Psychophysiology and motivated emotion:

Testing the affective touch hypothesis of C-tactile afferent function

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Highlights

- C-tactile afferents are unmyelinated low threshold mechanoreceptors.
- Their preferred stimulus is low force and velocity, skin temperature touch.
- CT targeted touch has a positive affective value and lowers arousal.
- This is consistent with their hypothesized social-affective function.
- Grounding studies in motivational theories of emotion will facilitate future research.

Abstract

The affective touch hypothesis posits a class of unmyelinated, low threshold mechanoreceptors form a distinct channel signaling the affective dimension of touch. The preferred stimulus of these CT afferents is a low force and velocity, skin temperature stroke, typical of a caress. A growing body of research has utilized psychophysiological techniques to study the implicit effects of CT targeted touch. Here we consider that literature in the context of an established, comparative model of motivated emotion. Consistent with their hypothesized social-affective function, preliminary evidence indicates CT targeted touch has a positive affective value, lowers arousal and modulates neural responses to concurrently experienced affective cues. We propose that psychophysiological research grounded in motivational theories of emotion adds unique value to the exploration of the affective touch hypothesis.

Keywords: Social; Touch; C-fibre; C-Tactile afferent; Motivation; Emotion

Introduction

The discovery of a system of unmyelinated cutaneous low threshold mechanoreceptor (LTMR) C-fibers in human hairy skin has challenged the canonical view of the sense of touch having only discriminative and haptic functions. These so-called C-tactile (CT) afferents have slow conduction velocities (~1 m s^{-1}) and are poorly suited for tactile discrimination [1–3]. The affective touch hypothesis posits that functionally, CTs form a distinct channel signaling the affective dimension of touch that has emotional and social relevance [1,4]. Central to the development of this hypothesis are the characteristic firing properties of CTs: human microneurographic recordings demonstrate that, while CTs respond to punctate stimuli [3], their preferred stimulus is caress-like slow, stroking touch [3,5]. Unlike discriminative, myelinated Aβ LTMR afferent firing, which increases linearly with increasing velocity of a gentle brushing stimulus, CTs spike most vigorously at velocities of 1-10 cm/s and significantly less for faster and slower stimuli [6,7] (See Figure 1A). Remarkably, this inverted U-shaped neural stimulus-response function shows a strong positive correlation with subjective ratings of touch pleasantness [6,7].

In human research to date, support for the affective touch hypothesis is primarily grounded in combined evidence from neuroimaging and psychophysics studies [1,8]. CT optimal velocities of touch are reliably rated more pleasant than faster or slower bouts of stroking, and fMRI contrast analysis shows greater activation in affective brain regions to CT optimal over faster, non-CT optimal stroking velocities [9,10]. However, less attention has been paid to the emotional and motivational consequences of CT stimulation. Here, we briefly highlight the limitations of fMRI and psychophysics for studying CT function, review recent psychophysiology studies and propose that grounding this body of research in motivational theories of emotion will facilitate further exploration of the affective touch hypothesis.

Affective Touch Perception – Subjective Pleasantness

A major challenge to testing the affective touch hypothesis is that it is impossible to stimulate CTs without co-stimulation of Aβ afferents [2]. In non-clinical studies, ratings of touch pleasantness, based upon the differential response characteristics of CT and Aβ fibers is a widely used proxy of CT mediated affective touch. Primarily, a CT optimal velocity stimulus is contrasted with a faster, Aβ afferent targeted stimulus [11]. Another approach compares CT optimal velocity touch delivered to hairy skin with the same stimulus applied to the glabrous skin of the palm [10,12], where CTs are not thought to innervate (though see [13]).

Support for this approach to understanding CT function came from studies in patients with selective deficits in either discriminative or affective touch pathways [2,14]. In individuals with Aα/β deafferentation resulting from a rare acquired neuronopathy syndrome, soft brush strokes are perceived on the forearm but not on the palm [2]. Neurally, this CT targeted touch activates the dorsal posterior insular cortex (PI) - a region thought to represent the gateway to social and affective cortical networks - but not primary sensory cortex [15]. However, while gentle stroking of hairy skin elicits a robust sympathetic skin response, the subjective effect was no more than a barely perceptible, faintly pleasant, and poorly localized tactile sensation [15,16]. This suggests, in healthy individuals, subjective experience of pleasant touch depends on concomitant Aβ inputs.

Further evidence supporting Aβ contributions to 'normal' pleasant touch perception is seen in a recent study of patients undergoing anterolateral cordotomy. This procedure, which lesions the spinothalamic tract [17], the major ascending relay for homeostatically relevant C-fiber inputs [18,19], failed to alter benchmark measures of affective touch, despite producing unambiguous impairments in pain, temperature and itch perception. Thus, in adulthood, information ascending in classical discriminative touch pathways is sufficient to preserve the inverted U-shaped stimulus-response that binds pleasantness ratings to velocity dependent CT firing.

Although recent evidence suggests a causal role for the insula in generating the perception of touch pleasantness to CT-targeted stimuli [20], tactile activation of this region is not CT specific.

Direct neural recordings in non-human primates [21] as well as human MEG studies [22,23] demonstrate the onset of robust activity in insular cortex, following gentle tactile stimulation, precedes the predicted arrival of CT inputs. Taken together, these data indicate that subjective ratings and measures focusing on the activity of individual brain regions may have limited utility in elucidating CT-specific affective processes. Therefore, both approaches should be supplemented by faster and/or more differentiated assessments of peripheral and central activity when testing the affective touch hypothesis.

From an evolutionary perspective, the observed relationship between stroking velocity and subjective pleasantness most likely has its genesis during development, arising as a surrogate of a CT mediated homeostatic role that, through autonomic, neurohormonal, as well as cortical networks, signals reassurance, comfort, and safety. Initial support for this view comes from rodent studies which show C-LTM activation, and C-LTM targeted skin stimulation, is motivating, rewarding and buffers against the physiological and behavioral consequences of stress [24–26]. In human research, a growing body of studies have investigated the psychophysiological effects of CT targeted touch. Here we first consider that literature in the context of an established, comparative model of motivated emotion [27] and subsequently make the case that designing future studies within this framework will facilitate testing of the affective touch hypothesis.

Positive Affect: Psychophysiological Markers of Valence, Arousal and Appetitive Motivation

Emotional responses to environmental stimuli can be considered to be organized around two motivational systems. The defense system is activated in contexts involving threat while the appetitive motivational system is activated in contexts that promote survival, including nurturance and caregiving. [28,29]. Importantly, within this motivational framework, affective reactions vary in hedonic valence (defensive or appetitive), arousal (the intensity of the motivational activation) and direction (promoting approach, avoidance or inactivity). Positive affective states high in arousal are likely to be associated with goal pursuit, while positive affective states low in arousal are more likely after a goal has been achieved [30]. Affective states that vary in motivational valence and intensity have different physiological and behavioral characteristics, and psychophysiological techniques allow investigation of reactions not open to conscious introspection [31,32] and classical modes of neuroimaging, such as fMRI. Considering responses to CT targeted versus non-CT targeted touch within this framework should facilitate multi-method, hypothesis driven approaches to characterizing the neural and autonomic consequences of CT stimulation.

If the CT system plays a specific role in signaling the social affective relevance of touch, CT excitation should activate appetitive motivational reflexes that function to increase attention and facilitate perceptual processing, thereby modulating behavioral responses to concurrently occurring events [27,33]. Thus, it can be hypothesized that, unlike affectively neutral control touch, brief CT-targeted touch will activate the same initial orienting responses seen to other positively valenced stimuli such as imagery [28], sounds [34], or loved faces [35]. This orienting response features an initial parasympathetically-induced heartrate deceleration, followed by a brief acceleration and accompanying increase in sympathetic responses such a pupil size change and skin conductance. Also, as CT stimulation is proposed to act in some circumstances as a stress buffer [36], sustained, mildly positive, low intensity CT-targeted touch might be expected to result in decreased sympathetic activity, and increased parasympathetic dominance, as indicated by measures of vagal tone such as heartrate variability (HRV). As a stimulus with a positive affective value, in comparison to control touch, CT- targeted touch might increase activity in the zygomaticus major ‘smile muscle’ and should decrease activity in the corrugator supercilii ‘frown muscle’.

Psychophysiological measures of stimulus intensity

Following the initial clinical report that brief (~3 second) applications of CT-optimal touch elicited short-lived skin conductance responses (SCRs) [16], further evidence for the predicted sympathetic orienting response was provided by a more recent study demonstrating increased SCRs in response to robotically delivered CT-touch [37]. However, significantly greater sympathetic activation, as evidenced by both larger SCRs [37–39] and greater pupil dilation [39], is consistently elicited to faster, non-CT optimal touch (Figure 1B). As sympathetic activation increases linearly with increasing stimulus intensity, any CT-related sympathetic effects are frequently likely to be overshadowed by orienting to the subjectively more intense Aβ input [39]. Similar relationships between stimulus intensity and sympathetic orienting have been tentatively suggested in orienting responses to valanced odors [40].

Psychophysiological measures of stimulus valence

Unlike skin conductance and pupil dilation measures, which vary in amplitude based on the intensity of a stimulus, cardiac responses differentiate depending on both the valence and the magnitude of an affective cue [28,41]. Thus, while brief exposure to an unpleasant visual image results in a rapid and sustained deceleratory response, viewing pleasant images is associated with a triphasic cardiac waveform. The slower, initial deceleration, which varies in magnitude depending on the perceived intensity of the image, is thought to reflect an initial orienting response. Subsequently there is a brief cardiac acceleration, which is highly consistent across stimuli and hypothesized to reflect semantic encoding or recognition [28], followed by further deceleration.

Fine-grained examinations of the triphasic heartrate response, seen following brief exposure to appetitive sensory stimuli [28] are currently lacking for affective touch. In infants, 10 seconds of CT-optimal touch, as compared to faster and slower, non-CT-optimal touch has been shown to reduce mean heartrate [42]. Behaviorally, there was also evidence that CT-optimal touch generated an orienting response, defined as longer attentional engagement with the brush, than in the faster or slower touch conditions. In adults, greater cardiac deceleration between the first five heartbeats post-touch onset has been reported after robot delivered CT-optimal, versus non-CT-optimal, velocity touch to the forearm [37]. A similar effect was found when the same pairing of speeds was applied manually to the palm [43]. Given here CT-optimal velocity touch to the palm and forearm were perceived as equally pleasant, the cardiac deceleration response may denote orienting to pleasantness rather than reflecting a CT-specific effect. Thus, further studies examining the affective touch evoked cardiac waveform in detail would be insightful (Figure 1C).

Longer-term autonomic responses to CT-targeted touch have also been investigated in infants and adults. Ten minutes of CT-optimal velocity stroking touch decreased preterm infants' heartrate, while the same period of static touch did not. This decrease was sustained over a 10-minute post-touch period [44]. Similarly, when mothers were asked to caress their infant for a 3-minute period, CT-optimal-velocity touch produced increased respiratory sinus arrhythmia, an index of HRV reflecting parasympathetic impact on the heart, which was again sustained into a subsequent post-touch period [45]. Likewise, in adults receiving 35 minutes of CT-optimal touch, HRV increased over time, plateauing at around 20 minutes [46]. No change was seen in the Aβ targeted control condition (Figure 1D). Interestingly, while CT-stimulation increased vagal influence over the heart, subjective ratings of touch pleasantness decreased over the same period, indicating a dissociation between physiological effects and subjective evaluations. Further theoretically grounded investigations of long-term tactile modulation of autonomic state are required in adults.

Facial electromyography (EMG) can be used to differentiate implicit responses to affective stimuli based on valence. It measures small changes in muscle activity that cannot be detected with the naked eye [47]. Processing unpleasant stimuli or events is associated with greater corrugator activity, while processing pleasant images or events is associated with increased zygomatic activity [28]. Several studies have investigated the affective valence of CT-targeted-touch using EMG measurements. Pawling and colleagues [43] found that CT-optimal touch to the volar forearm elicited a stronger but likely sub-perceptual zygomaticus response, compared to non-CT-optimal touch. Interestingly, this automatic facial response not only distinguished between CT-optimal and non-CT optimal velocity stimulation to the forearm, but also between CT-optimal velocity stimulation on the forearm and the palm, even when subjective ratings and heartrate measures failed to. Subsequent studies have however only found evidence in the corrugator for differential activity to CT-optimal and non-CT-optimal touch. In one, corrugator activity decreased during the first 6300ms of CT-optimal touch, whilst it increased to slower non-CT-optimal touch [48]. In another, faster touch resulted in greater corrugator activity, regardless of whether it was applied to the arm or palm [49] (Figure 1E). Interestingly, in both these latter studies the participant's view of the experimenter was occluded, whilst this was not the case in Pawling et al [43], where the participant sat eyes-closed but directly in front of two experimenters, a condition that is likely to induce stronger positively valenced facial responses to sensory stimuli [50]. Unlike the autonomic and somatic responses discussed so far, the magnitude of which reflect motivational engagement, facial responses are thought to be inherently social signals that can be modulated depending on the context [28,51]

Neural markers of valence, arousal and appetitive motivation.

Using EEG, a late positive potential (LPP) over centro-parietal electrodes has been established as a reliable index of the motivational relevance of an environmental stimulus [27]. Depending on stimulus aspects such a modality, this slow positive waveform may be apparent from about 300 msec post stimulus onset and, like skin conductance and pupil size measures, its amplitude varies monotonically with stimulus intensity not valence. However, since the slow conduction velocity of CTs means there is a delay of 500-1000 msec before an impulse reaches cortex, this LPP has not been a focus of CT research. Rather, a putative C-fiber specific ultra-late-potential (ULP) associated with CT-optimal, but not non-CT-optimal velocity input has been identified over mid-frontal electrodes with varying latencies dependent upon whether touch was precisely delivered using a robot or by hand and the duration of the touch [52,53]. Preliminary evidence suggests the amplitude of this response correlates with scores on the Autism Quotient (AQ), a widely used measure of social traits [53]. Thus, there is potential for future studies to investigate modulation of this ULP in tests of the affective touch hypothesis.

An alternative approach has been to explore whether CT-targeted touch modulates ERP responses to concurrently experienced affective stimuli. For example, an initial study exploring what effect CT-targeted touch has on orienting used EEG to investigate whether touch, applied with a brush to either hairy or glabrous skin, modulated perception of social auditory stimuli [54]. CT-optimal velocity touch on the arm but not the palm increased the LPP difference between affective and neutral voices. This differential neural effect was seen in the absence of any subjective differences in perceived touch pleasantness across skin sites, or changes in affective state. The fact the effect was specific to the affective content of the auditory stimuli is consistent with it reflecting a late enhancement of temporally associated socio-affective information.

Also using a within subject design, CT targeted touch, delivered by hand, reduced subjective ratings, plus early and late evoked neural responses to a subsequent noxious, laser evoked pin prick [55]. Interestingly, here participants' subjective ratings of touch pleasantness did not correlate with the magnitude by which their neural response to the noxious stimulus was modulated by touch. Also, although touch was delivered by the participants' romantic partner, who was hidden out of sight, attachment style only affected subjective pain ratings, not magnitude of the laser evoked potential. This suggests that bottom up, rather than top-down mechanisms are primarily at play, consistent with a similar neural modulation of noxious brain response to CT targeted brush stroking reported in new-born infants [56].

Asymmetry in alpha activity within frontal brain areas has been used as an index of affective response to a stimulus, with greater alpha activity in the left compared to the right hemisphere associated with greater positive affect and appetitive motivation [57]. To our knowledge, this has not to date been used to consider responses to CT optimal versus non-CT optimal touch.

Future Directions

If, as the affective touch hypothesis posits, CTs evolved to signal the rewarding value of affiliative tactile interactions, predictions can be made about the emotional and motivational consequences of CT optimal touch that should inform the design of future studies. For example, as an appetitive stimulus signaling comfort and safety, behaviorally CT optimal stimulation should drive inactivity (quiescence) rather than the motor readiness induced by high arousal positive affective states which initiate goal pursuit [30]. Physiologically, as a socially salient positive stimulus, CT optimal touch should produce a triphasic cardiac orienting response distinct from affectively neutral control touch [29]. Cognitively, as an innate safety signal, CT optimal touch, in comparison to affectively neutral control touch, should broaden attentional scope and heighten cognitive flexibility [30]. These hypotheses remain to be tested.

Future psychophysiological investigations might also focus on the notion that in participants reporting high motivation for social contact, CT-touch should theoretically induce larger autonomic and affective responses [28,29], than in those reporting low affiliative motivation, something for which there is some evidence in relation to positive facial expressions [58]. Finally, whilst human or robot delivered CT-touch may be subjectively perceived as equally pleasant [59], work is needed to determine whether implicit psychophysiological responses to CT-touch are influenced by the level of human-human interaction involved in touch delivery.

Conclusion

Recently, a growing body of research has used psychophysiology measures to contrast implicit responses to CT optimal over non-CT optimal touch. Taken together, these studies suggest that although CT-touch may indeed elicit the type of autonomic orienting associated with positive salient stimuli, this response may easily be masked by more intense concurrent input from Aβ-fibers. Tentatively, CT-touch does appear to induce an increase in parasympathetic activity, in line with the notion that it represents a safety-signal or stress buffer, it also appears to induce facial muscle activity associated with an increase in positive and decrease in negative affect. However, more work is needed to determine whether effects are CT-specific or related to any pleasantly perceived tactile stimulation. We propose, by grounding future studies in motivated theories of emotion, specific predictions about the implicit physiological, behavioral, and cognitive consequences of CT stimulation can be tested, facilitating empirical testing of the affective touch hypothesis in humans.

Figure Legend

Figure 1. A schematic comparing the response properties of myelinated Aβ and unmyelinated C-tactile afferents. The relative psychophysiological responses to CT-targeted and Aβ-targeted skin stimulation are also shown. A) While CT firing frequency shows a negative quadratic relationship with stimulus velocity, Aβ firing increases linearly with stimulus velocity. B) Both CT targeted and Aβ targeted touch elicit a robust SCR response, the response to the more intense Aβ targeted stimulation is of higher amplitude. C) CT targeted touch, both brief and prolonged, has been reported to decrease heart rate. However, fine grained analysis of the cardiac orienting response to CT versus Aβ targeted touch has not been conducted. The schematic shows the predicted waveforms based on established responses to appetitive and neutral visual stimuli. D) CT targeted touch has been reported to increase heart rate variability, while Aβ targeted vibrotactile stimulation produced no change in vagal tone. E) With facial EMG, while CT targeted touch has been reported to produce an increase in zygomaticus or decrease in corrugator activity, indicative of a positive affective response, Aβ targeted touch has been reported to increase corrugator activity. Corr. = Corrugator; Freq. = Frequency; µS = microsiemens; Zygo = Zygomaticus

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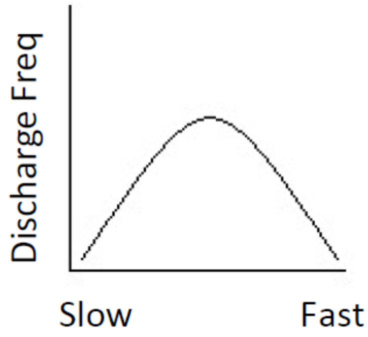
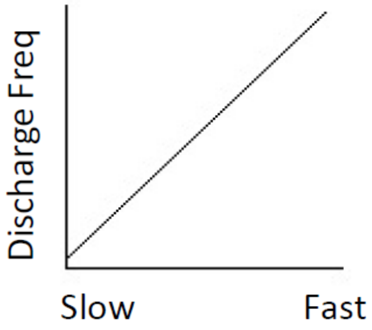
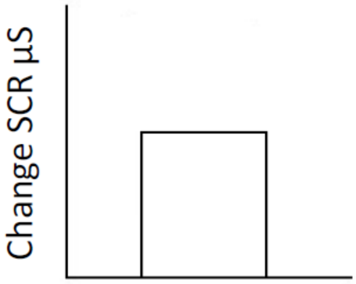
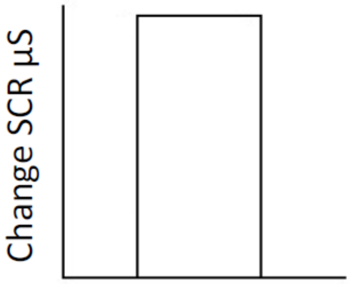
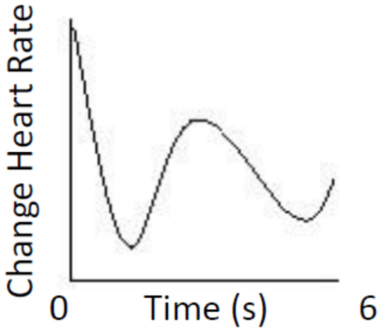
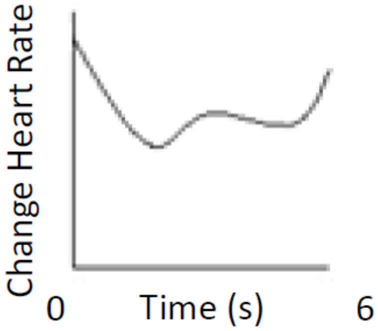
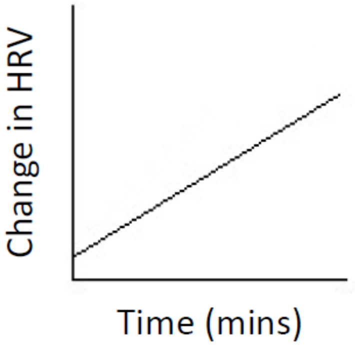
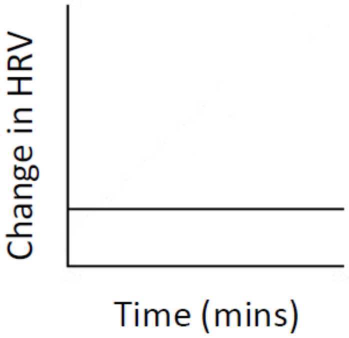
	Unmyelinated CT afferents	**Myelinated Aβ afferents**
A. DISCHARGE FREQUENCY		
	CT TARGETED (1-10 cm/s)	**Aβ TARGETED (e.g. ~ 30cm/s)**
B. SKIN CONDUCTANCE		
C. HEARTRATE (Hypothesized)		
D. HEART RATE VARIABILITY		
E. FACIAL EMG