensitive systems (fast A-Betas and slow CT), may impact the sensory scaffold on which the perceptual distinction between self and other is built (Bremner and Spence, 2017), further influencing social responses and abilities throughout development.

4.3. Toddlerhood and childhood

Social touch continues to influence brain development beyond infancy. As infants become toddlers and gain mobility, the repertoire of parent-child touch expands to include more kinds of pragmatic touch such as postural repositioning and support, as well as more complex and frequent grooming touch. The importance of grooming in maintaining primate social relationships has been emphasized from an evolutionary anthropological perspective (Dunbar, 2010) and is likely mediated by the reinforcing properties of touch-related oxytocin and endogenous opioid release. Touch is an important factor in family dynamics; touch within the nuclear family is a primary predictor of children's sustained expression of positive emotions (Bai et al., 2016). Childhood is a dynamic time during which the people and contexts surrounding social touch are in flux. During the transition to toddlerhood and preschool, the critical role of touch expands beyond caregivers and immediate family to include teachers and peers. As children get older and more independent, the sphere narrows again and children receive tactile input from fewer people and in fewer contexts than when they were very young.

Social touch plays a central role in play. In rats and many other mammalian species, juveniles engage in rough-and-tumble social play, a reinforcing experience that can induce a conditioned place preference (Trezza et al., 2011). Neural responses to physical play and tickling are tightly linked (Ishiyama and Brecht, 2016) and reflect positive affect mediated by the endogenous opioid-mediated reward system (Burgdorf and Panksepp, 2001). In humans, a recent study found that the frequency of maternal touch during a play session between mothers and their five-year-olds was associated with the strength of connectivity of the posterior superior temporal sulcus and other nodes in the social brain (Brauer et al., 2016). The positive effects of appropriate social

touch in early development seems particularly important to highlight at present with the climate of fear surrounding any tactile interaction with children (Selkar et al., 2017). Empowerment of children to seek, and permit touch when desired, while denying this when not desired will likely have positive developmental outcomes. More research is needed to consider how to facilitate this while remaining mindful of child protection issues.

There is also evidence for behavioral effects of physical touch from non-familial adults on children's behavior, although this kind of social touch is much less studied. Friendly touch from an experimenter increases the likelihood of a child delaying gratification by complying with the request to wait for permission before eating a piece of candy (Leonard et al., 2014). In the classroom, positive, contingent touch from teachers has been demonstrated to increase on-task behavior and decrease disruptive behavior in young children (Wheldall et al., 1986).

Finally, the pattern of neural responses to CT-targeted touch appears similar in school-age children as in adults, including posterior insula and posterior superior temporal sulcus responding in young children. Response intensity appears to increase with age between early childhood and adulthood, suggesting that the circuitry for social touch continues to mature as the brain develops (Björnsdotter et al., 2014).

4.4. Adolescence and adulthood

As children reach sexual maturity and embark on the transition to adulthood, corresponding changes in their tactile social world continue to shape brain and behavior. Response to social touch becomes heavily influenced by sexuality and romantic attraction that develops during this stage. Gender asymmetry, in which males are more likely to touch females than vice versa, is apparent in interpersonal touch between adults, but not children (Major et al., 1990). As adulthood continues, while discriminative touch abilities decline with age, perceived pleasantness of CT-targeted touch continues to increase into the ninth decade of life (Sehlstedt et al., 2016).

The effects of social touch in adolescents and adults are not limited to those relevant to romantic or sexual relationships. CT-targeted stroking touch that is non-romantic recruits neural networks involved in social cognition and reward more broadly, in contrast to non-CT-targeted touch delivered by the same experimenter (Gordon et al., 2010). Response to gentle stroking of the arm in brain regions such as the superior temporal sulcus and orbitofrontal cortex are negatively associated with subclinical autism traits in healthy adults (Voos et al., 2013).

The preceding paragraphs describe social touch during typical development, however, they do not address differences in individuals with developmental disabilities. While there is limited research on social touch in developmental disabilities, recent studies present an emerging picture of altered social touch in autism spectrum disorder (ASD). ASD is a developmental disorder that begins in very early childhood and affects individuals throughout their lives, impacting reciprocal social behavior, and thus relationships. Aberrant sensory reactivity is also a cardinal feature of the disorder, with altered reactivity to touch correlating strongly with both social and nonsocial symptoms (Foss-Feig et al., 2012). Thus, we turn now to the emerging research on social touch perception in ASD, highlighting the intersection of low-level sensory differences and higher-level reciprocal social behavior.

5. Social touch and disordered development: autism

The impact of social touch on the developing brain and the consequences of its altered trajectory in childhood are posited here to be highly relevant for autism spectrum disorder (Baranek, 1999). Animal models of ASD exhibit both impaired tactile discrimination and defensiveness to gentle touch, with associated developmental effects on social behavior (Orefice et al., 2016). Children with autism exhibit aberrant behavioral responses to touch (Cascio et al., 2016; Foss-Feig

et al., 2012; Schauder et al., 2015) which are strongly linked both with the core clinical symptoms of the disorder and with biomarkers such as distinct epochs in the somatosensory neural response (Cascio et al., 2015), white matter pathways (Pryweller et al., 2014), and genetic variants that increase serotonin transporter function (Schauder et al., 2015). Experimenter-delivered affective (pleasant and unpleasant) touch to children with autism elicits defensive reactions that are more severe in CT-innervated somatotopic regions (face and arm) than in non-CT-innervated regions (palm) (Cascio et al., 2016). A direct comparison of neural responses to CT- versus non-CT-targeted touch in children with autism suggests a dichotomous response, with reduced response in widespread social-affective brain networks to CT-targeted touch, and enhanced response in primary somatosensory cortex to non-CT-targeted touch (Kaiser et al., 2015).

Taken together, these results indicate that social touch is altered in autism, although it remains to be clarified how heterogeneous neural and behavioral responses to social touch in individuals with autism intersect *vis à vis* hyper-responsiveness and hypo-responsiveness. Both hypo-responsiveness and hyper-responsiveness to social touch may result in reduced input (occurring naturally or resulting from defensive/avoiding behaviors) that alters the trajectory of the developing social brain starting in infancy. Given the fundamental importance of social touch for infant's formation of secure attachment, cognitive and linguistic development, social reward, and emotion regulation, these differences are likely to have far-reaching effects indeed. A better understanding of these sensory-social developmental sequelae holds great promise for developing and refining early intervention approaches based on sensory features.

6. Conclusions

The themes that we have highlighted in this review cast the developmental nature of social touch as dynamic, integrative, and firmly rooted in reward learning processes that shape the developing brain and ultimately adult behavior. The landscape that defines social touch changes qualitatively from an intense and primary mode for associative learning and affiliative connection in the earliest stages of pre- and neonatal life, to part of a multisensory integrated environment throughout the lifespan. Changes with mobility, independence, widening spheres of social influence, sexual maturity, and aging all impact the perceptual experience of social touch. This perceptual experience is in and of itself the product of several overlapping integrative processes. At the neurobiological level, converging input from multiple afferent classes, with a primary role for CT afferents, is paired repeatedly over time with physiological and psychological processes that invoke feelings of comfort, security, and satisfaction. These peripheral processes and their corresponding pathways in the central nervous system are effectors of broader neurobiological systems including oxytocin and mu-opioid systems mediating the reinforcing properties of simple and more complex social bonding, respectively. These systems all interact with top-down contextual factors, including the nature of the relationships, culture, and social context, to create a highly complex, flexible platform in which the rich affective information conveyed through the skin exerts a powerful impact on behavior through learning over a lifetime.

Conflict of Interest

None.

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