ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Characterizing affiliative touch in humans and its role in advancing haptic design

James H. Kryklywy¹ | Preeti Vyas² | Karon E. Maclean² | Rebecca M. Todd^{3,4} 💿

¹Department of Psychology, Lakehead University, Thunder Bay, Ontario, Canada

²Department of Computer Science, University of British Columbia, Vancouver, British Columbia, Canada

³Department of Psychology, University of British Columbia, Vancouver, British Columbia, Canada

⁴Djavad Mowafaghian Centre for Brain Health, University of British Columbia, Vancouver, British Columbia, Canada

Correspondence

Rebecca M. Todd, Department of Psychology, University of British Columbia, 2136 West Mall, Vancouver, BC V6T 1Z4, Canada. Email: becket.todd@psych.ubc.ca

Funding information

Natural Sciences and Engineering Research Council of Canada, Grant/Award Numbers: PDF-532611-2019, RGPIN-2018-04828, RGPIN-2020-05354; Michael Smith Health Research BC, Grant/Award Number: 16897

Abstract

An emerging view in cognitive neuroscience holds that the extraction of emotional relevance from sensory experience extends beyond the centralized appraisal of sensation in associative brain regions, including frontal and medial-temporal cortices. This view holds that sensory information can be emotionally valenced from the point of contact with the world. This view is supported by recent research characterizing the human affiliative touch system, which carries signals of soft, stroking touch to the central nervous system and is mediated by dedicated C-tactile afferent receptors. This basic scientific research on the human affiliative touch system is informed by, and informs, technology design for communicating and regulating emotion through touch. Here, we review recent research on the basic biology and cognitive neuroscience of affiliative touch, its regulatory effects across the lifespan, and the factors that modulate it. We further review recent work on the design of haptic technologies, devices that stimulate the affiliative touch system, such as wearable technologies that apply the sensation of soft stroking or other skin-to-skin contact, to promote physiological regulation. We then point to future directions in interdisciplinary research aimed at both furthering scientific understanding and application of haptic technology for health and wellbeing.

KEYWORDS

affective touch, affiliative touch, emotion, haptic technology, self-regulation, valence

INTRODUCTION

From the literally searing pain you experience when you accidentally touch a hot burner to the comfort you feel from a loved one's caress, touch can feel intrinsically bad or good. An emerging perspective in affective cognitive neuroscience extends beyond the view that such affective coloring of perception is always the result of appraisal processes mediated by the central nervous system. This emerging perspective looks to evidence that perception can be emotionally valenced from the point of contact with the world.¹⁻³ As illustrated above, a paradigmatic example of a sensory system that carries valenced information from the periphery is the human tactile system. On the negative

end of the valence spectrum, the dedicated pain system has been well characterized; however, the identification of receptors mediating the positive end of the spectrum, a human affiliative touch system, is relatively recent. In addition to inspiring an explosion of research, the discovery of receptors dedicated to affiliative touch has informed-and is informed by-new technology design for communicating and regulating emotion through touch. In this paper, we review recent research on affiliative touch, its regulatory effects across the lifespan, and factors that modulate it. We also review recent work on the design of haptic technologies, devices that stimulate the affiliative touch system to promote physiological regulation. We then point to future directions in interdisciplinary research aimed at both furthering scientific

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

understanding and application of haptic technology for health and wellbeing.

BACKGROUND

Decades of research on the interplay between sensory experience and emotion has constructed a canonical picture of emotion-perception interactions. In this view, which we refer to as the central modulation view, brain regions sensitive to emotional/motivational relevance modulate activity in sensory cortices, altering the perception of sensory signals, and promoting adaptive behaviors.^{4–6} Here, the amygdala—along with other associative brain regions, such as the ventral prefrontal cortex, locus coeruleus, and ventral striatum-appraises the incoming sensory information to tag the emotional/motivational salience of objects and events. Feedback projections from these associative areas back into sensory cortices selectively enhance or inhibit perceptual processing. The central modulation view is well supported by a robust body of predominantly vision-oriented research; yet, it is not the whole picture. Examination of nonvisual sensory systems suggests that, rather than being solely dependent on central modulation, the perceptual experience can be valenced from the point of contact with the world.^{1,2,7} The tactile system is one such sense, as the skin itself contains receptors responsive to positive and negative sensation.⁸

The cognitive neuroscience of positive affective touch—a relatively new area of research-supports a view by which the emotional salience of sensation is conveyed from the periphery to the central nervous system. Note that here, and throughout this paper, the terms "emotion" or "emotional" refer to states elicited by events that act to motivate behavior.⁹ rather than discrete categorical emotions (e.g., happiness, fear, etc.¹⁰). In this view of peripheral affective coding, assessment of the affective or motivational salience of the world is no longer separate from, or superordinate to, raw sensation. Rather, the direct interface with physical characteristics of the environment can color perception with emotional meaning independently of appraisal by the central nervous system. This valenced contact in turn modulates perceptual experience as well as other cognitive processes. One major factor giving rise to this updated view of emotion/perception has been in response to recent work in characterizing affective somatosensation-signals of physical touch mediated by receptors that are sensitive to valenced information rather than discriminative properties.

Over the past 5 years, there has been an explosion of publications refining our understanding of positive affective touch-from its basic biology, to its role in emotion regulation and development, to individual differences in it, to contextual factors that modulate its effects. In parallel, an emerging field of haptic design has begun to integrate these same features into the development of technologies to support human emotional wellbeing. In the following review, we synthesize much of this recent work from psychology and cognitive neuroscience and integrate it with literature from computer science that incorporates emotion-related information into haptic design. We contextualize our review within a view of affective perception that stresses the role of affectively colored perception that is valenced from the initial point of contact with the world. Note that, because affect is, by definition, valenced, and nociception (pain perception, which is well-researched and beyond the scope of this review) is a form of negative affective touch, we will diverge from the more commonly used terminology of *affective touch* and refer to the subject of this paper as *affiliative touch*. We use the term affiliative because we are referring to a specific form of evolutionarily conserved positive touch thought to serve formation and maintenance of caregiving and social bonds in primates.^{8,11,12}

CHARACTERIZING AFFILIATIVE TOUCH

Of all the sensory organs, the skin receives information that is the most proximal to us. It provides an intimate experience of the environment and can act as a conduit of social-emotional communication. A simple touch alone can convey and evoke a range of positive (as well as negative) emotions. Although the experience of tactile sensation can be modulated by numerous factors, its valence is in part inherent to the structure and wiring of the peripheral nervous system. On the negative end of the valence spectrum, receptors dedicated to affective aspects of aversive touch sensation-pain-have been well-studied over the past century (e.g., Refs. 13 and 14). Signals of pain are carried from the skin by unmyelinated slow-conducting C fibers, as well as myelinated A-delta fibers, and are involved in both reflexive responses and the cognitive experience of pain.^{15,16} In contrast, it is only since the turn of the millennium that research on affiliative touch perception has taken off.

Prior to this point, investigation of human touch had focused on the glabrous, or nonhairy, skin of the palms, neglecting the hairy skin where C-tactile (CT) receptors are found.⁸ It took the investigation of receptor types in hairy skin to identify a type of low-threshold mechanoreceptor that responds preferentially to slow, sustained, caress-like touch.¹⁷ Although originally identified in cats in 1939,¹⁸ the presence of these affiliative receptors, known as C-tactile (CT) afferents in humans, was not reported in humans until 1988.¹⁹ Furthermore, it was not until 1999 that a pioneering study using microneurography (measuring nerve activity by inserting a needle electrode under the skin) reliably confirmed their existence.²⁰ Subsequent work has further found that the leaf-shaped CT receptors are arranged in what is poetically described as palisades around the hair follicle²¹ and are maximally sensitive to a gentle, stroking touch.²² CT receptors are distinct from nociceptors subserved by other unmyelinated C-fibers and from a range of A-beta receptors subserved by faster-conducting myelinated fibers that allow for discriminatory touch (i.e., tactile sensations that discriminate the characteristics of what is being touched) (Figure 1). CT receptors have small receptive fields,²³ fire preferentially to certain levels of pressure and stroking velocity (1-10 cm/s, often operationalized as 3 cm/s) as well as at a preferred temperature (32°C).²² They interact with fibers carrying discriminatory touch information^{21,24} and project directly or indirectly to multiple nodes of affective evaluation in the central nervous system.²⁵⁻²⁷ Importantly, stimuli that evoke

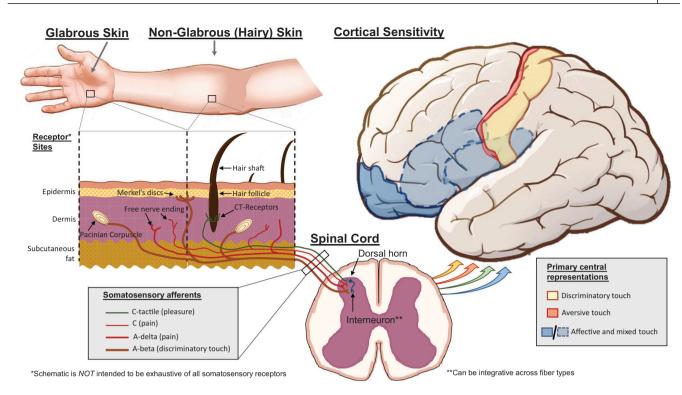


FIGURE 1 Schematic of parallel somatosensory pathways. Somatosensory information is received at the tactile receptors embedded within skin. While most receptor subtypes are present in both glabrous and nonglabrous (i.e., hairy) skin, CT fibers sensitive to affiliative touch are limited to nonglabrous regions. It should be noted that there is some evidence that A-beta fibers may also play a role in the experience of affiliative touch pleasantness. Signals of discriminatory, painful, and pleasant touch are conveyed to the central nervous system along distinct afferent fibers, with some integration of these signals occurring within the dorsal horn of the spinal cord. Within the cortex, somatosensory information is represented and processed across a number of brain regions, notably including primary/secondary somatosensory cortices (discriminatory touch) as well as orbitofrontal/ventromedial prefrontal, anterior cingulate, and insular cortices (affective and mixed-valence touch representations). Dashed outlines indicate areas not visible on the surface in the sagittal view presented. CT, C-tactile.

higher CT firing rates also typically evoke higher ratings of subjective pleasantness,²⁸ although the relationship between velocity and pleasantness is also modulated by the duration and spatial pattern of contact with the skin.²⁹ CT receptors may also be only one of a putative family of receptors, each sensitive to distinct qualities of affiliative social touch.^{21,30} There is also growing evidence that myelinated A fibers contribute to experienced pleasantness of soft stroking and pressure,^{29,31,32} although the precise mechanisms by which this occurs—and whether it is a function of centrally modulated associative processes—is still not known.³³

The findings summarized above first provided the foundation for the *affective*³⁴ and *social*^{12,35} *touch hypotheses*. These have proposed that CT afferents mediate affective rather than discriminatory aspects of touch, conveying information about affiliative body contact that is primarily (but not exclusively) associated with social emotions, such as comfort and affection, which in turn can promote social bonding. This is in stark contrast to the traditional conception of somatosensation that focuses on exteroceptive touch information conveyed by fast-conducting myelinated pathways. Together, this evidence suggests an important processing mechanism for affiliative touch signals, with likely correlates in the brain and behavior that show distinct developmental trajectories.

MEDIATION OF AFFILIATIVE TOUCH IN THE CENTRAL NERVOUS SYSTEM

A defining feature of the affiliative touch system is a functional and anatomical dissociation from discriminatory and aversive somatosensory pathways in the peripheral nervous system⁸-although this dissociation may not as be as absolute as previously thought.³³ CT receptors propagate their signals into the central nervous system along distinct afferent fiber pathways, parallel to those carrying discriminatory and aversive touch information. Although they may propagate within the same spinothalamic bundles, affiliative touch signals carried by CT afferents are not interrupted by pathway ablation in the same manner as signals carried by other unmyelinated afferent types.³³ Furthermore, although integration of affiliative and discriminatory touch signals has been observed as early as interneurons in the dorsal horn,³⁶ there is evidence that there is also some dissociable functional and anatomic processing of these signals within the brain as well. Within the canonical work investigating brain responses to tactile stimulation, a dissociation emerged between the roles of the posterior insula and primary somatosensory cortex (SI) related to their respective processing of affiliative and discriminative touch.³⁴ Subsequent work has supported these early findings, providing substantive evidence for

31

affiliative touch processing in the posterior insula^{26,37,38} with limited dependence on processing in S1.^{27,39,40} A meta-analysis of functional magnetic resonance imaging (fMRI) studies further elucidated the distinct processing roles of somatosensory and insula regions regarding their treatment of affiliative touch signals.³⁸ It was found that, across studies, insular and somatosensory regions not only differ in their processing of affiliative touch signals, but also engage dissociable functional networks. Moreover, temporal latencies in the neural responses to touch observed in posterior insula and S1 are consistent with those expected for unmyelinated and myelinated axons, respectively,⁴¹ suggesting that these regions are primarily receiving tactile signals from different channels. A final source of support for the critical role of the insula in affiliative touch processing can be found in work that investigated the perceptual outcome of insular damage. In this work, insular damage was associated with the impaired perception of both ipsi- and contra-lateral CT-mediated but not discriminatory touch,⁴² reinforcing its importance in affiliative touch processing.

With the explosion of recent interest in affiliative touch, a deeper understanding of how and where these signals are processed in the central nervous system beyond the canonical insular structures is also developing. A robust network of brain regions has emerged as responsive to affiliative touch signals. Regions consistently identified as responsive to affiliative touch signals are the anterior cingulate (ACC),^{25,27} orbitofrontal/mediofrontal (OFC),^{26,27,43} and insular cortices.^{26,37,38} Our own research used a multivariate approach to fMRI (representational similarity analysis) to model-specific information instantiated as distributed activation patterns in response to soft stroking versus pressure pain versus no active touch in these regions.²⁶ Model testing indicated a distinction between the way the ACC/insula and the ventromedial prefrontal cortex represented affective touch information (Figure 2). Of these regions, it was only the ventromedial prefrontal cortex/OFC activation patterns that instantiated information about affiliative touch independently from information about painful touch (Figure 2D). However, patterns of activation across 3 cm³ voxels within a large region do not preclude more differential representations at smaller, including neuronal, scales.

All three regions mentioned above (ACC, OFC, and insula) not only respond to affiliative touch signals, but also display patterns of robust functional connectivity between each other.⁴³ Whereas each of these structures independently displays dense interconnectedness across the brain, together they form a powerful core processing network for affiliative touch information that has the ability to influence widespread processes across the brain. For example, activation in striatal regions, known for their role in integrating social action with reward,⁴⁴ covaries with OFC and ACC activity during CT afferent activation.⁴³

Another structure that can play a role in affiliative touch processing is the amygdala. One of the canonical roles of this structure is the appraisal of incoming sensory information for affective salience.^{6,45} Activity in this region typically covaries with sensory experienceincluding somatosensation—in an event-related manner. We have also found that it is only the amygdala that represented information about the positive valence of affiliative touch as inversely related to information about the negative valence of painful touch.²⁶ Yet, during the experience of affiliative touch, amygdala activity appears to functionally decouple from sensory input.⁴⁶ This suggests that affiliative touch, as coded by the peripheral nervous system, may act as a signal to turn centralized affective processing away from sensory appraisal.⁴⁷ It is as if the sensation of gentle affiliative touch is an indicator that we are cared for and not in harm's way—a potent signal of environmental safety that allows us to turn down our other affective monitoring systems. Consistent with this, there is evidence of touch-induced vagal tone, reduced vigilance,⁴⁶ and oxytocin release^{48,49} in response to CT afferent stimulation. Affiliative touch may just signal that everything is ok.³³

EFFECTS OF AFFILIATIVE TOUCH ON SELF-REGULATION

The idea that soft gentle stroking has a calming effect is intuitive. Immediate social regulatory effects of CT-mediated touch include reduced behavioral and autonomic stress indices. For example, receiving CToptimal stroking—often operationalized as light stroking at 3 cm/s—has been found to increase indices of vagal tone, including heart rate deceleration and heart rate variability^{50,51} Additionally, studies using facial electromyography as an objective measure of valenced response have found that activation of the corrugator, or "frowning," muscle often used as an index of the presence of negative affect (e.g., Ref. ⁵²)—is consistently reduced during CT-optimal stimulation compared to either faster or slower touch.^{53,54} In a correlational study, selfreported receipt of social touch (alongside social support) was also found to predict self-reported loneliness, although this effect was not associated with individual differences in heart rate variability at rest.⁵⁵

CT-optimal touch can also play an important role in pain regulation. In a recent study, both subjective pain ratings and electroencephalography (EEG) indices elicited by a painful laser stimulation were demonstrated to be reduced during the experience of CT-optimal touch compared to a faster rate of stroking.⁵⁶ This demonstrates the influence of affiliative touch on pain signaling through changes to both the subjective experience of nociceptive signals and the alteration of quantitative cortical responses.

Beyond regulating stress and pain, some researchers have proposed that affiliative touch plays an active role in establishing and maintaining social bonds by reciprocally modulating the release of endogenous opioids and oxytocin (e.g., Ref. ⁴⁹). In nonhuman primates, blocking mu-opioid receptors canonically implicated in analgesia and reward⁵⁷ increases the tendency to groom and seek grooming.^{58,59} This suggests that mu-opioid receptors help establish and reinforce affiliative relationships through physical interaction. Building on these findings, a rare human study investigating mu-opioid receptor activity used positron emission tomography (PET) to demonstrate a reduced activation of the endogenous opioid system during affiliative (nonsexual) touch.⁶⁰ In the PET scanner, participants received pleasurable caresses from their partners in one condition and lay alone in the other. Effects of touch versus its absence (alone condition) were observed in primary

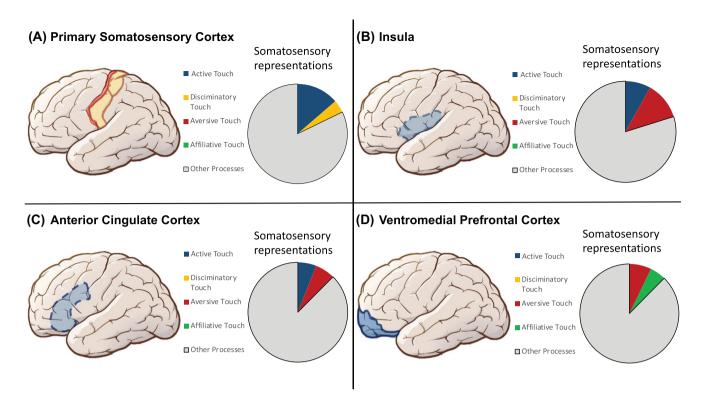


FIGURE 2 Representational weight of somatosensory information in the cortex. Results of pattern component modeling with representational similarity analysis of fMRI data indicating that cortical regions sensitive to somatosensory information show distinct pattern of representation for varying somatosensory information. (A) Primary somatosensory cortex displays the greatest response to discriminatory tactile (i.e., valence independent) experience as well as active, transient touch experience (operationalized as the equivalent representation of positive and negative tactile manipulation relative to no manipulation). (B, C) Insular and anterior cingulate cortices display distinct patterns of activation that reflect the experience of painful and affiliative touch as highly similar (active touch), as well as pain-specific representations. Dashed outlines indicate areas not visible on the surface in the sagittal view presented. (D) Ventromedial prefrontal cortex displays activation consistent with unique representations of both painful and affiliative touch experience. Data are summarized from Kryklywy et al.²⁶ fMRI, functional magnetic resonance imaging. *Note:* Cortical regions outlined here are not meant to be reflective of the precise neuroanatomy but are rather intended to demonstrate the variability of expected cortical response as it relates to affiliative and nonaffiliative somatosensory signaling.

and secondary somatosensory cortices, the amygdala, medial PFC, and canonical hubs of the reward system. Notably, effects of the affiliative touch condition on endogenous opioid activity were also observed in the ventromedial prefrontal cortex and the insula,⁶⁰ which are both known targets of CT afferent pathways.^{26,43} It is, however, important to note that while the pleasurable touch used in this design likely activated CT afferents, it was not specific to CT-optimal stroking—or necessarily to touch at all given the lack of a no-touch control in the presence of a romantic partner.

Finally, when we think of pleasurable interpersonal touch, the first association that often comes to mind is erotic touch. A natural question concerns the degree to which CT-optimal stroking is associated with erotic experience. Whereas CT-optimal velocities have been associated with higher eroticism as well as pleasantness ratings in both men and women, peak eroticism ratings are found to be elicited by a slower velocity than the peak CT-optimal velocity when operationalized as 3 cm/s. This has been interpreted as an indication that sensations of eroticism likely involve a distinct pattern of activation of both CT and other (e.g., A-beta) fibers.⁶¹

Taken together, this body of literature highlights the critical role of affiliative touch on the development and maintenance of mental wellness. It also suggests a potential set of novel clinical applications that leverage the unique ability of affiliative touch in mediating feelings of pain and connectedness to address conditions previously resistant to treatment. Note that while specific treatment targets and approaches lie outside of the scope of this review, the breadth and strength of influence that affiliative touch signals—and other forms of peripherally identified valence—have on mood and pain perception suggest that the topic warrants considerable further investigation (for additional discussion of potential future work, see Box 1). Finally, by broadening the conceptualization of sensory-focused therapies to incorporate the effects of affiliative touch, we may better understand the mechanism of action in current, or previous, examples of successful sensory-focused treatments (e.g., Ref. 62).

BOX 1 Questions for future affiliative touch research

Can the direct influence of affiliative touch signals (and other sources of valenced peripheral information) on associative brain structures involved in emotion regulation be leveraged to assist with overcoming treatment-resistant mental health conditions?

How might altered sensitivity to affiliative touch information be related to social-behavioral profiles characteristic of specific clinical syndromes?

What brain systems and processes enable interactions between sensory modalities that modulate responses to affiliative touch?

How and where do sensory signals of affiliative touch, generated in the periphery, interact with contextual cues, such as the gender or identity of the toucher, to mediate social bonding (e.g., expression of affection to others)?

What is the long-term impact of social interaction with haptic technology designed to target affiliative touch pathways on social connectedness, relationship outcomes, and emotional wellbeing?

THE AFFILIATIVE TOUCH SYSTEM IN DEVELOPMENT

The CT afferent system is thought to be highly conserved and structured across the lifespan and across species. Its regulatory capacity is a likely influence on infant-caregiver relations and should be observable very early in development. Thus, developmental research is crucial to testing claims about any potential role in mammalian coregulation. Anecdotally, nearly any parent can testify to the importance, and effectiveness, of stroking, hugging, and jiggling for calming a fussy new baby. Indeed, a whole body of developmental work on social touch was generated decades ago, originally in response to nonhuman primate and rodent research finding effects of maternal grooming of infants on optimal development of the stress system (for review, see Ref. ⁶¹). Yet, much of this research focused on the broad category of social touch, which includes many forms of touch outside the forms of soft stroking typically used to activate CT receptors.⁶³ More recently, with the boom in research on affective touch systems, there has been increasing attention to aspects of social touch that our somatosensory system denotes as positive from the point of contact: CT-mediated touch.⁶³

Claims that the CT afferent system is highly conserved across species are supported by consistent responses to gentle stroking observed in species from rodents to nonhuman primates to human infants (for review, see Ref. ⁶³). Convergent evidence also supports claims that the CT-mediated affiliative touch system, which does not rely on slow-maturing myelination processes, is already "online" almost from birth. For example, increased parasympathetic responses to stroking, relative to static touch, can be observed in preterm

infants.^{64,65} suggesting the system is pretuned to affiliative stroking prior to social interaction. Moreover, video evidence indicates that mothers spontaneously stroke their young infants at velocities that activate CT afferents. Later in childhood, once they are old enough to reliably report subjective experiences, children (5-8 years of age) rate 3 cm/s stroking velocities as more pleasant than other velocities, just as adults do.⁶⁶ A body of evidence that maternal stroking mitigates the effects of maternal depression on infants in the early months further supports the importance of CT-mediated touch on healthy infant-caregiver relations. For example, the effects of maternal postpartum depression, which is associated with more negative emotional responses and physiological stress reactivity at 6 months, have been found to be limited to infants whose mothers reported infrequent stroking of their infants.⁶⁷ A further study found that higher levels of reported maternal stroking were associated with reduced methylation of the glucocorticoid receptor gene (a gene implicated in the physiological stress response) in infants whose mothers experienced a sharp increase in depression after birth.⁶⁸

Neuroimaging studies in infants have further elucidated the impact that CT afferent touch systems have on development.^{69,70} Studies conducted with fMRI and diffuse optical tomography have shown consistent evidence that activation in the insula, as a primary target of CT afferent fibers,^{37,38} is already sensitive to CT-optimal touch from early in infancy. Furthermore, there is additional neuroimaging evidence that the central nervous system is involved in mediating the effects of CT-optimal stroking on the pain response in young infants. One study⁷¹ found that CT-optimal stroking can reduce the pain response in infants, as indexed by EEG recordings, by 60%; however, this effect diminished over repeated pain exposures. Interestingly, a second experiment from the same authors did not find consistent neural habituation to the analgesic effects of CT-optimal touch. The authors concluded that interval timing is crucial to maintain the effects of CT-optimal stroking on pain regulation.⁷¹

Thus, developmental studies support claims that the CT-mediated affiliative touch system serves to regulate pain and stress from the first days of life. Reduced stroking may be one pathway by which maternal depression may result in hypersensitive stress systems in offspring, while more stroking can mitigate effects. Finally, insula activation sensitivity, which is observed in adults, is also present in very young infants. Outstanding developmental questions center on understanding the degree to which lower-level perceptual sensitivity to CT-optimal touch comes to increasingly interact with contextual factors (reviewed below) that modulate it,⁶³ and how the CT afferent system comes to interact with sensory systems in social regulation processes.

INDIVIDUAL AND CONTEXTUAL DIFFERENCES IN AFFILIATIVE TOUCH RESPONSES

Following an early phase of research characterizing the basic properties of the CT afferent system and how its signaling influences perception and development, a second wave of research has begun to elucidate contextual factors that modulate the initial response to CT-optimal touch. To date, these include sex differences, cultural differences, mood state, and the social intent and identity of the toucher.

One reliable, and unsurprising, factor that influences the perceived pleasantness of CT-optimal touch is sex/gender. Although some findings in the domain of gender differences have been equivocal, a recent robustly powered study found that women and men gave equivalent pleasantness ratings for touch velocities that ranged around CT-optimal velocities; however, women expressed comfort with touch from a wider range of social partners, particularly female ones, than men did.⁷² This study also reported cultural differences in female comfort with opposite-sex partners. Moreover, although average pleasantness ratings are highest for CT-optimal touch in general, that may not be true for a given individual or may even vary over time within an individual. A recent study tested the stability of reliable findings of affective habituation and discovered a reduction of pleasantness ratings for CT-optimal stroking over time. This study found that 43% of participants showed a pattern of response to repeated affiliative touch stimulation that reflected habituation to the subjective pleasantness, while only 36% showed a stable response over time.⁷³ This suggests that (1) rather than being a universal phenomenon, there is considerable variability in canonical habituation patterns, and (2) rather than being a stable phenomenon, the experience of affiliative touch is influenced by state/contextual factors.

A few specific state factors have been measured to date. An intuitive factor to investigate is loneliness and desire for touch. During COVID-19 shutdowns, participants who reported more longing for touch, and experienced more stringent social isolation, rated videos of CT-optimal touch as more pleasant.⁷⁴ To test the hypothesis that CT-optimal touch engages affiliative processes modulated by serotonin, a team in the United Kingdom used tryptophan depletion to reduce serotonin levels before administering CT-optimal touch to the forearm in the MRI scanner.⁷⁵ Tryptophan depletion did not reduce pleasantness ratings. However, the fMRI data revealed an elegant dissociation between discriminatory and affectively salient stimulation. The placebo group, but not the serotonin-depleted group, showed more activation in a region of the orbitofrontal cortex for strokes on the forearm versus strokes to the CT receptor-free ventral surfaces of the left fingers, suggesting depletion reduced CT afferent mediated touch responses in a brain region sensitive to affective valence. The placebo group also showed somatosensory cortex sensitivity to ventral finger strokes relative to strokes to the forearm.⁷⁵ These results suggest that serotonin does not simply tune brain regions that are sensitive to the affective salience of social touch. Rather, its role may be to tune the central nervous system's capacity to selectively respond to tactile information by enhancing the discriminatory activation of regions sensitive to affective touch, enervated by CT afferents, as well as regions sensitive to discriminatory touch enervated by A-beta fibers.

Another fMRI study manipulated context by using olfactory stimuli to create state changes that influence the brain and subjective responses to touch pleasantness.⁷⁶ It was found that the presence of a disgusting odor reduced the perception of touch pleasantness. Furthermore, individual differences in subjective ratings of odor unpleasantness were correlated with activation of the somatosensory as well 17496632, 2023, 1, Downloaded from https://nyaspubs.onlinelibrary.wiley.com/doi/10.1111/nyas.15056 by Cochrane Canada Pro Wiley Online Library on [19/10/2023]. See the Terms and Conditions (https: on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Comm

as the orbitofrontal cortex (albeit assessed in a sample of only 22 participants, which is underpowered to detect reliable correlations). If replicated in a larger sample, such findings would suggest that context alters perceptual aspects of affiliative touch as well as those associated with affective salience. Moreover, interactions between sensory modalities may also influence the predisposition to produce affiliative touch. A pair of studies has reported suggestive results indicating that viewing images of bonding versus nonbonding human pairs increased muscle activity in finger flexor muscles and reduced EEG signals of motor readiness prior to the instructed finger movement.^{77,78} Such findings highlight the complex interplay between the senses.

Unsurprisingly, another contextual feature known to modulate the pleasantness of affiliative touch is the identity of the toucher. At a basic level, strokes at velocities rated as more human are consistently perceived as more pleasant.²⁹ Touch from people perceived to be more attractive is also experienced as more pleasant.⁷⁹ Consistent with this finding, heterosexual men showed greater activation in S1 in response to sensual touch when they thought the toucher was an attractive woman versus a man. This again suggests that affective context in the form of the toucher influences activation in a region thought to be primarily dedicated to discriminatory processing.⁸⁰ In this case, the observation of activation in S1-a region less involved in processing the relatively raw CT afferent signals-suggests that it is the result of centralized modulation of experience rather than differences in the strength of the initial CT afferent signals of valence. In a more recent study, which was powered to detect individual differences, the administration of oxytocin was found to intensify activation in the anterior cingulate cortex as well as the nucleus accumbens, a key node in dopaminergic reward anticipation circuitry, in response to the touch of a perceived partner compared to that of a stranger. Differential activation in the nucleus accumbens was correlated with the degree to which the participants reported themselves to be passionately in love. Although CT-optimal touch is typically experienced as rewarding, the nucleus accumbens is not among the regions often reported as sensitive to CT-optimal touch. This finding suggests that an oxytocin boost, or an element of anticipation or prediction error, may be required to engage the midbrain reward circuitry in response to affiliative touch. What remains unknown, however, is how or where in the brain the relationship-specific modulation of the response to affiliative touch is instantiated. Work in human neuroimaging has demonstrated dissociable representations for different touchers (stranger vs. partners) in the orbitofrontal cortex and amygdala as well as somatosensory cortices. This study revealed additional refinement in activation patterns (samesex vs. opposite-sex stranger) observed in the insula.⁸¹ This suggests that, of the nodes of systems sensitive to affiliative touch, the insula, a primary target of CT afferents, can be highly influenced by additional nonsomatosensory information, including the identity of the toucher.

Finally, sources of individual differences in affiliative touch sensitivity have begun to be elucidated, with a focus on neurodivergence. Allodynia, which results from neuronal injury, is a condition of extreme sensitivity to touch such that normally pleasant or innocuous touch is experienced as aversive.⁸² In a study in which it was experimentally induced, allodynia was associated with reduced pleasantness of CT-optimal touch as well as impaired discriminatory touch accuracy, implicating an influence on both CT and A-beta signal processing.⁸² Autistic traits, measured on a continuous scale, have also been associated with reduced pleasantness ratings for CT-optimal touch in both participants with autism spectrum disorder and in controls.⁸³ Moreover, participants with anorexia have also shown reduced pleasantness ratings for affiliative touch;⁸⁴ however, a recent study found this response was not specific to CT-optimal touch and was more a function of beliefs or general interoceptive sensitivity.⁸⁵ As the study of individual differences in both neurotypical and neurodivergent populations is still nascent, a good deal of future work will likely be devoted to it.

In the sections above, we reviewed key experimental findings on the role of the affiliative touch system in self-regulation as well as factors that in turn modulate its response. In the section that follows, we now discuss examples of how this knowledge has been applied in haptic technology designed to enhance human self-regulation and wellbeing.

HAPTIC TECHNOLOGY AND AFFILIATIVE TOUCH

Haptic technology

Haptic technology, as studied and developed within the broader context of robotics and human-computer interaction within computer science and engineering, is found today in many consumer and professional products. Such technology provides the capability to create, modulate, or replicate an experience of touch using a diverse range of mechanisms, and targets the full range of cutaneous, kinesthetic, and proprioceptive receptors. In these fields, the term haptic is understood to refer to devices that generate both tactile and kinesthetic sensations rather than just tactile sensations. Tsetserukou and colleagues⁸⁶ described affective haptics as "an emerging area of research which focuses on the design of devices and systems that can elicit, enhance, or influence the emotional state of a human by means of sense of touch." Since at least 2002, researchers have been using and developing many forms of haptic technology in the service of "affective haptics." Building on findings from psychology and neuroscience, this technology has the potential to harness the power of our growing understanding of CT-optimal touch. It can be used to devise applications that leverage our knowledge of the affiliative touch system's capacity to mediate self-regulation to reduce stress and improve health and wellbeing.

In the next section, we focus on technologies that stimulate the CT afferent system, and highlight two research foci that have received substantial attention in the last decade: haptics used to (1) communicate, display, or render emotion, and (2) facilitate self-regulation.⁸⁷

Technologies that stimulate the CT afferent system

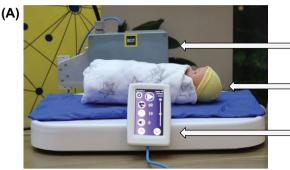
In this domain, researchers have explored wearable, tabletop, and hand-held forms of technology that serve the need for human-tohuman touch through technologically mediated touch. The technologies have been studied in the context of rendering remote social touch between partners,⁸⁸ family members,⁸⁹ friends,⁹⁰ and patients and their loved ones.⁹¹ The growing neuroscientific understanding of CT afferent systems supports the importance of emotional communication in contexts of physical isolation, such as those experienced by vulnerable populations during COVID-19 shutdowns. These technologies can be designed to directly mimic human-to-human social touch interactions⁹² and replicate these naturally occurring behaviors in interactive systems that activate the CT afferent system by stroking (e.g., Refs. 93 and 94). Using stroking speeds (1-10 cm/s) and optimum temperatures (32°C) based on prior neuroscientific work,^{28,95} Liu et al.'s device attempts to render a caress-like sensation through a pneumatic-actuated sleeve. The sleeve encompasses an array of microblowers and inflatable pouches that apply pressure and thermal stimuli. The device renders discrete tactile stimulation from haptic actuators embedded in a sleeve, sequentially activating them at an optimum speed to create an illusory sensation of continuous stroking. Although it has only been evaluated by a metric of pleasantness at this stage, stroking patterns associated with high pleasantness play a crucial role in regulating stress and pain responses as described above in the section on the role of affiliative touch on self-regulation.

Self-regulation

Haptic technology used to facilitate self-regulation is often designed to influence biological processes that are, at least indirectly, subject to voluntary influences on such physiological processes as heart rate and breathing.⁹⁶⁻⁹⁸ However, other technologies have been successfully used to target visceral, nonconscious control loops. Notably, Calmer is a robotic device that is placed in an incubator to directly simulate multiple components of touch that have been found to reduce pain in preterm infants during medical procedures.⁹⁹ Inspired by a core design known as Haptic Creature,¹⁰⁰ Calmer (Ref. 101; https://www. youtube.com/watch?v=x35P24MDliA) simulates human skin-to-skin contact to infants in incubators (Figure 3). Specifically, it administers a breathing motion through a rhythmically moving, pneumatically powered bellows; the sound of a human heart-beat rendered as pressure waves via a subwoofer; and skin-like tactility. A randomized clinical trial demonstrated the health benefits of Calmer.99 Infants who had Calmer installed in their incubators demonstrated equivalent pain and heart rate variability following a heel lance to those who experienced facilitated tucking, a common human-touch intervention. It is likely this technology has components of affiliative touch that show promise for enabling self-regulation in infants when a human touch is unavailable.

In other forms of affective haptic design,⁸⁷ common configurations for self-regulatory devices include robotic companions, wearables (e.g., smart watch, smart sleeve jackets), and objects (e.g., chair, cushion, plushie, fidget-spinner) chosen for ease of adaptation to a user's day-to-day practices and contextual use.^{102,103} Often these applications use closed-loop regulation processes wherein the haptic stimulus changes are triggered or modulated based on the user's physiological state^{98,104} or touch interaction.^{105,106} The physiological state in turn is estimated by sensors that are embedded in the physical object of interaction or worn by participants. These easy-to-use wearable devices and ambient objects lay the groundwork for future identification of affec-

Application of affiliative touch signalling in neonatal healthcare



Integrated motor to simulate heartbeat and breathing rate of the mother

Bassinette covered in skin-like surface material to support premature infant too fragile for normal contact

 Ongoing real-time monitoring of both parental and infant physiology

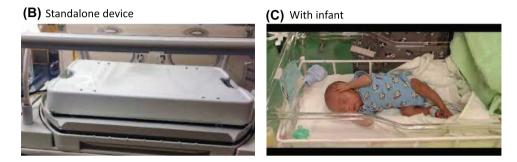


FIGURE 3 Illustration of versions of the Calmer device used to mimic skin-to-skin contact for premature infants as described in Holsti et al.⁹⁹ and Hauser et al.¹⁰¹ (A) Full setup of the Calmer device with doll for illustration. (B) Illustration of the standalone Calmer device without skin-like surface material or peripheral devices. (C) Illustration of the Calmer device inserted into a bassinet and in active use with an infant in a neonatal intensive care unit.

tive states that can automatically trigger stroking-like tactile actuation to activate the CT afferent system, thus facilitating self-regulation in a wide range of populations.

Looking forward

To date, the bulk of the research described above has been designoriented and exploratory in nature. Many of the cited works seek to assess basic feasibility (e.g., the degree to which interventions produce a measurable visceral response). Beyond feasibility, contemporary computational methods promise interactive emotion recognition and training on individualized models. Machine-learning methods have recognized markers of affective state, or its shifts, through individuals' touch patterns at levels comparable to conventional affective computing modalities such as brain activity, with implications for creating nonintrusive, personalized interactive applications.¹⁰⁷

Much of the research in this area has been conducted in singlesession laboratory studies due to the challenges of deploying hardware prototypes in users' daily life—despite the evidence for individual differences in response to affiliative touch as described in this paper. There is a need for longitudinal *in situ* evaluation of such technologies, with an open challenge of how the designs of remote social touch can be personalized to suit individual preferences and context of use. With current empirical evaluations in terms of design preference, acceptability, and usability,⁸⁷ next steps involve studying the longitudinal effects of such technologies on social connectedness, relationship outcomes, and emotional satisfaction. They also involve fine-tuning technology based on the growing understanding of the neurobiology of the human haptic system reviewed in this paper. This requires an interdisciplinary approach that incorporates cognitive science, psychology, and neuroscience¹⁰⁸ to provide theoretical foundations and methods for interaction quality and their effectiveness in affective communication or regulation. These in turn can provide crucial tools for further developing our understanding of human affiliative touch.

CONCLUSION

In this review, we have discussed recent findings in the cognitive neuroscience of affiliative touch in conjunction with research in haptic technology design that is informed by and informs psychology and neuroscience research. We reviewed what is known about the basic biology of CT afferent fibers as well as their primary targets and the instantiation of hedonic touch information in the human brain. We then examined evidence of the role of the CT afferent system in affecting regulation in adulthood and development, as well as individual differences in and contextual influences on its function. These findings were contextualized in an evolving view of emotion-perception interactions in which peripheral stimulation evokes signals that are valenced by virtue of the receptors that are activated, and thus does not depend on centralized assessment to determine affective salience. This emerging view in cognitive neuroscience emphasizes the importance of continuing to delineate the family of putative affiliative touch receptors and the specific information they convey for a biologically grounded approach to haptic design. It also suggests numerous crucial applications in a historical period where many people, often from vulnerable populations, are experiencing high levels of isolation or distance from loved ones. It can further spur the development of haptic technologies that are increasingly efficient at targeting these systems for effective technological interventions aimed at improving health and quality of life.

AUTHOR CONTRIBUTIONS

J.H.K. and R.M.T. were responsible for the overall framing of the paper and wrote the first drafts of the sections focused on scientific research on affiliative touch. P.V. and K.M. wrote the first drafts of the sections on haptic technology. All authors contributed to the synthesis of the sections. J.H.K. created the figures.

ACKNOWLEDGMENTS

J.H.K. has been supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Fellowship Award (PDF-532611-2019). R.M.T. has been supported by a Michael Smith Foundation for Health Research Scholar Award (16897), and an NSERC Discovery Grant (RGPIN-2020-05354). K.M. is supported by an NSERC Discovery Grant (RGPIN-2018-04828).

COMPETING INTERESTS

The authors declare no competing interests.

ORCID

Rebecca M. Todd D https://orcid.org/0000-0002-7566-9476

PEER REVIEW

The peer review history for this article is available at https://publons. com/publon/10.1111/nyas.15056

REFERENCES

- Li, W., & Keil, A. (2023). Sensing fear: Fast and precise threat evaluation in human sensory cortex. *Trends in Cognitive Sciences*, 27(4), 341–352. https://doi.org/10.1016/j.tics.2023.01.001
- Todd, R. M., Miskovic, V., Chikazoe, J., & Anderson, A. K. (2020). Emotional objectivity: Neural representations of emotions and their interaction with cognition. *Annual Review of Psychology*, 71(8), 25. https://doi.org/10.1146/annurev-psych-010419-051044
- Kryklywy, J. H., Ehlers, M. R., Anderson, A. K., & Todd, R. M. (2020). From architecture to evolution: Multisensory evidence of decentralized emotion. *Trends in Cognitive Sciences*, 24(11), 916–929. https:// doi.org/10.1016/j.tics.2020.08.002
- Markovic, J., Anderson, A. K., & Todd, R. M. (2014). Tuning to the significant: Neural and genetic processes underlying affective enhancement of visual perception and memory. *Behavioural Brain Research*, 259, 229–241. https://doi.org/10.1016/j.bbr.2013.11.018
- Pourtois, G., Schettino, A., & Vuilleumier, P. (2013). Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. *Biological Psychology*, 92(3), 492–512. https://doi.org/ 10.1016/j.biopsycho.2012.02.007

- Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, 9(12), 585–594. https://doi.org/10.1016/j.tics.2005.10.011
- Kryklywy, J. H., Ehlers, M. R., Anderson, A. K., & Todd, R. M. (2020). From architecture to evolution: Multisensory evidence of decentralized emotion. *Trends in Cognitive Sciences*, 24, 916–929. https://doi. org/10.1016/j.tics.2020.08.002
- Mcglone, F., Wessberg, J., & Olausson, H. (2014). Discriminative and affective touch: Sensing and feeling. *Neuron*, 82(4), 737–755. https:// doi.org/10.1016/j.neuron.2014.05.001
- Rolls, E. T. (2013). What are emotional states, and why do we have them? *Emotion Review*, 5(3), 241–247. https://doi.org/10.1177/ 1754073913477514
- Ekman, P. (1992). An argument for basic emotions. Cognition and Emotion, 6(3-4), 169-200. https://doi.org/10.1080/ 02699939208411068
- Jablonski, N. G. (2021). Social and affective touch in primates and its role in the evolution of social cohesion. *Neuroscience*, 464, 117–125. https://doi.org/10.1016/j.neuroscience.2020.11.024
- Morrison, I., Löken, L. S., & Olausson, H. (2010). The skin as a social organ. Experimental Brain Research, 204(3), 305–314. https://doi.org/ 10.1007/s00221-009-2007-y
- Willis, W. D., & Westlund, K. N. (1997). Neuroanatomy of the pain system and of the pathways that modulate pain. *Journal of Clinical Neurophysiology*, 14(1), 2–31. https://doi.org/10.1097/00004691-199701000-00002
- Xiao, X., & Zhang, Y.-Q. (2018). A new perspective on the anterior cingulate cortex and affective pain. Neuroscience & Biobehavioral Reviews, 90, 200–211. https://doi.org/10.1016/j.neubiorev.2018.03.022
- Kragel, P. A., Kano, M., Van Oudenhove, L., Ly, H. G., Dupont, P., Rubio, A., Delon-Martin, C., Bonaz, B. L., Manuck, S. B., Gianaros, P. J., Ceko, M., Reynolds Losin, E. A., Woo, C.-W., Nichols, T. E., & Wager, T. D. (2018). Generalizable representations of pain, cognitive control, and negative emotion in medial frontal cortex. *Nature Neuroscience*, 21(2), 283–289. https://doi.org/10.1038/s41593-017-0051-7
- Rustamov, N., Northon, S., Tessier, J., Leblond, H., & Piché, M. (2019). Integration of bilateral nociceptive inputs tunes spinal and cerebral responses. *Scientific Reports*, 9(1), 7143. https://doi.org/10.1038/ s41598-019-43567-y
- Abraira, V. E., & Ginty, D. D. (2013). The sensory neurons of touch. Neuron, 79(4), 618–639. https://doi.org/10.1016/j.neuron.2013.07. 051
- Zotterman, Y. (1939). Touch, pain and tickling: An electrophysiological investigation on cutaneous sensory nerves. *Journal* of Physiology, 95(1), 1–28. https://doi.org/10.1113/jphysiol.1939. sp003707
- Johansson, R. S., Trulsson, M., Olsson, K. Å., & Westberg, K.-G. (1988). Mechanoreceptor activity from the human face and oral mucosa. *Experimental Brain Research*, 72(1), 204–208. https://doi.org/ 10.1007/BF00248518
- Vallbo, Å. B., Olausson, H., & Wessberg, J. (1999). Unmyelinated afferents constitute a second system coding tactile stimuli of the human hairy skin. *Journal of Neurophysiology*, 81(6), 2753–2763. https://doi. org/10.1152/jn.1999.81.6.2753
- Bohic, M., & Abraira, V. E. (2022). Wired for social touch: The sense that binds us to others. *Current Opinion in Behavioral Sciences*, 43, 207–215. https://doi.org/10.1016/j.cobeha.2021.10.009
- Ackerley, R. (2022). C-tactile (CT) afferents: Evidence of their function from microneurography studies in humans. *Current Opinion in Behavioral Sciences*, 43, 95–100. https://doi.org/10.1016/j.cobeha. 2021.08.012
- Wessberg, J., Olausson, H., Fernström, K. W., & Vallbo, Å. B. (2003). Receptive field properties of unmyelinated tactile afferents in the human skin. *Journal of Neurophysiology*, 89(3), 1567–1575. https:// doi.org/10.1152/jn.00256.2002

- Walker, S. C., Marshall, A., & Pawling, R. (2022). Psychophysiology and motivated emotion: Testing the affective touch hypothesis of Ctactile afferent function. *Current Opinion in Behavioral Sciences*, 43, 131–137. https://doi.org/10.1016/j.cobeha.2021.10.004
- Gordon, I., Voos, A. C., Bennett, R. H., Bolling, D. Z., Pelphrey, K. A., & Kaiser, M. D. (2013). Brain mechanisms for processing affective touch. *Human Brain Mapping*, 34(4), 914–922. https://doi.org/10. 1002/hbm.21480
- Kryklywy, J. H., Ehlers, M. R., Beukers, A. O., Moore, S. R., Todd, R. M., & Anderson, A. K. (2023). Decomposing neural representational patterns of discriminatory and hedonic information during somatosensory stimulation. *eNeuro*, 10(1), ENEURO.0274-22.2022. https://doi.org/10.1523/ENEURO.0274-22.2022
- Rolls, E. T. (2003). Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. *Cerebral Cortex*, 13(3), 308–317.
- Ackerley, R., Backlund Wasling, H., Liljencrantz, J., Olausson, H., Johnson, R. D., & Wessberg, J. (2014). Human C-tactile afferents are tuned to the temperature of a skin-stroking caress. *Journal of Neuroscience*, 34(8), 2879–2883. https://doi.org/10.1523/JNEUROSCI. 2847-13.2014
- Schirmer, A., Cham, C., Lai, O., Le, T.-L. S., & Ackerley, R. (2023). Stroking trajectory shapes velocity effects on pleasantness and other touch percepts. Journal of Experimental Psychology: Human Perception and Performance, 49(1), 71–86. https://doi.org/10.1037/xhp0001079
- Schirmer, A., Chiu, M. H., & Croy, I. (2021). More than one kind: Different sensory signatures and functions divide affectionate touch. *Emotion (Washington, D.C.),* 21(6), 1268–1280. https://doi.org/10. 1037/emo0000966
- Case, L. K., Madian, N., Mccall, M. V., Bradson, M. L., Liljencrantz, J., Goldstein, B., Alasha, V. J., & Zimmerman, M. S. (2023). Aβ-CT affective touch: Touch pleasantness ratings for gentle stroking and deep pressure exhibit dependence on A-fibers. *eNeuro*, 10(5), ENEURO.0504-22.2023. https://doi.org/10.1523/ENEURO.0504-22.2023
- Marshall, A. G., Sharma, M. L., Marley, K., Olausson, H., & Mcglone, F. P. (2019). Spinal signalling of C-fiber mediated pleasant touch in humans. *eLife*, 8, e51642. https://doi.org/10.7554/eLife.51642
- Marshall, A. G., & Mcglone, F. P. (2020). Affective touch: The enigmatic spinal pathway of the C-tactile afferent. *Neuroscience Insights*, 15, 2633105520925072. https://doi.org/10.1177/2633105520925072
- Olausson, H., Lamarre, Y., Backlund, H., Morin, C., Wallin, B. G., Starck, G., Ekholm, S., Strigo, I., Worsley, K., Vallbo, Å. B., & Bushnell, M. C. (2002). Unmyelinated tactile afferents signal touch and project to insular cortex. *Nature Neuroscience*, 5(9), 900–904. https://doi.org/10. 1038/nn896
- Olausson, H., Wessberg, J., Morrison, I., McGlone, F., & Vallbo, Å. (2010). The neurophysiology of unmyelinated tactile afferents. *Neuroscience & Biobehavioral Reviews*, 34(2), 185–191. https://doi.org/10. 1016/j.neubiorev.2008.09.011
- Abraira, V. E., Kuehn, E. D., Chirila, A. M., Springel, M. W., Toliver, A. A., Zimmerman, A. L., Orefice, L. L., Boyle, K. A., Bai, L., Song, B. J., Bashista, K. A., O'neill, T. G., Zhuo, J., Tsan, C., Hoynoski, J., Rutlin, M., Kus, L., Niederkofler, V., Watanabe, M., ... & Ginty, D. D. (2017). The cellular and synaptic architecture of the mechanosensory dorsal horn. *Cell*, 168(1–2), 295–310.e19. https://doi.org/10.1016/j.cell. 2016.12.010
- Björnsdotter, M., Löken, L., Olausson, H., Vallbo, Å., & Wessberg, J. (2009). Somatotopic organization of gentle touch processing in the posterior insular cortex. *Journal of Neuroscience*, 29(29), 9314–9320. https://doi.org/10.1523/JNEUROSCI.0400-09.2009
- Morrison, I. (2016). ALE meta-analysis reveals dissociable networks for affective and discriminative aspects of touch. *Human Brain Mapping*, 37(4), 1308–1320. https://doi.org/10.1002/hbm.23103

- Case, L. K., Čeko, M., Gracely, J. L., Richards, E. A., Olausson, H., & Bushnell, M. C. (2016). Touch perception altered by chronic pain and by opioid blockade. *eNeuro*, 3(1), ENEURO.0138-15.2016. https://doi. org/10.1523/ENEURO.0138-15.2016
- Case, L. K., Laubacher, C. M., Richards, E. A., Spagnolo, P. A., Olausson, H., & Bushnell, M. C. (2017). Inhibitory rTMS of secondary somatosensory cortex reduces intensity but not pleasantness of gentle touch. *Neuroscience Letters*, 653, 84–91. https://doi.org/10.1016/j. neulet.2017.05.006
- Eriksson Hagberg, E., Ackerley, R., Lundqvist, D., Schneiderman, J., Jousmäki, V., & Wessberg, J. (2019). Spatio-temporal profile of brain activity during gentle touch investigated with magnetoencephalography. *Neuroimage*, 201, 116024. https://doi.org/10.1016/j. neuroimage.2019.116024
- Kirsch, L. P., Besharati, S., Papadaki, C., Crucianelli, L., Bertagnoli, S., Ward, N., Moro, V., Jenkinson, P. M., & Fotopoulou, A. (2020). Damage to the right insula disrupts the perception of affective touch. *eLife*, *9*, e47895. https://doi.org/10.7554/eLife.47895
- Sailer, U., Triscoli, C., Häggblad, G., Hamilton, P., Olausson, H., & Croy, I. (2016). Temporal dynamics of brain activation during 40 minutes of pleasant touch. *Neuroimage*, 139, 360–367. https://doi.org/10.1016/ j.neuroimage.2016.06.031
- Báez-Mendoza, R., & Schultz, W. (2013). The role of the striatum in social behavior. Frontiers in Neuroscience, 7, 233. https://doi.org/10. 3389/fnins.2013.00233
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a "low road" to "many roads" of evaluating biological significance. *Nature Reviews Neuroscience*, 11(11), 773–782. https:// doi.org/10.1038/nrn2920
- Gothard, K. M., & Fuglevand, A. J. (2022). The role of the amygdala in processing social and affective touch. *Current Opinion in Behavioral Sciences*, 43, 46–53. https://doi.org/10.1016/j.cobeha.2021.08.004
- Morrison, I. (2022). Affective and discriminative touch: A reappraisal. *Current Opinion in Behavioral Sciences*, 43, 145–151. https://doi.org/ 10.1016/j.cobeha.2021.09.007
- Uvnäs Moberg, K., & Petersson, M. (2022). Physiological effects induced by stimulation of cutaneous sensory nerves, with a focus on oxytocin. Current Opinion in Behavioral Sciences, 43, 159–166. https:// doi.org/10.1016/j.cobeha.2021.10.001
- Walker, S. C., Trotter, P. D., Swaney, W. T., Marshall, A., & Mcglone, F. P. (2017). C-tactile afferents: Cutaneous mediators of oxytocin release during affiliative tactile interactions? *Neuropeptides*, 64, 27– 38. https://doi.org/10.1016/j.npep.2017.01.001
- Pawling, R., Trotter, P. D., Mcglone, F. P., & Walker, S. C. (2017). A positive touch: C-tactile afferent targeted skin stimulation carries an appetitive motivational value. *Biological Psychology*, 129, 186–194. https://doi.org/10.1016/j.biopsycho.2017.08.057
- Triscoli, C., Croy, I., Steudte-Schmiedgen, S., Olausson, H., & Sailer, U. (2017). Heart rate variability is enhanced by long-lasting pleasant touch at CT-optimized velocity. *Biological Psychology*, 128, 71–81. https://doi.org/10.1016/j.biopsycho.2017.07.007
- Larsen, J. T., Norris, C. J., & Cacioppo, J. T. (2003). Effects of positive and negative affect on electromyographic activity over zygomaticus major and corrugator supercilii. *Psychophysiology*, 40(5), 776–785. https://doi.org/10.1111/1469-8986.00078
- Mayo, L. M., Lindé, J., Olausson, H., Heilig, M., & Morrison, I. (2018). Putting a good face on touch: Facial expression reflects the affective valence of caress-like touch across modalities. *Biological Psychology*, 137, 83–90. https://doi.org/10.1016/j.biopsycho.2018.07.001
- Ree, A., Mayo, L. M., Leknes, S., & Sailer, U. (2019). Touch targeting C-tactile afferent fibers has a unique physiological pattern: A combined electrodermal and facial electromyography study. *Biological Psychology*, 140, 55–63. https://doi.org/10.1016/j.biopsycho. 2018.11.006

- 55. Araújo, C. R. V., Mota, B. E. F., Campagnoli, R. R., Rocha-Rego, V., Volchan, E., & Souza, G. G. L. (2022). Decreased self-reported receiving of social touch and social support predict loneliness in healthy adults. *Psicologia: Reflexão e Crítica*, 35(1), 25. https://doi.org/10. 1186/s41155-022-00228-w
- Von Mohr, M., Krahé, C., Beck, B., & Fotopoulou, A. (2018). The social buffering of pain by affective touch: A laser-evoked potential study in romantic couples. *Social Cognitive and Affective Neuroscience*, 13(11), 1121–1130. https://doi.org/10.1093/scan/nsy085
- 57. Pasternak, G. W., & Pan, Y.-X. (2013). Mu opioids and their receptors: Evolution of a concept. *Pharmacological Reviews*, *65*(4), 1257–1317. https://doi.org/10.1124/pr.112.007138
- Fabre-Nys, C., Meller, R. E., & Keverne, E. B. (1982). Opiate antagonists stimulate affiliative behaviour in monkeys. *Pharmacology Biochemistry and Behavior*, 16(4), 653–659. https://doi.org/10.1016/ 0091-3057(82)90432-4
- Keverne, E. B., Martensz, N. D., & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, 14(1–2), 155– 161. https://doi.org/10.1016/0306-4530(89)90065-6
- Nummenmaa, L., Tuominen, L., Dunbar, R., Hirvonen, J., Manninen, S., Arponen, E., Machin, A., Hari, R., Jääskeläinen, I. P., & Sams, M. (2016). Social touch modulates endogenous μ-opioid system activity in humans. *Neuroimage*, 138, 242–247. https://doi.org/10.1016/j. neuroimage.2016.05.063
- Jönsson, E. H., Backlund Wasling, H., Wagnbeck, V., Dimitriadis, M., Georgiadis, J. R., Olausson, H., & Croy, I. (2015). Unmyelinated tactile cutaneous nerves signal erotic sensations. *Journal of Sexual Medicine*, 12(6), 1338–1345. https://doi.org/10.1111/jsm.12905
- Willemsen, M. (2020). Reclaiming the body and restoring a bodily self in drama therapy: A case study of sensory-focused trauma-centred developmental transformations for survivors of father-daughter incest. Drama Therapy Review, 6(2), 203–219. https://doi.org/10. 1386/dtr_00028_1
- Gliga, T., Farroni, T., & Cascio, C. J. (2019). Social touch: A new vista for developmental cognitive neuroscience? *Developmental Cognitive Neuroscience*, 35, 1–4. https://doi.org/10.1016/j.dcn.2018.05.006
- Fairhurst, M. T., Mcglone, F., & Croy, I. (2022). Affective touch: A communication channel for social exchange. *Current Opinion in Behavioral Sciences*, 43, 54–61. https://doi.org/10.1016/j.cobeha.2021.07.007
- Manzotti, A., Cerritelli, F., Esteves, J. E., Lista, G., Lombardi, E., La Rocca, S., Gallace, A., Mcglone, F. P., & Walker, S. C. (2019). Dynamic touch reduces physiological arousal in preterm infants: A role for ctactile afferents? *Developmental Cognitive Neuroscience*, *39*, 100703. https://doi.org/10.1016/j.dcn.2019.100703
- Croy, I., Sehlstedt, I., Wasling, H. B., Ackerley, R., & Olausson, H. (2019). Gentle touch perception: From early childhood to adolescence. *Developmental Cognitive Neuroscience*, 35, 81–86. https://doi. org/10.1016/j.dcn.2017.07.009
- Sharp, H., Pickles, A., Meaney, M., Marshall, K., Tibu, F., & Hill, J. (2012). Frequency of infant stroking reported by mothers moderates the effect of prenatal depression on infant behavioural and physiological outcomes. *PLoS ONE*, 7(10), e45446. https://doi.org/10.1371/ journal.pone.0045446
- Murgatroyd, C., Quinn, J. P., Sharp, H. M., Pickles, A., & Hill, J. (2015). Effects of prenatal and postnatal depression, and maternal stroking, at the glucocorticoid receptor gene. *Translational Psychiatry*, 5(5), e560. https://doi.org/10.1038/tp.2014.140
- Jönsson, E. H., Kotilahti, K., Heiskala, J., Wasling, H. B., Olausson, H., Croy, I., Mustaniemi, H., Hiltunen, P., Tuulari, J. J., Scheinin, N. M., Karlsson, L., Karlsson, H., & Nissilä, I. (2018). Affective and non-affective touch evoke differential brain responses in 2-monthold infants. *Neuroimage*, 169, 162–171. https://doi.org/10.1016/j. neuroimage.2017.12.024

- Tuulari, J. J., Scheinin, N. M., Lehtola, S., Merisaari, H., Saunavaara, J., Parkkola, R., Sehlstedt, I., Karlsson, L., Karlsson, H., & Björnsdotter, M. (2019). Neural correlates of gentle skin stroking in early infancy. *Developmental Cognitive Neuroscience*, 35, 36–41. https://doi.org/10. 1016/j.dcn.2017.10.004
- Gursul, D., Goksan, S., Hartley, C., Mellado, G. S., Moultrie, F., Hoskin, A., Adams, E., Hathway, G., Walker, S., Mcglone, F., & Slater, R. (2018). Stroking modulates noxious-evoked brain activity in human infants. *Current Biology*, 28(24), R1380–R1381. https://doi.org/10. 1016/j.cub.2018.11.014
- Schirmer, A., Cham, C., Zhao, Z., Lai, O., Lo, C., & Croy, I. (2022). Understanding sex differences in affective touch: Sensory pleasantness, social comfort, and precursive experiences. *Physiology & Behavior*, 250, 113797. https://doi.org/10.1016/j.physbeh.2022.113797
- Bendas, J., Ree, A., Pabel, L., Sailer, U., & Croy, I. (2021). Dynamics of affective habituation to touch differ on the group and individual level. *Neuroscience*, 464, 44–52. https://doi.org/10.1016/j.neuroscience. 2020.12.024
- 74. Meijer, L. L., Hasenack, B., Kamps, J. C. C., Mahon, A., Titone, G., Dijkerman, H. C., & Keizer, A. (2022). Affective touch perception and longing for touch during the COVID-19 pandemic. *Scientific Reports*, 12(1), 3887. https://doi.org/10.1038/s41598-022-07213-4
- Trotter, P. D., Mcglone, F., Mckie, S., Mcfarquhar, M., Elliott, R., Walker, S. C., & Deakin, J. F. W. (2016). Effects of acute tryptophan depletion on central processing of CT-targeted and discriminatory touch in humans. *European Journal of Neuroscience*, 44(4), 2072–2083. https:// doi.org/10.1111/ejn.13298
- Croy, I., Drechsler, E., Hamilton, P., Hummel, T., & Olausson, H. (2016). Olfactory modulation of affective touch processing—A neurophysiological investigation. *Neuroimage*, 135, 135–141. https://doi.org/10. 1016/j.neuroimage.2016.04.046
- 77. Campagnoli, R. R., Krutman, L., Vargas, C. D., Lobo, I., Oliveira, J. M., Oliveira, L., Pereira, M. G., David, I. A., & Volchan, E. (2015). Preparing to caress: A neural signature of social bonding. *Frontiers in Psychology*, 6, 16. https://doi.org/10.3389/fpsyg.2015.00016
- Grichtchouk, O., Oliveira, J. M., Campagnoli, R. R., Franklin, C., Correa, M. F., Pereira, M. G., Vargas, C. D., David, I. A., Souza, G. G. L., Gleiser, S., Keil, A., Rocha-Rego, V., & Volchan, E. (2022). Visuomotor affective interplay: Bonding scenes promote implicit motor pre-dispositions associated with social grooming–A pilot study. *Frontiers in Psychology*, 13, 817699. https://doi.org/10.3389/fpsyg.2022. 817699
- Novembre, G., Etzi, R., & Morrison, I. (2021). Hedonic responses to touch are modulated by the perceived attractiveness of the caresser. *Neuroscience*, 464, 79–89. https://doi.org/10.1016/j.neuroscience. 2020.10.007
- 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. https://doi.org/10.1073/pnas. 1113211109
- Suvilehto, J. T., Renvall, V., & Nummenmaa, L. (2021). Relationshipspecific encoding of social touch in somatosensory and insular cortices. *Neuroscience*, 464, 105–116. https://doi.org/10.1016/j. neuroscience.2020.09.015
- Liljencrantz, J., Marshall, A., Ackerley, R., & Olausson, H. (2014). Discriminative and affective touch in human experimental tactile allodynia. *Neuroscience Letters*, 563, 75–79. https://doi.org/10.1016/ j.neulet.2014.01.041
- Croy, I., Geide, H., Paulus, M., Weidner, K., & Olausson, H. (2016). Affective touch awareness in mental health and disease relates to autistic traits – An explorative neurophysiological investigation. *Psychiatry Research*, 245, 491–496. https://doi.org/10.1016/j.psychres. 2016.09.011

- Crucianelli, L., Cardi, V., Treasure, J., Jenkinson, P. M., & Fotopoulou, A. (2016). The perception of affective touch in anorexia nervosa. *Psychiatry Research*, 239, 72–78. https://doi.org/10.1016/j.psychres.2016. 01.078
- Crucianelli, L., Demartini, B., Goeta, D., Nisticò, V., Saramandi, A., Bertelli, S., Todisco, P., Gambini, O., & Fotopoulou, A. (2021). The anticipation and perception of affective touch in women with and recovered from anorexia nervosa. *Neuroscience*, 464, 143–155. https://doi.org/10.1016/j.neuroscience.2020.09.013
- Tsetserukou, D., Neviarouskaya, A., Prendinger, H., Kawakami, N., & Tachi, S. (2009). Affective haptics in emotional communication. 2009 3rd International Conference on Affective Computing and Intelligent Interaction and Workshops, 1–6. https://doi.org/10.1109/ACII. 2009.5349516
- Vyas, P., Desai, U. M., Yamakawa, K., & McLean, K. E. (2023). A descriptive analysis of a formative decade of research in affective haptic system design. Proceedings of the 2023 CHI Conference on Human Factors in Computing Systems.
- Park, Y.-W., Bae, S.-H., & Nam, T.-J. (2012). How do couples use CheekTouch over phone calls? *Proceedings of the SIGCHI Conference* on Human Factors in Computing Systems, 763–766. https://doi.org/10. 1145/2207676.2207786
- Fong, A., Ashktorab, Z., & Froehlich, J. (2013). Bear-with-me: An embodied prototype to explore tangible two-way exchanges of emotional language. CHI '13 Extended Abstracts on Human Factors in Computing Systems on - CHI EA '13. https://doi.org/10.1145/ 2468356.2468537
- Nunez, E., Hirokawa, M., Perusquia-Hernandez, M., & Suzuki, K. (2019). Effect on social connectedness and stress levels by using a huggable interface in remote communication. 2019 8th International Conference on Affective Computing and Intelligent Interaction (ACII), 1–7. https://doi.org/10.1109/ACII.2019.8925457
- Jeong, S., Breazeal, C., Logan, D., & Weinstock, P. (2018). Huggable: The impact of embodiment on promoting socio-emotional interactions for young pediatric inpatients. *Proceedings of the 2018 CHI Conference on Human Factors in Computing Systems*, 1–13. https://doi. org/10.1145/3173574.3174069
- Hauser, S. C., McIntyre, S., Israr, A., Olausson, H., & Gerling, G. J. (2019). Uncovering human-to-human physical interactions that underlie emotional and affective touch communication. 2019 IEEE World Haptics Conference (WHC), 407–412. https://doi.org/10.1109/ WHC.2019.8816169
- Liu, Y., Nishikawa, S., Seong, Y., Niiyama, R., & Kuniyoshi, Y. (2021). ThermoCaress: A wearable haptic device with illusory moving thermal stimulation. Proceedings of the 2021 CHI Conference on Human Factors in Computing Systems, 1–12. https://doi.org/10.1145/3411764. 3445777
- Nunez, C. M., Huerta, B. N., Okamura, A. M., & Culbertson, H. (2020). Investigating social haptic illusions for tactile stroking (SHIFTS). 2020 IEEE Haptics Symposium (HAPTICS), 629–636. https://doi.org/ 10.1109/HAPTICS45997.2020.ras.HAP20.35.f631355d
- Cascio, C. J., Moore, D., & Mcglone, F. (2019). Social touch and human development. *Developmental Cognitive Neuroscience*, 35, 5–11. https:// doi.org/10.1016/j.dcn.2018.04.009
- Frey, J., Grabli, M., Slyper, R., & Cauchard, J. R. (2018). Breeze: Sharing biofeedback through wearable technologies. Proceedings of the 2018 CHI Conference on Human Factors in Computing Systems, 1–12. https:// doi.org/10.1145/3173574.3174219
- Jung, A., Alfaras, M., Karpashevich, P., Primett, W., & Höök, K. (2021). Exploring awareness of breathing through deep touch pressure. Pro-

ceedings of the 2021 CHI Conference on Human Factors in Computing Systems, 1–15. https://doi.org/10.1145/3411764.3445533

- Miri, P., Flory, R., Uusberg, A., Culbertson, H., Harvey, R. H., Kelman, A., Peper, D. E., Gross, J. J., Isbister, K., & Marzullo, K. (2020). PIV: Placement, pattern, and personalization of an inconspicuous vibrotactile breathing pacer. ACM Transactions on Computer-Human Interaction, 27(1), 1–44. https://doi.org/10.1145/3365107
- 99. Holsti, L., Maclean, K., Oberlander, T., Synnes, A., & Brant, R. (2019). Calmer: A robot for managing acute pain effectively in preterm infants in the neonatal intensive care unit. *Pain Reports*, 4(2), e727. https://doi.org/10.1097/PR9.00000000000727
- 100. Yohanan, S. J. (2012). The Haptic Creature: Social human-robot interaction through affective touch. University of British Columbia.
- 101. Hauser, S., Suto, M. J., Holsti, L., Ranger, M., & MacLean, K. E. (2020). Designing and evaluating Calmer, a device for simulating maternal skin-to-skin holding for premature infants. *Proceedings of the 2020 CHI Conference on Human Factors in Computing Systems*, 1–15. https:// doi.org/10.1145/3313831.3376539
- 102. Geva, N., Uzefovsky, F., & Levy-Tzedek, S. (2020). Touching the social robot PARO reduces pain perception and salivary oxytocin levels. *Scientific Reports*, 10(1), Article 1. https://doi.org/10.1038/s41598-020-66982-y
- Sefidgar, Y. S., Maclean, K. E., Yohanan, S., Van Der Loos, H. F. M., Croft, E. A., & Garland, E. J. (2016). Design and evaluation of a touchcentered calming interaction with a social robot. *IEEE Transactions on Affective Computing*, 7(2), 108–121. https://doi.org/10.1109/TAFFC. 2015.2457893
- 104. Lee, J., Elhaouij, N., & Picard, R. (2021). AmbientBreath: Unobtrusive just-in-time breathing intervention using multi-sensory stimulation and its evaluation in a car simulator. *Proceedings of the ACM on Interactive, Mobile, Wearable and Ubiquitous Technologies*, 5(2), 1–30. https:// doi.org/10.1145/3463493
- 105. Cang, X. L., Bucci, P., Rantala, J., & Maclean, K. E. (2021). Discerning affect from touch and gaze during interaction with a robot pet. *IEEE Transactions on Affective Computing*, 14, 1598–1612. https://doi.org/ 10.1109/TAFFC.2021.3094894
- Isbister, K., Cottrell, P., Cecchet, A., Dagan, E., Theofanopoulou, N., Bertran, F. A., Horowitz, A. J., Mead, N., Schwartz, J. B., & Slovak, P. (2022). Design (not) lost in translation: A case study of an intimatespace socially assistive "robot" for emotion regulation. ACM Transactions on Computer-Human Interaction, 29(4), 1–36. https://doi.org/10. 1145/3491083
- 107. Cang, X. L., Guerra, R. R., Bucci, P., Guta, B., MacLean, K., Rodgers, L., Mah, H., Hsu, S., Feng, Q., Zhang, C., & Agrawal, A. (2022). Choose or fuse: Enriching data views with multi-label emotion dynamics. 2022 10th International Conference on Affective Computing and Intelligent Interaction (ACII), 1–8. https://doi.org/10.1109/ACII55700.2022. 9953882
- Maclean, K. E. (2022). Designing affective haptic experience for wellness and social communication: Where designers need affective neuroscience and psychology. *Current Opinion in Behavioral Sciences*, 45, 101113. https://doi.org/10.1016/j.cobeha.2022.101113

How to cite this article: Kryklywy, J. H., Vyas, P., Maclean, K. E., & Todd, R. M. (2023). Characterizing affiliative touch in humans and its role in advancing haptic design. *Ann NY Acad Sci.*, 1528, 29–41. https://doi.org/10.1111/nyas.15056