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What are C-tactile afferents and how do they relate to "affective touch"?

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ABSTRACT

Since their initial discovery in cats, low-threshold C-fiber mechanoreceptors have become a central interest of scientists studying the affective aspects of touch. Their pursuit in humans, here termed C-tactile (CT) afferents, has led to the establishment of a research field referred to as "affective touch", which is differentiated from "discriminative touch". Presently, we review these developments based on an automated semantic analysis of more than 1000 published abstracts as well as empirical evidence and the solicited opinions of leading experts in the field. Our review provides a historical perspective and update of CT research, it reflects on the meaning of "affective touch", and discusses how current insights challenge established views on the relation between CTs and affective touch. We conclude that CTs support gentle, affective touch, but that not every affective touch experience relies on CTs or must necessarily be pleasant. Moreover, we speculate that currently underappreciated aspects of CT signaling will prove relevant for the manner in which these unique fibers support how humans connect both physically and emotionally.

" […] affection is a pleasurable sensation, it generally causes a gentle smile and some brightening of the eyes. A strong desire to touch the beloved person is commonly felt; and love is expressed by this means more plainly than by any other. Hence, we long to clasp in our arms those whom we tenderly love." – Charles Darwin, 1897, The Expression of the Emotions in Man and Animals (pg. 213).

1. Introduction

It has long been recognized, that strong affective bonds prompt close physical contact. Indeed, most intimate relationships such as those between a parent and child or between romantic partners thrive on touch. Their tactile basis has inspired touch research and prompted neuroscientific investigations into the mechanisms and functions linking socio-affective and tactile processes (Field, 2003; Jakubiak and Feeney, 2017; Schirmer and McGlone, 2022).

A key discovery has been a class of unmyelinated cutaneous mechanosensory afferents that appear ideal for the encoding of gentle indentation and motion across the skin (Nordin, 1990; Vallbo et al., 1993; Zotterman, 1939) and that have been termed C-tactile afferents (CTs). CTs have been functionally linked to the term "affective touch" and this has prompted growing interest from a range of academic disciplines (McGlone et al., 2014; Olausson et al., 2010; Vallbo et al., 2009). This growth has been accompanied by a broadening of touch research, and with this, an increasing heterogeneity of opinions and theoretical positions leading, ultimately, to an uncertainty about the role of CTs and the meaning of affective touch. Here, we aim to tackle this uncertainty. Moreover, we document the history and current state of research on CTs and affective touch, we review and analyze the semantic usage of both terms in the scientific literature and by experts in the field, and we discuss open issues and challenges. In doing so, we wish to clarify fundamental terminology to facilitate prospective research into the manner by which we connect with others both physically and emotionally.

2. A historical perspective on CT afferent research

In 1926, Adrian and Zotterman published seminal electrophysiological recordings from peripheral nerves in cats and provided evidence

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for specific afferent nerve fibers signaling proprioception, touch (i.e., mechanoreception), and pain (i.e., nociception), (Adrian and Zotterman, 1926). This early research focused on myelinated fibers because of their large and evident response to stimulation. Later, Zotterman (1939) examined both myelinated and unmyelinated fibers. Moreover, he found that gentle skin touch activated many afferents ranging from those with larger spike heights and faster conduction velocities (~60 m/s) originating from myelinated Aβ mechanoreceptors to the smallest spike heights and slowest conduction velocities originating from unmyelinated C-fibers (~2 m/s). Zotterman postulated that "the itching after-sensation to light touch is most probably due to fibres conducting at C rates" and implicated these C-fiber afferents in encoding after-sensations of touch and tickle. This work paved the way for new and exciting research on C-mechanoreceptive afferents in non-human animals, which were eventually termed C-low threshold mechanoreceptors (CLTMs), to distinguish them from nociceptive C-high threshold mechanoreceptors (CHTMs) (Lawson et al., 1997; Shea and Perl, 1985).

For a long time, insights into somatosensory afferent activity were limited to non-human animals. This changed with the development of a technique called microneurography (Vallbo and Hagbarth, 1967), which enabled the study of axonal responses in humans via the insertion of a microelectrode through the skin into a peripheral nerve. Initial work using the technique, which is conducted at only a few places in the world, has demonstrated the complex firing of cutaneous myelinated Aβ mechanoreceptors to various mechanical events (e.g., the classic review from Vallbo and Johansson, 1984). After many years of microneurography, further evidence emerged that, as well as Aβ mechanoreceptive afferents, C-mechanoreceptive afferents also existed in human skin. In microneurography recordings from the face, Johansson et al. (1988) found a potential C-fiber that was highly responsive to gentle touch and Nordin (1990) produced additional and unequivocal evidence for such an afferent. As previous work had readily documented nociceptive C-fiber responses in human limbs (Torebjörk, 1974), Nordin concluded that "C mechanoreceptors, being 'primitive' sense organs, are comparatively rare in man". Yet, in a series of subsequent papers, Vallbo, Wessberg and colleagues showed that these low threshold C-mechanoreceptors are abundant in the hairy skin of the arm. They named them "tactile C afferents" (Vallbo et al., 1999), which later became widely accepted as "C-tactile" (CT) afferents. CTs are abundant on the arm and face, have been found to a lesser extent on the leg (Edin, 2001; Löken et al., 2022) and likely exist throughout the hairy skin of the body. A recent study, aiming to investigate Aβ fibers in the glabrous skin of the hand, also found a couple of CT afferents there, suggesting they are not constrained to hairy skin (Watkins et al., 2021).

Although CLTMs in non-human animals and CTs in humans share many characteristics (Nordin, 1990; Watkins, 2022), their terminological distinction has persisted. This is in part due to some differences in response characteristics (e.g., less fatigue to repeated touch in humans and differences in the stroking velocity tuning, where some non-human animals show response peaks at substantially lower velocities), but also due to divergence in CLTM gene expression profiles (for an overview see Watkins, 2022).

Remarkably, scientists started to seriously hypothesize a possible functional role for low threshold C-fibers only years after their discovery (Vallbo et al., 1999). Laying the path for this, was a long series of experiments by Vallbo, Wessberg, Olausson and colleagues, which highlighted that, unlike Aβ mechanoreceptive afferents, CTs are not well-suited to provide discriminative touch information, here defined as the information that lets us locate, identify, or manipulate a tactile object. CTs encode the timing of touch poorly and can display variable firing to the same stimulus, yet their firing frequency shows a positive relationship with perceived tactile pleasantness leading the authors to formulate the *affective touch hypothesis* (Vallbo et al., 2009). In this hypothesis they argue that "the essential role of the CT system is to convey pleasant aspects of light touch, particularly of skin-to-skin contact with affiliative human beings". Moreover, Vallbo and colleagues state that although a number of sensory mechanisms and psychological factors are inherently at play in tactile interactions, the touch itself, from the moment of skin contact, is the driving force giving rise to positive tactile affect. Although postulating a key role for CTs in this positive tactile affect, they also emphasized that other sensory afferents likely contribute. Notably, this latter point has often gone unnoticed in subsequent work.

Building on the affective touch hypothesis, several groups postulated that Aβ and CT afferents support central representations of discriminative and affective touch, respectively (Fig. 1, left), (McGlone et al., 2007, 2014; Morrison et al., 2010). This proposal resembles another sensory system proposal, which is that pain processing involves two major, dissociable dimensions (Auvray et al., 2010; Hofbauer et al., 2001; Kulkarni et al., 2005; Rainville et al., 1997). That is, for both touch and pain, a sensory-discriminative dimension supports the encoding of physical stimulus properties including, for example, spatial location and intensity, while an affective-motivational dimension encodes stimulus valence (e.g. pleasantness/unpleasantness) and thus how imperative that stimulus is for behavior (Fig. 1, right). As with the affective touch hypothesis, nuances of this proposal have often been "lost in translation" including the idea that the proposed pathways are but partly dissociable and that "it is likely that sensory-discriminative and motivational-affective pathways for touch interact" (Morrison et al., 2010).

2.1. *Affective touch – then and now*

Alongside the neurophysiology of touch, there has been an increasing interest in the psychology of touch. Around 60 years ago, Harlow and Zimmerman demonstrated the importance of tactile comfort in primate development (Harlow, 1958, p. 19). They separated macaque offspring from their mothers offering them surrogates made of wire or terrycloth. The offspring naturally preferred clothed surrogates and this was true irrespective of which surrogate was paired with food. These results led Harlow to speculate that "contact comfort is a variable of overwhelming importance in the development of affectional responses". Following this work, psychologists began to study the role of touch for human infant development (e.g., Ainsworth, 1979; Feldman et al., 2002) and adult relationships (Debrot et al., 2021; Jakubiak, 2022). Moreover, a large body of data emerged pointing to a significant function of gentle skin contact for both physical and mental health across the lifespan (e.g., Araújo et al., 2022; Hasenack et al., 2023; Schulze et al., 2022) and raising questions as to the underlying mechanisms (for reviews see Morrison, 2016; Schirmer and McGlone, 2022).

Given insights from neurophysiology, the CT system was deemed potentially relevant and explored as a mechanism for the benefits of touch. Thus, it was shown, for example, that touch presented at CT optimal stroking velocities (i.e. gentle moving touch delivered around 1–10 cm/s; Ackerley, Backlund Wasling et al., 2014; Löken et al., 2009), reduces heart rate in full and pre-term infants (Manzotti et al., 2019; Püschel et al., 2022) and pain responses in full-term infants undergoing painful medical procedures (Gursul et al., 2018). This suggests that touch with CT optimal velocities is suited to change an infant's interoceptive state and to promote homeostasis (Püschel et al., 2022). Additionally, there is some indication that gentle touch may be relevant for promoting pro-social processes and the developing social brain with causal evidence from non-human animals (Champagne et al., 2008; Simpson et al., 2019) and correlational evidence from humans (Brauer et al., 2016; Della Longa et al., 2019; Reece et al., 2016).

Work in human adults suggests that social touch effects are at play also in the mature brain. Gentle stroking at velocities that optimally excite CTs feel pleasant, but also more human than stroking at other velocities (Schirmer et al., 2023; Wijaya et al., 2020). Additionally, this type of touch enhances the processing of concurrent social signals such as a speaker's voice (Schirmer and Gunter, 2017). A reason may be that gentle and positive skin-to-skin contact naturally addresses CTs: when

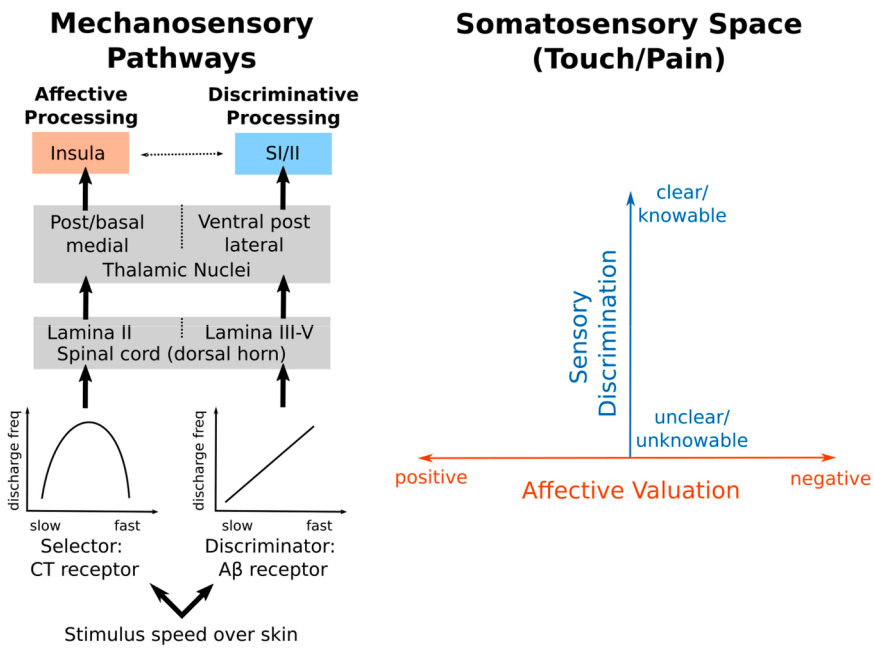

Fig. 1. Illustrated on the left is a schematic model of affective and sensory-discriminative pathways for dynamic touch (adapted from Morrison et al., 2010). Illustrated on the right is a two-dimensional somatosensory space, visualizing that affective valuation, guided by C-fiber input, and sensory discrimination, guided by Aβ input, inform touch perception.

asked to caress a romantic partner, one's child, or a pet, humans more readily stroke slower than faster (Croy et al., 2016; Lo et al., 2021; Van Puyvelde et al., 2019). Indeed, in a laboratory setting, stroking speed appears to decrease linearly with one's emotional closeness to a touch target (Strauss et al., 2020), albeit on average it is faster than what is considered the CT optimum. Further, pro-socially motivated stroking is both temporally and spatially more variable than non-social stroking, which reduces predictability and enhances self-other differentiation for the receiver thus possibly contributing to tactile pleasure (Lo et al., 2021).

Exciting new insights from non-human animals further strengthen the link between CT relevant touch and both affective and social responding. A study in mice showed that tactile interactions with conspecifics preferably activate a population of oxytocin neurons and that a selective inhibition of these neurons reduces social interactions (Tang et al., 2020). Using genetic ablation, it has also been found that blockage of CLTM processing in mouse spinal cord interneurons markedly reduces prosocial behavior and the affective value of gentle touch (Huzard et al., 2022; Liu et al., 2022).

Interestingly, it has been shown in both rodents (Liu et al., 2022; Vrontou et al., 2013) and humans (Fu et al., 2018) that CT targeted touch is naturally reinforcing and shapes preferences for touch-associated stimuli. For example, humans will rate neutral faces as more pleasant and gentle when these faces had been previously paired with forearm stroking at 4 cm/s as compared to when no stroking had been administered. Thus, touch addressing the CT system likely serves as an unconditioned stimulus prompting a conditioned response to the individual who offers such touch (Della Longa et al., 2019; Francis et al., 1999; Fu et al., 2018; Triscoli et al., 2017). Individuals may learn to associate the induced positive affect with a person or person group and may become motivated to seek out relevant social contact (for a review see Croy et al., 2022).

2.2. *Semantic coupling of the terms "affective touch" and "C-tactile" in the literature*

It is unsurprising that emergent empirical and theoretical links between the positive feeling of gentle touch and CT activity have associated the terms affective touch and CTs in our minds. However, to date, our field has failed to properly reflect on the nature of this link and to what extent it may adequately describe available data. We, therefore, sought to address this issue by quantifying the semantic associations between terms in the literature and by evaluating them on the backdrop of both established theory and more recent evidence.

In a first step, we explored scientific publications with the search terms *affective touch* and/or *C-tactile* in title, abstract or keywords (449 publications, see Supplementary Materials for details). One approach we took entailed analyzing available abstracts for semantic overlap. To this end, we parsed abstracts into nouns, verbs, adverbs, and adjectives, counted their occurrence, and selected the 100 most frequent words. Next, we identified the intersection among these words for data retrieved with the search term *affective touch* and data retrieved with the search term *C-tactile*. The results are illustrated in Fig. 2 and entailed a 67% overlap. While both data sets included typical somatosensory research terms such as "body", "system" or "velocity", they also shared in their CT relevance as evident from terms such as "hairy" and "glabrous" and their reference to C fibers. Notably, the common terms "positive", "caress", "affiliative" and "arousal" indicate that both "affective touch" and "C-tactile" typically denote a similar, affectively positive experience.

As a second step, we examined how frequently the search terms *affective touch* and *C-tactile* pointed to the same publication and compared this with other words typically used in the context of touch research. Thus, we retrieved additional data with the search terms *affectionate touch*, *affiliative touch*, *emotional touch*, *interpersonal touch*, *pleasant touch*, and *social touch* (1000 publications). These terms are semantically related to the terms *affective touch* and *C-tactile*. In Fig. 3, we illustrate our understanding of their relationships as well as the results of our analysis. The latter show a close association between *affective touch* and *C-tactile* that was unmatched by any of the other search terms. Looking across years, starting with 1980, we also found a stark rise in publications for the search terms *affective touch* and *C-tactile* that was rivaled only by publications for the search term *social touch*.

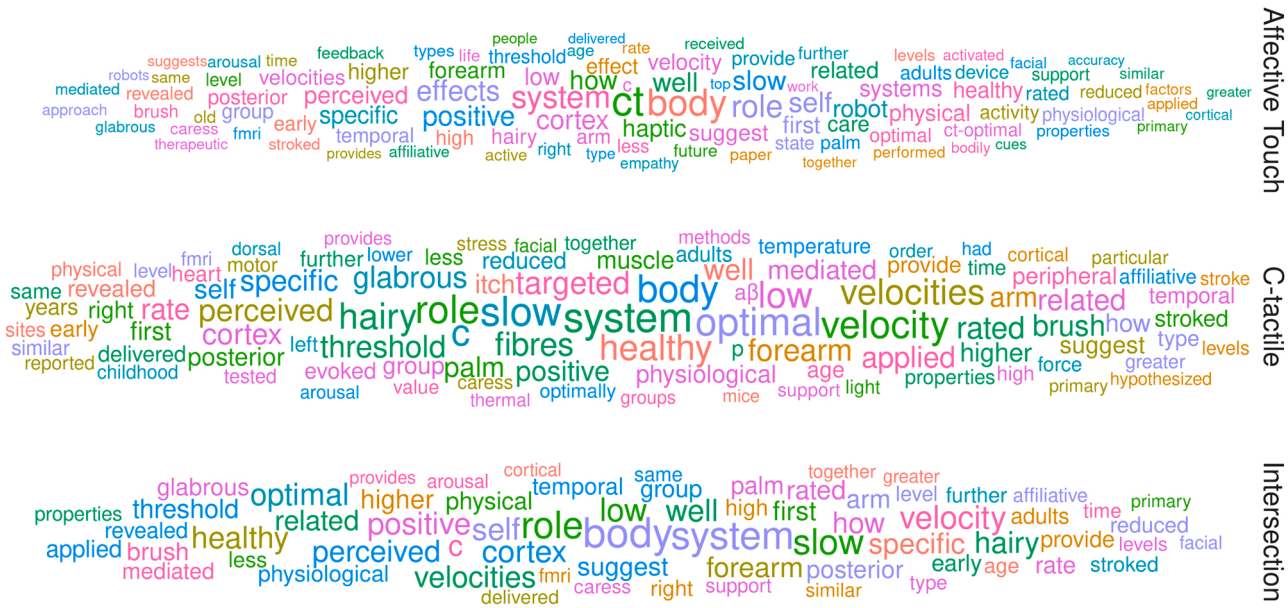

Fig. 2. Illustration of the relative frequencies of tokens in abstracts identified with the search terms affective touch (top) and CT afferents (middle). Both groups of tokens show a 67% overlap (bottom).

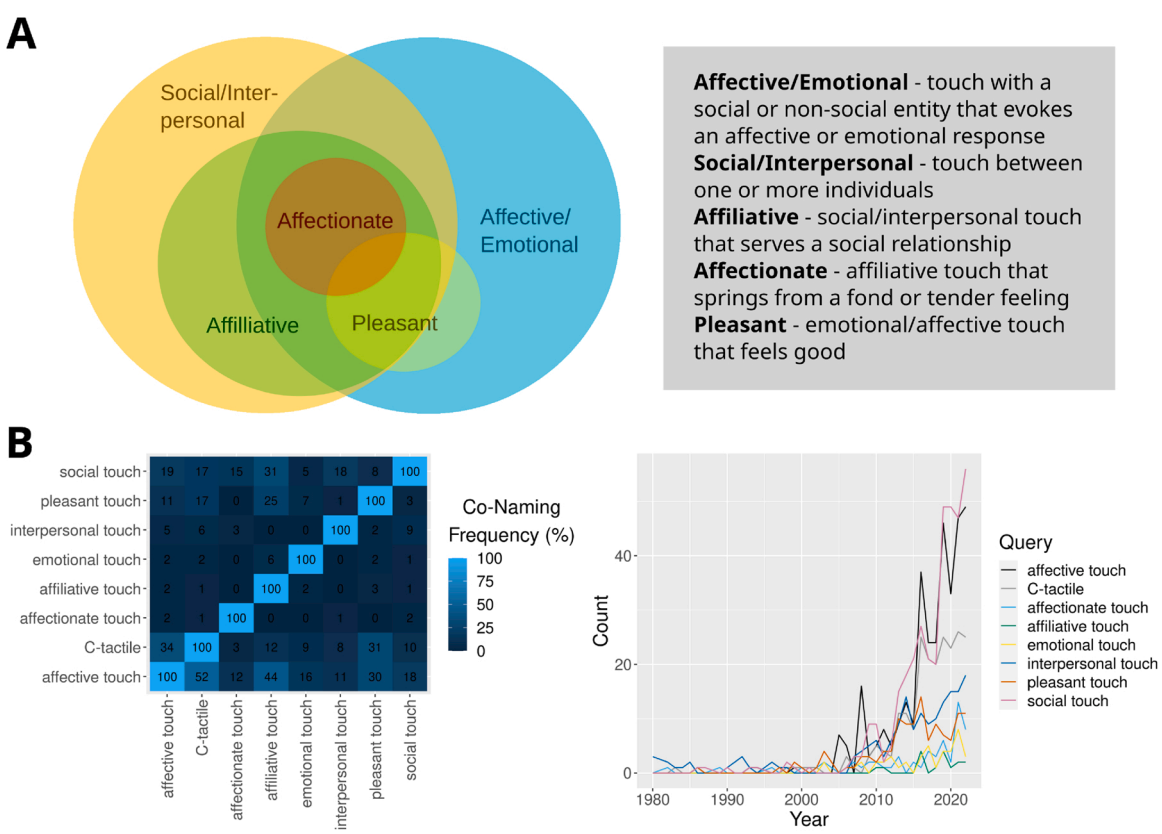

Fig. 3. A – Illustration of how the present authors understand the semantic relationships between the search terms in their analysis. B – Visualization of Scopus search term results from 01/1980 to 08/2022. Illustrated on the left is a heat map of the co-occurrence of search terms. Illustrated on the x-axis is the search term for which we checked how frequently other search terms illustrated on the y-axis were used in the same publication. For example, of publications with the search term "affective touch", 34% also had the search term "C-tactile". Illustrated on the right is the number of publications for the different search term queries plotted as a function of publication year. Both affective touch and social touch have gained significant popularity relative to other terms in the literature in the last few years.

2.3. The relationship between affective touch and CT afferents is complex

Together, our observations of the relevant literature identify a greatly increasing interest in affective touch and CTs showing that both terms are strongly conceptually associated. The majority of research contributions echo the affective touch hypothesis (Vallbo et al., 2009) and the notion that CTs present a special fiber system that functionally dissociates from the Aβ fiber system in that it supports affective rather

than discriminative tactile representations in the brain (McGlone et al., 2014; Morrison et al., 2010). Additionally, we found that the way the literature refers to affective touch and CTs insinuates that the term "affective touch" specifies touch that activates CTs and that is inherently pleasant (e.g., CTs defined as "responsible for the so-called "affective touch" (Fidanza et al., 2021)).

This has parallels with the classical Wason problem, which entails the presentation of four cards together with a rule that problem solvers must test by turning over one or more of the cards. In our case, the problem might entail four cards showing a somatosensory fiber on one face and a type of touch on the other face (Fig. 4). Here, in line with the analysis of published abstracts, affective touch is understood as gentle and pleasant touch. Discriminative touch is understood as informing about the physical aspects of a tactile object. Our instruction to problem solvers would be to test the proposition that "if a card shows 'CT' on one face, then its opposite face is 'Affective Touch' or expressed differently, if we excite CTs then the resulting tactile experience is pleasant". According to Wason's results, we would expect a tendency to turn the cards with "CT" and "Affective Touch" on the upper face. The logical fallacy here is the assumption that because CTs are linked with touch pleasantness, touch pleasantness requires CT stimulation and that CT touch equals affective touch. In truth, however, one would need to turn the cards with "CT" and "Discriminative Touch" on the upper face. That is, because our proposition does not exclude the possibility that other skin receptors like Aβ mechanoreceptors are affectively relevant and can excite pleasure.

In line with our proposition, affective touch and CT signaling cannot be mapped one-to-one (Morrison, 2022). Instead their relationship is more complex and in fact cannot be easily described with a simple set of rules. In what follows, we list some points about this complexity.

First, we would like to raise that the term "affective" specifies any stimulus that influences one's feelings positively or negatively. Moreover, that stimulus can be self-generated or come from another human, animal, or inanimate source (Schirmer, 2014). As such, it is fairly broad and clearly relevant for touch involving more afferents than just CTs. For example, painful or ticklish stimuli, that likely excite different combinations of Aβ, Aδ and/or C fibers, are clearly affective. Thus, whereas touch that excites CTs likely prompts affectively relevant brain responses, an affective touch experience does not necessitate the activation of CTs. Indeed, it might be driven by other C fibers relevant for pain perception or any other afferents. Note that this converges with the fact that, in general, the relationship between sensory perception and our representation of the world is nondeterministic (de Araujo et al., 2005; McGurk and MacDonald, 1976).

A second point concerns the presumed functional division between CT and Aβ fibers and between affective and discriminative touch. Such a strict division was not intended originally in the affective touch hypothesis, which acknowledged the contribution of Aβ fibers to affect (Vallbo et al., 2009). It has also been challenged recently by evidence from both humans and non-human animals. In humans, touch with CT optimal velocity directed at glabrous skin densely innervated by Aβ fibers can be as pleasant as that directed at hairy skin densely innervated with CTs (Löken et al., 2011; Luong et al., 2017; Novembre et al., 2021), although the quality of the pleasure may differ (e.g., activating vs calming, Ackerley, Saar et al., 2014; Guest et al., 2011; McGlone et al., 2012). Additionally, deep pressure touch directed at Aβ fibers is pleasant (Case et al., 2021) and a peripheral nerve block of Aβ input to the brain nearly abolishes the pleasantness of both gentle stroking and deep pressure touch (Case et al., 2022).

In non-human animals, the tracing of neuronal connections in the dorsal horn of the spinal cord revealed that first-order CLTM neurons, considered functionally equivalent to human CTs, interface with second-order Aβ neurons, thus allowing CLTM input to be expedited to the brain (Abraira et al., 2017). Notably, this finding helps explain data from human patients who incurred spinal lesions that impaired all C but preserved Aβ projections to the brain (Marshall et al., 2019). These patients showed no difference in their affective rating of touch before and after the injury possibly because first-order CT input could travel along higher-order Aβ projections. In support of this conjecture is recent evidence from the EEG, which identified a relatively early somatosensory response that would accommodate the timing of a CT to Aβ signaling pathway and that was specific to CT rich, hairy skin (Schirmer, Lai, McGlone et al., 2022).

In all, it is quite possible that input from different fiber systems including those that convey, for example, temperature or pain, interact very early and send a mixture of information to the brain. Further research is needed to probe this possibility and to examine CT and Aβ fiber projections and interactions at different levels of the nervous system.

A third line of evidence weakening the strong conceptual tie between affective touch and CTs is that other psychological attributes may be equally, if not more, relevant in describing the mental effects of CT stimulation. For example, perceptions of touch intensity or roughness show quadratic responses as a function of touch velocity reminiscent of the well-established pleasantness effect (Sailer et al., 2020; Schirmer et al., 2023). Additionally, stroking at intermediate velocities feels more human than stroking at faster and slower velocities and humanness ratings positively predict perceived pleasantness (Schirmer et al., 2023; Wijaya et al., 2020). CTs also appear to prefer touch at skin temperature over warmer and colder touch (Ackerley, Backlund Wasling et al., 2014) and their velocity-tuning overlaps, albeit only partially, with that of natural human touch (Bytomski et al., 2020; Croy et al., 2016; Lo et al., 2021). Interestingly, CT relevant touch is not preferred by all (Croy et al., 2021; Schirmer, Lai, Cham et al., 2022) and there is some evidence that certain changes in its processing are linked to autism (Kaiser et al., 2015) and attachment anxiety (Krahé et al., 2018) among others (Löffler et al., 2022; Schaefer et al., 2022; Spitoni et al., 2020). Thus, one may speculate that instead of simply inducing positive affect, CT input conveys gentle touch from conspecifics and evolved to specifically reinforce such touch. This idea was preconceived in the original affective touch

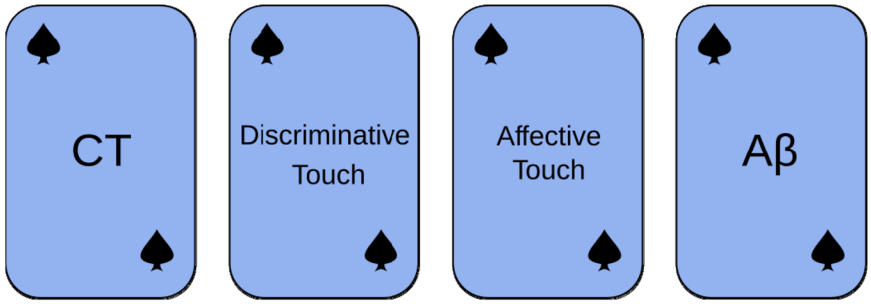

Fig. 4. Wason problem. You are shown a set of four cards placed on a table, each of which has a somatosensory fiber on one side and a type of touch on the other side. Which card(s) must you turn over in order to test the truth of the proposition that if a card shows "CT" on one face, then its opposite face is "Affective Touch"? This problem is modeled after the classic Wason problem which used numbers and colors. The data from the classic Wason problem imply that most problem solvers would opt for turning the cards showing "CT" and "Affective Touch". The cards that should be turned, however, are "CT" and "Discriminative Touch". Indeed, if the card showing "Affective Touch" had Aβ on its other side, it would not break the stipulated rule. However, if the card showing "Discriminative Touch" had "CT" on its other side, it would break the rule.

hypothesis and sharpened in the social touch hypothesis (Morrison et al., 2010; Olausson et al., 2010), which understands CTs as selectors that promote the processing of positive body contact with conspecifics.

Last, but not least, it is important to highlight that we are just at the beginning of understanding CTs. Since the first thorough documentation of CT properties (Nordin, 1990), certain aspects about their firing have been noted, but little investigated. Most of the handful of papers that report CTs recordings note that slow stroking produces high activity. To quantify this, previous work has focused on mean instantaneous firing rate measured across the duration of a tactile stimulus. However, there are other ways to quantify CT responses, including number of spikes, maximum firing frequency, spectral analyses, and the modeling of responses (e.g. using information theory). Indeed, CT firing is more than a simple on/off response. Moreover, it has been associated with a range of interesting phenomena such as after-discharge (a burst of impulses after a stimulus has ended) (Ackerley et al., 2018; Johansson et al., 1988; Nordin, 1990; Vallbo et al., 1999; Watkins et al., 2017), adaptation to a sustained skin indentation (Johansson et al., 1988; Vallbo et al., 1999), fatigue from repeated stimulation (Edin, 2001; Nordin, 1990; Vallbo et al., 1999), and varying receptive field properties (Nordin, 1990; Wessberg et al., 2003), which are phenomena also observed in CLTM studies (for an overview see Watkins, 2022).

Currently, insights into these aspects are based on just a handful of qualitative observations that leave us with many important questions. For example, we do not yet know the functional significance of after-discharge and cannot explain why it varies across seemingly similar touch stimuli. Further, CTs have been shown to respond equally well to blunt or sharp indentation at forces around 150 mN, with firing rates as high as for stroking (Nordin, 1990; Vallbo et al., 1999). Recent work has investigated the response of CTs to monofilament indentation and found a positive linear relationship between mean firing frequency and force, from very gentle (4 mN) to quite forceful (100 mN) stimulation (Middleton et al., 2022). Going forward it will be relevant to specify exactly what forces and types of touch (e.g. rough vs. smooth textures, sharp vs. blunted objects) stimulate CTs optimally. Indeed, their complex receptive fields, likely supporting their velocity tuning, could also prove relevant for encoding other characteristics of touch. Furthermore, the adaptation of CTs to prolonged indentation requires examination. This has been classed as 'intermediate-adaptation', but is somewhat vague, as CTs can have a bi-phasic response to sustained skin contact. They often show a significant burst of firing to initial touch and then some responses that eventually stop (adaptation) but start-up again later (delayed acceleration) (Vallbo et al., 1999). CTs somewhat decrease in firing after repeated stimulation (fatigue), but this has not yet been formally quantified and is less prominent than for CLTMs. A further question concerns the functionality of CT receptive fields. Although, in publications, CTs tend to be depicted as a single spot to display their location, they can have a various number of 'hot spots' that can influence the firing of the afferent (Vallbo et al., 1993; Watkins et al., 2017; Wessberg et al., 2003). CT hot spots may have different force activation thresholds, where with increased numbers of hot spots, there may be an interaction in the response to different tactile forces and their direction (Wessberg et al., 2003). What, if any, effect these signaling patterns have on upstream neural and psychological processes is currently unknown. Finally, CTs respond to more than just gentle stroking and their firing depends on more than just stimulus velocity including, for example, stimulus temperature (Ackerley, Backlund Wasling et al., 2014; Ackerley et al., 2018). More research is needed to explore other physical properties such as skin stretch (Edin, 2001; Nordin, 1990) or touch duration (often left uncontrolled due to an emphasis on controlling touch distance) that could be equally relevant and to pursue the possibility of different CT sub-types.

2.4. How do experts think about CTs and affective touch?

In light of these issues, we contacted leading experts (see Supplementary Materials) in the field of affective touch and held an online meeting to discuss the potential relationship between affective touch and CTs with the ambitious intention of developing working definitions with majority consensus. This proved difficult as these experts voiced various perspectives in part driven by different disciplines. They, and several others we contacted later, then kindly offered their written definitions of affective touch and the presumed function of CTs allowing us to better understand the existing diversity of opinions. An analysis of all obtained definitions (N = 13), conducted analogously to that of published abstracts above, indicated that the majority of our expert group defined affective touch as something going beyond the activation of CTs (Fig. 5). Moreover, the majority clearly dissociated both terms with the overall overlap reaching only 23% (as opposed to 67% in published abstracts). Whereas affective touch was described using higher-level perceptual terms such as "positive", "desire", or "subjective", CTs were described using more lower-level sensory terms such as "low", "velocity", or "receptors". Notably, affectively positive associations did not dominate and did not emerge as common to affective touch and CTs.

A comparison between the analysis of published abstracts and the expert statements reveals a striking gap in how the terms "affective touch" and "C-tactile" are used. This gap may be explained in several ways including that it is often appealing and necessary to simplify a complex problem when communicating with a broad or non-expert audience. Unfortunately, empirical work can be over-simplified and misinterpreted and this impedes scientific advances, especially in a fast-moving and growing field.

2.5. Re-visiting the meaning of CTs and affective touch

After three decades of CT research and over a decade of probing the affective touch hypothesis, it seems pertinent to reflect on how we link physiology and psychology in communicating research findings. Early proposals of CT functionality implicating affect were well founded in our knowledge at that time. Activating these fibers has been linked convincingly to pleasurable affect and the term "affective" is broad enough to encompass a host of psychological phenomena thus serving well when the functionality of CTs is still incompletely understood. Yet, over time, touch directed at CTs has become synonymous with the term "affective touch" and this creates unwanted practical and theoretical issues. Therefore, we would like to highlight the intriguing and still mysterious nature of CTs and redefine affective touch for the field of CT directed research.

In light of evidence from microneurography, we wish to stress that there is still a lot to uncover about CTs. Yet, one empirical observation that stands out is that CT firing is variable – after-discharge, biphasic responses and receptive field properties converge onto a signal with low predictability. Thus, we speculate that this low predictability is functionally relevant in that it could reduce the predictability of tactile pleasure at the level of the brain and there increase prediction error signals. Indeed, such signals are critical in shaping dopaminergic responses in the brain's reward system and for promoting learning. The more uncertain pleasure is, the larger is the prediction error and the more rewarding and memorable is the experience (Glimcher, 2011; Rouhani and Niv, 2021; Schultz, 2017). Thus, together with the variation that's present in natural touching (Lo et al., 2021), variation in CT firing undoubtedly promotes pleasure and strengthens mental associations between an affective outcome and the stimulus that produced it (e.g., a specific person), (Croy et al., 2022).

In line with current theories of emotion (Barrett, 2017; Moors et al., 2013), we conceive that affective touch results from the basic evaluation or appraisal of mechanical and other somatosensory (e.g., temperature, nociceptive) input that feeds into higher-order processes, supporting the construction of an emotion, and that often, but not always, leads to an awareness of the touch and how it feels. The resulting emotion is positive or negative and may be affiliative, erotic, aggressive, fearful or

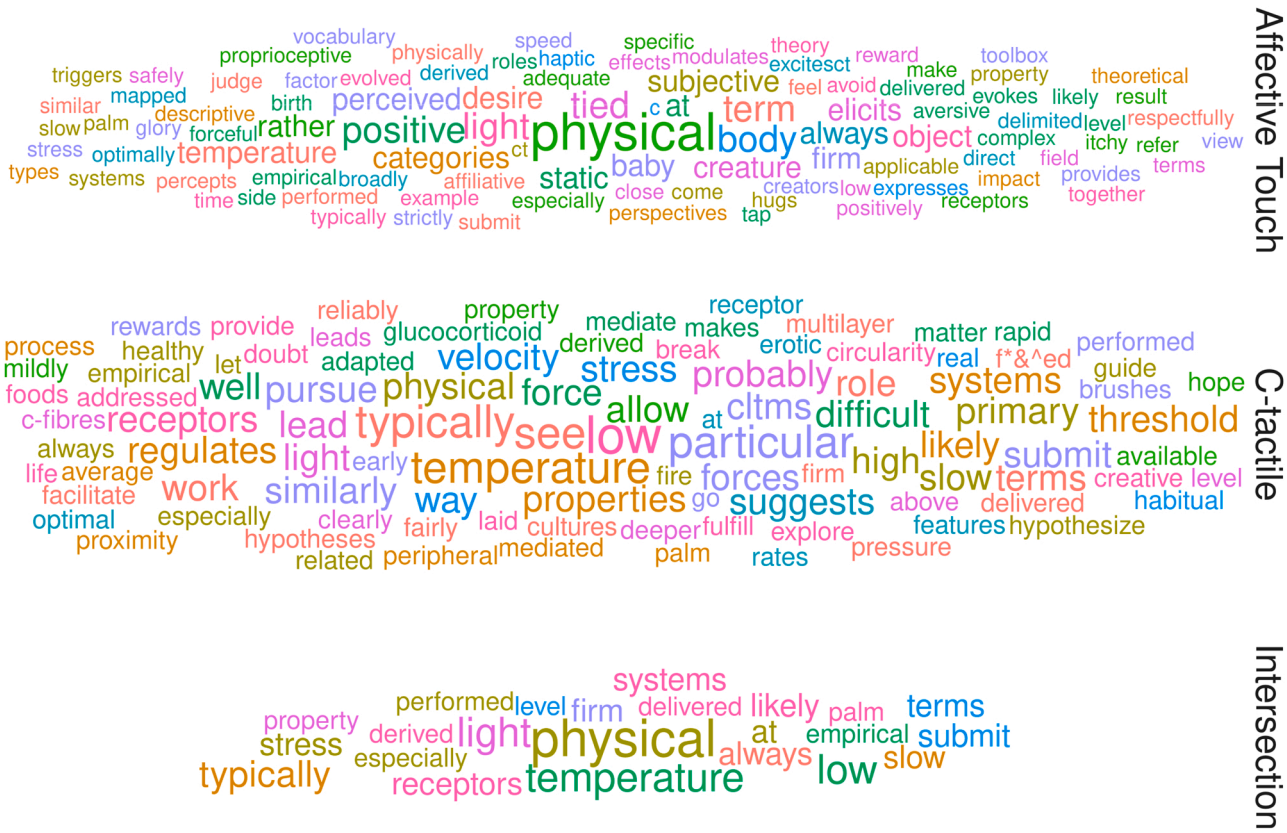

Fig. 5. Illustration of the relative frequencies of tokens in the definition of experts as relates to affective touch (top) and CT afferents (middle). Both groups of tokens show 23% overlap (bottom).

disgusted to name just a few. It entails central and peripheral changes such as those associated with the autonomic nervous system that motivate and prepare individuals to either seek out or avoid the touch.

Together the present conceptualizations of CTs and affective touch help clarify their relation. They hold that while CT targeted stimuli may produce affective touch, such touch can also be experienced from somatosensory stimuli not specifically addressing CTs. Thus, when one wishes to discuss the kind of tactile experiences aroused by activating CTs, the term affective touch may be unsatisfactory. Instead, it may be better to characterize the nature of the experimental stimulus as, for example, gentle stroking or to specify the manner in which a concrete touch experience, such as pleasure or human-likeness, was traced back to the activity of CTs. Indeed, given the many open questions surrounding the mechanisms of CTs and their role in affect and emotion, a scientific language that is stimulus rather than function-focused seems warranted.

3. Conclusions

The discovery of CTs and initial insights into their function have inspired the affective touch hypothesis (Olausson et al., 2010; Vallbo et al., 2009). This hypothesis has shaped an emergent subfield within the broader area of somatosensation and created a strong association between the terms “affective touch” and “C-tactile” in our minds. Yet, as we have shown here, this association must be understood quite loosely as there is but partial overlap in the actual meaning of “affect” and the function of CTs as they are understood today. Whereas tactile affect denotes both positive and negative experiences that are conveyed by a range of receptors apart from CTs, CT signaling appears particularly relevant for reinforcing the consequences of gentle touch. Yet, this appearance is tied to a still fragmentary understanding of CTs, as indeed we are just beginning to appreciate their computational complexity and how their signaling characteristics allow for a simple physical connection to instill an affectionate one that fundamentally supports physical and mental well-being.

Declaration Of Competing Interest

The authors declare no competing interests.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2023.105236.

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