

Accepted Manuscript

Title: Social touch: a new vista for developmental cognitive neuroscience?

Author: Teodora Gliga

PII: S1878-9293(18)30114-2
DOI: <https://doi.org/10.1016/j.dcn.2018.05.006>
Reference: DCN 577



To appear in:

Author: Teresa Farroni

PII: S1878-9293(18)30114-2
DOI: <https://doi.org/10.1016/j.dcn.2018.05.006>
Reference: DCN 577

To appear in:

Author: Carissa J. Cascio

PII: S1878-9293(18)30114-2
DOI: <https://doi.org/10.1016/j.dcn.2018.05.006>
Reference: DCN 577

To appear in:

Please cite this article as: Gliga T, Farroni T, Cascio CJ, Social touch: a new vista for developmental cognitive neuroscience?, *Developmental Cognitive Neuroscience* (2018), <https://doi.org/10.1016/j.dcn.2018.05.006>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Social touch: a new vista for developmental cognitive neuroscience?

Editorial

Teodora Gliga¹, Teresa Farroni² and Carissa J. Cascio³¹Centre for Brain and Cognitive Development, Birkbeck, University of London, UK²Developmental Psychology and Socialization Department, Padua University, Italy³Vanderbilt University Medical Center, Department of Psychiatry and Behavioral Sciences, Nashville, TN, USA

The past years have seen a renewed interest in measuring neural, physiological or cognitive, immediate and longer-term effects of human interaction through touch. The term “social touch” was rapidly adopted, implying the existence of (stimulus) selective and (functionally) specific mechanisms. It has been suggested that decreased exposure to social touch during development, either due to its unavailability (e.g. as in the case of pre-term infants placed in incubators or of infants of mothers with post-partum depression) or to atypical touch perception (e.g. as might be the case in autism) has serious consequences for subsequent brain and cognitive development. Despite the excitement surrounding this topic, and its clinical relevance, its object of study remained poorly defined and understood.

The interest in social touch has a decades long history. The first rigorous studies into the importance of maternal physical contact for (monkey) development were carried out in the 1960s, by Harlow and col. (e.g. Harlow & Zimmermann, 1959). A few decades later, in the 1990s, Meaney and col. work reinforced the idea that close physical contact through licking and grooming, early in (rats’) life, was critical for the survival and thriving of the pups e.g. Liu et al, 1997). This group also revealed stable individual differences in the amount of care provided by mothers. It was only natural that researchers would ask whether similar phenomena can be described in human infants. Studying longitudinal cohorts, Field and col. and Feldman and col., demonstrated the beneficial effects of infant skin-to-skin contact or massage on later physical and mental development (e.g. Field, Diego & Hernandez-Reif, 2010; Feldman, Rosenthal & Eidelman, 2013). These decades of very fruitful research have strongly reinforced the idea that caregiving through touch has a special and critical role in early development, and that interfering with it has long lasting effects (measurable still 10 years later, Feldman, Rosenthal & Eidelman, 2013 or from one

generation to the next, Champagne, 2008). The consistency across rodent, non-human primate, and human studies also seems to support the idea of a conserved mechanisms (in mammals). Differences in the nature of the critical stimulation (being able to cling to the surrogate mother matters in monkeys, Harlow & Zimmerman, 1959, while brushing the anal-genital region is sufficient to induce beneficial effects in mice, Evoniuk, Kuhn & Schanberg, 1979) could simply reflect species-specific ecological peculiarities, but ultimately serving the same function. Indeed, in both animal and human studies, parental touch was shown to modulate stress responsivity. However, even within one species – humans - the variety of types of stimulation that have this effect (skin-to-skin contact or pressure massage) cannot but raise questions about how infants may identify caregiving touch across these instances. This is further complicated by the recent discovery of strong correlations between the perceived pleasantness of different stroking speeds and the tuning curves of a particular class of skin receptors, the CT-fibers (Loken, 2009). This research suggests that the speed and temperature of tactile stimulation might be the key properties triggering the effects of social touch. However, another mechanism needs to mediate the effect of skin-to-skin contact, which involves mainly static stimulation, and is therefore suboptimal for CT-fibers. In addition, many other studies showed that, in human adults, top-down factors, such as the identity of the person providing the stroking, matters more than the low-level properties of touch (Gazzola et al., 2012). Understanding the contribution of low level physical properties of touch versus that of the high level, social context, seems critical for understanding the role touch plays in development (and whether a unitary role can be at all ascribed to all touch provided by other human beings).

Thus, this special issue emerged from the need to acknowledge, on one hand, a growing field of research into the role and the mechanisms of social interaction through touch and, on the other, the still lingering difficulties with defining the object of this research and understanding underlying developmental mechanisms. Introducing this special issue, **Cascio et col.** acknowledge the breadth of the research into social touch, which now includes molecular and physiological studies of skin receptors, studies of the social modulation of the perceived pleasantness of touch in human adults and of the atypicalities associated with developmental disorders, such as autism. They also review the small but growing literature looking into the mechanisms and neural substrates of social touch in infants. These authors highlight the need to integrate studies of social touch investigating low level properties of sensory systems with higher level aspects of social interaction. Interestingly, they suggest that few human touches are not social (i.e. non-intentional, accidental). While top-down cues

to intentionality may be critical for perceived touch pleasantness later in life, other mechanisms must mediate the effects of social touch in the first months of life, before infants can judge the intentionality or goal-directedness of action.

Defining social touch. Most developmental studies in this special issue adopt a definition of social touch that is based on stroking speed, a testament to the impact the discovery of CT-fibers has had on the field. **Croy et col.** show that children 5 to 12 years old have a similar dependence of pleasantness rating on stroking speed, as found in adults. **Miguel et col., Della Longa et col., Pirazzoli et col.** and **Tuulari et col.** used CT-targeted velocity stroking as their social touch stimulus, contrasting it to tapping (**Miguel et col., Della Longa et col.**), sub-optimal temperature touch (**Pirazzoli et col.**) or no control (**Tuulari et col.**). A comparison of different velocity stimuli is used also by **Sailer et col.**, to investigate the role of touch experience for adults' pleasantness ratings. CT-optimal stroking versus vibration was used by **Davidovic et col.**, to study the neural underpinnings of touch in adults.

Others have included a variety of interpersonal touches in their social touch category. Social stimulation was provided by an experimenter holding, swaddling and stroking newborn monkeys, in **Simpson et col. Peled-Avron et col.** showed participants pictures of hugging, handshakes or holding hands (in contrast to no-touch interactions).

Mantis et col. further discriminate the between the affective and playful use of touch in mother-infant interaction. Stroking but also massage or patting was classified as affective touch and contrasted to playful touch, which included tickling, lifting or rhythmic touches. This grouping emerged from how frequently mothers used these types of touches (i.e. factor analysis) suggesting that mothers themselves (just like the experimenters) used these touches with different functions. While these studies acknowledge the larger variety in the expression of social touch they raise the question of how we come to classify together actions as dissimilar as patting, stroking and holding hands. Six-month old infants can already extract common goals across different manner of execution, as for example reaching for a particular object, when different trajectories of reaching are used (**Biro & Leslie, 2007**), but no study yet has investigated when they can appreciate the common affective aim of actions as physically dissimilar as patting and stroking. **Crucianelli et col.** make a further distinction between touch that was used contingently on infant's own behaviour or not (e.g. stroking a crying infant vs. stroking and thus distracting an infant engaged with a book). Many other studies have demonstrated the importance of contingent responding in caregiver-infant

interaction (e.g. Begus, Gliga & Southgate, 2014) and it may be that this is a critical aspect for touch to exercise its roles (see further on), in human development.

Yet other studies in this special issue investigated the contribution of other modalities to how social touch is perceived. Could touch be perceived as social not because of how it is felt on the skin but because they see it is delivered by a human hand? **Keizer et col.** asked whether seeing the arm performing the touch matters for its perceived pleasantness in adults. Veridical vision of the arm increased the pleasantness of intermediate velocity stroking. In **Rigato et col.** 4-month-old infants responded differently to tactile stimulation on their hands when it was accompanied by concurrent images depicting a hand being touched, versus images of the table next to the hand being touched. While this demonstrates an understanding of the mapping between visual and tactile bodily coordinates, which may be important for learning about social touch (see further on), it is unclear whether the social component of touch was of importance in this particular study (infants saw a brush touching the hand and felt vibratory stimuli, a touch stimulus that is non CT-targeted and was used by others as a control to social touch). **Lee-Williams et col.**, also use a touch other studies used as control stimulation; they showed that tapping on infant's body helps learning auditory patterns. Could it be that infants did perceive this stimulus as social since infants could see that the stimulation was delivered by a human being and tapping was delivered in structured patterns (possibly betraying intentionality)?

In sum, although a CT-fibers based definition of social touch is currently favoured, a mixture of other physical, inter-relational (e.g. contingency) and intentional (e.g. affective) properties are used as basis for defining social touch. Showing that stimuli with varied structural properties activate common neural substrates or have a similar impact on an organism's physiology or cognition is a better way to ascertain shared mechanisms.

Neural substrates of social touch. The search for neural substrates of social touch has yielded intriguing findings. In this special issue, Tuulari et col. used fMRI to capture somatosensory and insular activation in one-month-old infants experiencing CT-targeted touch during sleep. Insular activation is in line with another recent finding by Jonsson et al (2018), who used diffused optical tomography. These results are particularly exciting given the association between insular activation and both CT-stimulation (Olausson et al, 2002) and the perceived affective or pleasantness of touch, in human adults (Bjornsdotter & Olausson, 2011). This would suggest that from very early on in life (therefore it could be independent of experience) CT-targeted tactile stimulation has motivational value. However, in this special

issue, Davidovic et col. show that both social (stroking) and non-social (vibration) stimuli increase functional connectivity between posterior and anterior insula in adults, but differentially for the dorsal and ventral partitions of the anterior insula. Given the disparity in the age of the samples and the lack of dorsal-ventral specification of insular ROIs in the Tuulari and Jonsson papers, it is difficult to directly compare the results of adult and infant studies.

The posterior STS (pSTS) is another area shown to be recruited by social touch in adults (Bennett et al., 2014; Gordon et al., 2013, but see Davidovic et col., 2016 for not replicating pSTS activation). Intriguingly, two infant studies in this special issue, Miguel et col. and Pirazzoli et col., did not find differences between CT-targeted and non-targeted touch in the STS. Finally, Peled-Avron et col. interrogated the neural mechanisms of vicarious, or observed, social touch using transcranial direct current stimulation. They report a role for the inferior frontal gyrus, part of the putative human mirror neuron system, in the emotional responses to vicarious touch. This effect was modulated by self-reported emotional empathy.

These studies advance our understanding of mechanisms underlying social touch perception in development but have only started to address the questions of which aspects of interpersonal touch are critical to elicit response from key areas of the “social brain”. While CT-targeted touch per se seems sufficient to activate the insula (in sleeping infants), additional contextual cues may be needed for STS activation. Exploration of neural mechanisms for vicarious touch extends the relevant neural network to include the putative mirror neuron system. More importantly than defining a neural network for social touch, we need to better understand whether and how nodes of this network interact, and what the functional implications are of both typical and aberrant interactions at different stages of development.

The function of social touch. Why should infants need to identify touch provided by a human being from other tactile stimulation they perceive? As is the case for other social stimuli, such as the human voice, there need not be a sole answer to this question. Humans use vocal signals, for example, to communicate, sooth or recognize each other. There have been two major theories explaining the putative functions of social touch. Because, across species, social touch decreases stress reactivity (true for licking and grooming in mice, Kangaroo care or massage in human infants), a conserved mechanism was proposed, where parental touch signals the quality of the environment in which the infant develops, thus

allowing them to adapt to this environment (Meaney, 2001). Social touch signals to infants that they are in a resource full environment, one where caregivers have the energy to engage in this type of stimulation. Triggered by tactile stimulation from caregivers or by stimulation that simulates caregiver touch, a chain of physiological and epigenetic processes leads, across species, to decreased stress responses to novel stimulation and an increase in exploration. In this special issue, Simpson et col. carry out a comprehensive study of the effects of early deprivation of tactile contact, in monkeys. Using an animal model means one can better control the environment the infant was exposed to, allowing for causal inferences to be made about the role of touch per se. When raised in isolation, tactile stimulation provided by an experimenter was sufficient to decrease the latency with which monkeys approached novel objects and their anxiety when faced with a new experimenter. Furthermore, Brummelman et col. also suggest that parental touch makes children feel safe in their exploration of the environment. In their paper they demonstrate that parental touch lowered children's implicit attentional bias for social threat and, among socially anxious children, raised trust in unfamiliar others. These effects occur in late childhood, when children still readily rely on their parents for safety, but seems to disappear in adolescence when, according to the authors, they seek independence from their parents. These papers, as many others investigating the effects of touch on stress reactivity, stop short of discussing in which way these behavioural changes allow the organism to adapt to a good/poor environment. We can speculate that, in a poor environment in which parents are less available, children might have to make themselves decisions on whether to approach novel stimuli; in this context children would be at an advantage if they and were more alert to the presence of threat or novelty but took longer to process them before approaching them.

A second theoretical perspective gives social touch a key role in establishing affective or affiliative bonds. This view is supported by evidence that CT fibers innervate the insula, a structure associated with generating affiliative behaviors (Caruana et al, 2011) and that stroking elicits oxytocin release in both those experiencing and providing this stimulation (Crockford et al, 2013; Cong et al., 2015). In this special Tuulari et col. describe insular activation by CT-targeted touch as early as the first month of life. However, the insula is also involved in interoception as for example the perception of heart beats (Critchley et al, 2004) and social touch was shown to produce changes in heart rate (Feldman, Singer & Zagoory, 2010). Thus, what is seen as evidence for an affiliative role of social touch may also be evidence for its role in stress regulation.

Much less investigated has been the role social touch may have in communication. Other social signals, such as direct gaze or infant directed speech, are used by caregivers in an ostensive-communicative manner to promote early learning (e.g. Senju & Csibra, 2008). Direct gaze, for example, facilitates the learning of both the identity of the person communicating and of the information she conveys (e.g. Farroni et al, 2007). In this special issue, Della Longa et col. show that social touch has an equivalent role to direct gaze, since 4-month-old infants encode better the identity of a human face, despite its averted gaze, when they experienced concurrent stroking. Pirazzoli et col show that stroking activates the posterior Superior Temporal Sulcus, a region also associated with processing direct gaze or the human voice (Grossmann et al., 2008; Blasi et al., 2011). Lee-Williams et col. finding that touching infant's body in a particular pattern helps them extract words from an auditory stream may be explained by the fact that the structured nature of the tactile stimulus conveys communicative intent. This study goes one step further and attempts to characterize the prevalence of this type of touch in mother infant interaction. Findings are not yet straightforward - the pattern of touch that is most effective for auditory learning is found to rarely occur spontaneously.

Thus, papers in this special issue brings support three potential roles of social touch: regulatory, affiliative and communicative. However, we cannot but ask to what extent these are distinct roles, given they are triggered by the same signal – i.e. CT-targeted touch? A similar question has been asked with respect to the role played by pitch variation in motherese: does it convey communicative intent or emotional valence (Saint-Georges et al, 2013), or both? Could it be that the same (touch) signal fulfils concurrently all three roles, decreasing anxiety and (as a by product ?) promoting learning about the caregiver (an affiliative function) and the environment (a communicative role)?

Experience dependent? Key to developmental work is understanding to what extent mechanisms depend on experience and characterizing the nature of this experience. Given the role social touch is supposed to have in signalling the quality of the environment an organism is born into, we'd expect that genetically specified mechanisms were available to help newborns identify social touch. The discovery of CT-fibers and evidence for very early responsiveness to CT-targeted stimulation in human infants (Tuulari et col., in this special issue) encourages this view. But this special issue also contains work that suggests experience may be needed to define what social touch is. Sailer et col. show that adults with reduced exposure to touch do not rate CT-targeted stroking as more pleasant. However,

individual differences in exposure to touch could result from individual differences in the propensity to enjoy touch or to engage in social interaction, more broadly. Rather than experience, genetically determined traits may explain the Sailer et col. findings. But is it plausible that the (CT-fibers) tuning to intermediate velocity of stroking is learned? 3-10 cm/sec is the speed most commonly used by adults when stroking or imagining they stroke another human being, including an infant (Croy et al., 2016). If this experience led to the “training” of CT-fibers, what constrains the use of this speed to start with (if not the specific tuning of skin receptors)? If the tuning of CT-fibers is unlikely to be experience dependent, could the pleasantness or social role of interpersonal touch be learned by association with other social cues? In this special issue, Keizer et col. show that intermediate velocity stroking increases in pleasantness if adults see the hand performing the touch. The associated visual experience of inter-personal touch might be needed for infants to perceive it as social (and pleasant). To build on this experience, infants should be able to map the visual and somatosensory experience of touch on their bodies. According to Rigato et col, infants as young as 4-month-old do that. Future studies will tell us whether visual experience of interpersonal touch contributes to how the perception and functions of this type of touch changes during development.

Two papers in this special issue, Mantis et col. and Crucianelli et col. suggest potential avenues for investigating the role of early experience. Mantis et col. document less frequent use of touch, especially of playful and stimulating touch, by mothers suffering from post-natal depression. When investigating the role of touch in this population, studies will have to carefully control for the broader effects depression has on parent child interaction. Crucianelli et col. found that variation in the frequency of non-attuned mind-related comments associates with the amount of touch behaviours that were not contingent with the infant’s emotions. Both these studies observe variation in particular types of social touch (playful, contingent), which opens the possibility of investigating their specific roles.

Looking to the future

The breadth of approaches to investigating social touch that this special issue attracted, have helped clarify important avenues for future research. We identify the following open questions:

(1) *How to reconcile evidence for bottom up and top down contributions to touch perception, in early development?* Could inconsistencies in findings actually reflect a developmental progression where bottom up (evolutionarily conserved) mechanisms allow the identification

of social touch initially and have a regulatory effect, while later, additional social cues, experienced concurrently with touch, help infants recognize this signal as affiliative and communicative?

(2) *Is touch special amongst other social and communicative cues?* Some have suggested a complementary use of cues such as mutual gaze, infant directed speech and touch.

Specifically, it was suggested that touch may populate those moments in interaction when face to face communication was not possible. The role of touch might also decrease as children become mobile and therefore spend less time in proximity with caregivers. Yet, few studies have assessed the communicative role of touch in the same way as it has been done for gaze or voice cues.

(3) *Which mechanisms are conserved and which human specific?* There is now good evidence for touch playing a role in stress regulation in mammals (and possibly other species dependent on parental care). In contrast, given some social cues have gained a particular role in communication in human evolution, the communicative role of touch is likely to be unique to our species. The use of grooming for social bonding, in primates (Dunbar, 2010), might be the reason why CT-fibers are mainly present in hairy skin.

(4) *Which aspects of social touch are impaired in autism?* While there is some evidence for deficits in the CT system, aberrant touch perception in autism does not appear to be limited to the perception of CT-targeted touch. Understanding the scope of deficit and the relative roles of top-down versus bottom-up mechanisms will be important for the development of relevant therapeutic approaches in this population.

Acknowledgments: TG is funded by UK Medical Research Council (G0701484); TF is supported by the Wellcome Trust (073985/Z/03/Z) and by the Pro Beneficentia Stiftung (Liechtenstein). CJC is funded by the U.S. National Institute of Mental Health (MH 102272).

References

- Begus, K., Gliga, T., & Southgate, V. (2014). Infants learn what they want to learn: Responding to infant pointing leads to superior learning. *PloS one*, *9*(10), e108817.
- Biro, S., & Leslie, A. M. (2007). Infants' perception of goal-directed actions: development through cue-based bootstrapping. *Developmental science*, *10*(3), 379-398.
- Björnsdotter, M., & Olausson, H. (2011). Vicarious responses to social touch in posterior insular cortex are tuned to pleasant caressing speeds. *Journal of Neuroscience*, *31*(26), 9554-9562.
- Blasi, A., Mercure, E., Lloyd-Fox, S., Thomson, A., Brammer, M., Sauter, D., Deeley, Q., Barker, G.J., Renvall, V., Deoni, S., Gasston, D., Williams, S.C.R., Johnson, M.H.,
- Caruana, F., Jezzini, A., Sbriscia-Fioretti, B., Rizzolatti, G., & Gallese, V. (2011). Emotional and social behaviors elicited by electrical stimulation of the insula in the macaque monkey. *Current Biology*, *21*(3), 195-199.
- Cascio, Carissa J., David Moore, and Francis McGlone. "Social touch and human development." *Developmental cognitive neuroscience* (2018).
- Champagne, D. L., Bagot, R. C., van Hasselt, F., Ramakers, G., Meaney, M. J., De Kloet, E. R., ... & Krugers, H. (2008). Maternal care and hippocampal plasticity: evidence for experience-dependent structural plasticity, altered synaptic functioning, and differential responsiveness to glucocorticoids and stress. *Journal of Neuroscience*, *28*(23), 6037-6045.
- Cong, X., Ludington-Hoe, S. M., Hussain, N., Cusson, R. M., Walsh, S., Vazquez, V., ... & Vittner, D. (2015). Parental oxytocin responses during skin-to-skin contact in pre-term infants. *Early Human Development*, *91*(7), 401-406.
- Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B*, *280*(1755), 20122765.

- Croy, I., Luong, A., Tricoli, C., Hofmann, E., Olausson, H., & Sailer, U. (2016). Interpersonal stroking touch is targeted to C tactile afferent activation. *Behavioural Brain Research SreeTestContent1*, 297, 37-40.
- Croy, I., Sehlstedt, I., Wasling, H. B., Ackerley, R., & Olausson, H. (2017). Gentle touch perception: From early childhood to adolescence. *Developmental cognitive neuroscience*.
- Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature neuroscience*, 7(2), 189.
- Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B*, 280(1755), 20122765.
- Crucianelli, L., Wheatley, L., Filippetti, M. L., Jenkinson, P. M., Kirk, E., & Fotopoulou, A. K. (2018). The mindedness of maternal touch: An investigation of maternal mind-mindedness and mother-infant touch interactions. *Developmental cognitive neuroscience*.
- Cong, X., Ludington-Hoe, S. M., Hussain, N., Cusson, R. M., Walsh, S., Vazquez, V., ... & Vittner, D. (2015). Parental oxytocin responses during skin-to-skin contact in pre-term infants. *Early Human Development*, 91(7), 401-406.
- Davidovic, M., Jönsson, E. H., Olausson, H., & Björnsdotter, M. (2016). Posterior superior temporal sulcus responses predict perceived pleasantness of skin stroking. *Frontiers in human neuroscience*, 10, 432.
- Davidovic, M., Göran, S., & Håkan, O. (2017). Processing of affective and emotionally neutral tactile stimuli in the insular cortex. *Developmental cognitive neuroscience*.
- Della Longa, L., Gliga, T., & Farroni, T. (2017). Tune to touch: Affective touch enhances learning of face identity in 4-month-old infants. *Developmental cognitive neuroscience*.

- Dunbar, R. I. (2010). The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews*, *34*(2), 260-268.
- Evoniuk, G. E., Kuhn, C. M., & Schanberg, S. M. (1979). The effect of tactile stimulation on serum growth hormone and tissue ornithine decarboxylase activity during maternal deprivation in rat pups. *Communications in Psychopharmacology*, *3*(5), 363.
- Farroni, T., Massaccesi, S., Menon, E., & Johnson, M. H. (2007). Direct gaze modulates face recognition in young infants. *Cognition*, *102*(3), 396-404.
- Feldman, R., Rosenthal, Z., Eidelman, A.I., 2013. Maternal-Preterm Skin-to-Skin Contact Enhances Child Physiologic Organization and Cognitive Control Across the First 10 Years of Life. *Biol. Psychiatry* *75*, 56–64. doi:10.1016/j.biopsych.2013.08.012
- Feldman, R., Singer, M., & Zagoory, O. (2010). Touch attenuates infants' physiological reactivity to stress. *Developmental Science*, *13*(2), 271-278.
- Field, T., Diego, M., & Hernandez-Reif, M. (2010). Preterm infant massage therapy research: a review. *Infant Behavior and Development*, *33*(2), 115-124.
- Gazzola, V., Spezio, M. L., Etzel, J. A., Castelli, F., Adolphs, R., & Keysers, C. (2012). Primary somatosensory cortex discriminates affective significance in social touch. *Proceedings of the National Academy of Sciences*, *109*(25), E1657-E1666.
- Gordon, I., Voos, A. C., Bennett, R. H., Bolling, D. Z., Pelphey, K. A., & Kaiser, M. D. (2013). Brain mechanisms for processing affective touch. *Human Brain Mapping*, *34*(4), 914-922.
- Grossmann, T., Johnson, M.H., Lloyd-Fox, S., Blasi, A., Deligianni, F., Elwell, C., Csibra, G., 2008. Early cortical specialization for face-to-face communication in human infants. *Proc. R. Soc. London B Biol. Sci.* *275*, 2803–2811. doi:10.1098/rspb.2008.0986
- Harlow, H. F., & Zimmermann, R. R. (1959). Affectional responses in the infant monkey. *Science*, *130*(3373), 421-432.

Keizer, A., de Jong, J. R., Bartlema, L., & Dijkerman, C. (2017). Visual perception of the arm manipulates the experienced pleasantness of touch. *Developmental cognitive neuroscience*.

Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., ... & Meaney, M. J. (1997). Maternal care, hippocampal glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress. *Science*, 277(5332), 1659-1662.

Löken, L.S., Wessberg, J., Morrison, I., McGlone, F., Olausson, H., 2009. Coding of pleasant touch by unmyelinated afferents in humans. *Nat. Neurosci.* 12, 547–548.
doi:10.1038/nn.2312

Mantis, I., Mercuri, M., Stack, D. M., & Field, T. M. (2018). Depressed and non-depressed mothers' touching during social interactions with their infants. *Developmental cognitive neuroscience*.

Meaney, M. J. (2001). Nature, nurture, and the disunity of knowledge. *Annals of the New York Academy of Sciences*, 935(1), 50-61.

Miguel, H. O., Lisboa, I. C., Gonçalves, Ó. F., & Sampaio, A. (2017). Brain mechanisms for processing discriminative and affective touch in 7-month-old infants. *Developmental cognitive neuroscience*.

Olausson, H., Lamarre, Y., Backlund, H., Morin, C., Wallin, B. G., Starck, G., ... & Bushnell, M. C. (2002). Unmyelinated tactile afferents signal touch and project to insular cortex. *Nature neuroscience*, 5(9), 900.

Peled-Avron, L., Glasner, L., Gvirts, H. V., & Shamay-Tsoory, S. G. (2018). The role of the inferior frontal gyrus in vicarious social touch: A transcranial direct current stimulation (tDCS) study. *Developmental Cognitive Neuroscience*.

Pirazzoli, L., Lloyd-Fox, S., Braukmann, R., Johnson, M.H. & Gliga, T. (2018) Hand or spoon? Exploring the neural basis of affective touch in 5-month-old infants. *Developmental Cognitive Neuroscience*.

Rigato, S., Banissy, M. J., Romanska, A., Thomas, R., van Velzen, J., & Bremner, A. J. (2017). Cortical signatures of vicarious tactile experience in four-month-old infants. *Developmental cognitive neuroscience*.

Sailer, U., & Ackerley, R. (2017). Exposure shapes the perception of affective touch. *Developmental cognitive neuroscience*.

Senju, A., & Csibra, G. (2008). Gaze following in human infants depends on communicative signals. *Current Biology*, 18(9), 668-671.

Simmons, A., Murphy, D.G.M., 2011. Early specialization for voice and emotion processing in the infant brain. *Curr. Biol.* 21, 1220–1224. doi:10.1016/j.cub.2011.06.009

Simpson, E. A., Sclafani, V., Paukner, A., Kaburu, S. S., Suomi, S. J., & Ferrari, P. F. (2017). Handling newborn monkeys alters later exploratory, cognitive, and social behaviors. *Developmental cognitive neuroscience*.

Tuulari, J. J., Scheinin, N. M., Lehtola, S., Merisaari, H., Saunavaara, J., Parkkola, R., ... & Björnsdotter, M. (2017). Neural correlates of gentle skin stroking in early infancy. *Developmental cognitive neuroscience*.