Chapter 12
CT Afferent-Mediated Affective Touch: Brain Networks and Functional Hypotheses

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Abstract Investigating the role of C-tactile (CT) afferents in affective touch requires exploration of the subcortical and cortical brain regions which receive information from the CT afferent pathway. This chapter summarizes the major known cortical targets and wider networks associated with CT-mediated touch, particularly the posterior insula and parietal operculum. It concludes with an outline of three hypotheses regarding the possible function of CT afferents. A central feature of each is the idea that C mechanoreceptive afferents contribute to physiological regulation, particularly of the sympathetic nervous system, in a manner which can extend to the social domain.

Keywords Neural processing • Affective touch • CT-mediated touch • C-tactile (CT) afferents • Cortical brain • Subcortical brain • Cortical targets

Introduction

Neural processing of affective touch starts in the skin. As evidence presented in other chapters in this volume demonstrates, mechanoreceptive CT afferents contribute to the signaling of light touch, associated with affectively valenced percepts. However, this implies neither that CT afferent signaling directly *codes* such affective qualities of tactile stimulation, nor that affective touch is *limited* to CT signal processing at any level of the nervous system. To explore how CT-mediated touch attains hedonic value, and what role CTs play in such processes, it is important to investigate the neuroanatomical details of higher-level cortical networks. The discussion in this chapter will address this, hinging mainly on a distinction between "cortical targets" and "cortical networks."

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In the following sections, cortical targets are considered as the earliest synapses from thalamic nuclei conveying the signal from the periphery, spinal cord, and brainstem—thus reflecting a high, though not exclusive, specificity for peripheral tactile information. These first cortical synapses are generally third-order neurons from spinothalamic projections. From these cortical targets, subsequent processing of the signal is elaborated in highly interconnected cortical networks, which extend throughout the brain and which are less likely to be domain specific for touch. These networks involve fourth-order connections and beyond. The identification of cortical targets involves tracing a pathway, either physically (by following axons) or functionally (by tracking responses to a stimulus). The identification of cortical networks, on the other hand, involves a less direct, more inferential approach—partly because of their complexity and multidimensionality, and partly because they are less experimentally accessible, especially in humans. Because a cortical target is also part of a cortical network, the distinction between the two is mainly heuristic.

Cortical Targets

One of our best tools for probing both CT cortical targets and networks in the brains of human volunteers is neuroimaging, especially MRI (magnetic resonance imaging). This technique can measure both structural and functional properties of the brain. Structurally, it can provide contrast images between grey matter and other types of brain tissue, such as white matter and cerebrospinal fluid. It can also highlight white matter tracts. Functionally, it provides measurements of regional changes in cerebral blood flow, which indirectly reflect changes in neurovascular regulation as a result of localized neuronal metabolic activity. However, it is important to note that the low temporal resolution of functional MRI (fMRI) makes it impossible to distinguish between early and late processing in the brain—though in some cases it is possible to infer the likelihood that an activation reflects a "cortical target" based on other considerations, such as the anatomical pathways established by research in nonhuman mammals. This section focuses on data obtained by MRI measurements relevant to affective touch in general, and CT stimulation in particular.

On the way to the brain, unmyelinated C afferents (including CTs) synapse in neural populations in the dorsal horn of the spinal cord (e.g., Craig 1995; Andrew 2010; this volume). There is little direct evidence about where CTs might go from there, especially in humans, but it is likely that the CT pathway ascends to the thalamus via the spinothalamic tract (STT; but see Abraira and Ginty 2013; Zimmerman et al. 2014). In contrast, Aβ tactile afferents associated with discriminative function follow a pathway up to the brain via the dorsal column of the spinal cord. These two pathways terminate in relatively distinct sets of thalamic nuclei, which project in turn to relatively distinct sets of cortical regions (Dum et al. 2009; Friedman and Murray 1986). Human neuroimaging cannot shed light on the exact course the CT pathway takes before the level of its thalamic projections, but CT signaling properties and tactile stimulation of hairy skin can be used to probe hemodynamic responses in the brain using functional fMRI.

fMRI gives us a small but growing toolkit for inferences about cortical targets of the CT pathway. First, we can use known CT properties as a "probe" to investigate related hemodynamic responses in the brain. The more we know about CT afferents, the more precisely we can tailor stimulation likely to elicit responses from the cortical targets. For example, we can manipulate the speed of stroking, to which CTs are sensitive (Löken et al. 2009; Björnsdotter, this volume). We can also exploit the differential innervation of hairy and glabrous skin: tactile stimulation of hairy skin activates both CT and Aβ fibers, whereas glabrous (e.g., palm) stimulation activates Aβs only. We can investigate populations with pathologies or disturbances in either their CT or Aβ innervation. We can also focus on experimental manipulations that change the participants' subjective experience or behavior related to affective touch stimulation. Finally, we can mine the existing published reports and apply inferential statistics for the meta-analytical picture across larger data sets.

Each of these approaches has yielded evidence pointing to posterior insula as the prime candidate for a first cortical target of the CT pathway (see also Björnsdotter, this volume). First, posterior insula shows preferential activation to "CT-optimal" stroking speeds of 1–10 cm/s (peaking at about 3 cm/s), compared to "CT-nonoptimal" speeds of 30 cm/s (Morrison et al. 2011a, b) and 0.3 cm/s (Perini et al. 2015), consistent with peripheral afferent response profiles (Löken et al. 2009; Ackerley et al. 2014). Second, comparing arm and palm stroking stimulation reveals partly distinct activations for each, with arm (hairy skin) responses limited to posterior insula (Perini et al. 2015). Third, Aβ-denervated patients with preserved CT afferents show insula activation when stroked on the hairy skin (Olausson et al. 2002, 2010; Cole, this volume), suggesting that CT signals reach this region of cortex in the absence of Aβ-mediated tactile information. In patients with a rare mutation resulting in a selective reduction in C-afferent density, on the other hand, posterior insula shows no modulation by stroking speed (Morrison et al. 2011a, b).

In a recent study investigating stroking preferences and behavior, posterior insula activation increased for stroking speeds that the participants preferred at above-chance levels (Perini et al. 2015). Finally, a recent meta-analysis created a spatial map of brain areas highly likely to be reported as active for pleasant touch in the existing fMRI literature, using activation likelihood estimate (ALE) analysis (Morrison, 2016). The posterior insula showed the highest probability of selective activation by pleasantly rated gentle touch, as opposed to tactile stimulation in the context of detection or discrimination tasks. The weight of the above evidence thus supports the posterior insula as a cortical target for the CT afferent pathway. This is consistent with a proposed pathway for all thin-diameter, unmyelinated C afferents in rodents and nonhuman primates (Craig 2004; see Andrew, this volume).

The posterior insula is activated by a broad range of visceral, somatosensory, and nociceptive stimulation in humans (e.g., Kurth et al. 2010; Segerdahl et al. 2015) and is highly interconnected with parietal sensorimotor cortices (Deen et al. 2011; Cauda et al. 2011; Cerliani et al. 2012). Distinct cytological subdivisions have been identified in insular cortex, with posterior granular areas Ig1 and Ig2 implicated in somatosensory and nociceptive processing (e.g., Kurth et al. 2010; Segerdahl et al. 2015). Granular insular cortex responses to affective touch fall predominantly around the long gyri and within the insular central sulcus (Morrison et al. 2011a).

This region also exhibits distinct somatotopic responses for stroking on the arm and thigh within the range of CT afferents' preferred speed (Björnsdotter et al. 2009, 2010; this volume). The granular region of posterior insular cortex might therefore provide a fundamental, early contribution to such stimulus processing, and may be critical for the efficient integration of affectively relevant somatosensory information (Lovero et al. 2009; Lucas et al. 2014; Perini et al. 2015).

Apart from the posterior insula, there are also parallel or minor cortical targets for affective touch. These may receive a proportionally smaller or less selective contribution of input from the CT-spinothalamic pathway than posterior insula, but could likewise reflect early projections to cortex. One such region may be the secondary somatosensory (SII) cortices on the parietal operculum. These can be regarded as cortical targets by virtue of major input from the STT via anatomical projections from ventroposterior inferior (VPI) nucleus, and minor input from the posterior-suprageniculate complex (Po-Sg; of which posterior ventromedial nucleus, VMpo, is considered a part; but see Willis et al. 2002, Graziano and Jones 2004). In the macaque monkey, parietal opercular cortex receives 29 % of STT inputs, in second place behind granular posterior insular areas which receive 41 % (Dum et al. 2009). In contrast, primary somatosensory cortex (SI) receives 4 % of the projections from STT. The parietal opercular regions most relevant for affective touch are discussed further in following section.

Cortical Networks

So far, then, granular posterior insula is the region most likely to be selectively activated by affective touch in fMRI studies and is anatomically well-situated to be a cortical target for a CT afferent pathway. However, it is improbable that activation of posterior insula singlehandedly exhausts any hedonic content of affective touch. For example, its selectivity for stroking speed outweighed pleasantness differences between soft- and coarse-haired brushes (Morrison et al. 2011a), and its activity consistently fails to correlate with subjective ratings (e.g., Morrison et al. 2011a; Ebisch et al. 2011; Perini et al. 2015). Despite this, posterior insula is doubtless a robust participant in a brain-wide network of different areas specializing in various aspects of tactile and affective processing. Specific relationships among such nodes in a wider network have not yet been experimentally tested, but several candidates have been identified as consistently implicated in affective touch processing.

As mentioned in the foregoing section, parietal opercular somatosensory areas may be parallel or minor cortical targets of the CT-spinothalamic pathway, alongside posterior insula (Fig. 12.1). Alternatively—or additionally—these regions may form part of a wider network that contributes to the processing of gentle, dynamic touch by virtue of its direct corticocortical connections (Friedman et al. 1986; zu Eulenburg et al. 2013; Ebisch et al. 2011; Morrison et al. 2010; Wei and Bao 2013). In fact, the term "operculo-insular cortex" has been used to capture the functional similarity among these areas. Yet although these insular and opercular

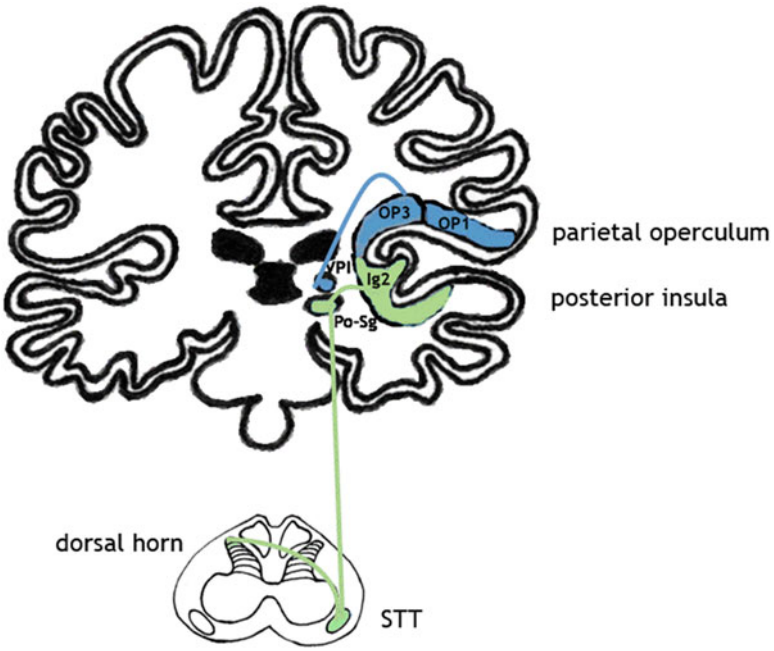

Fig. 12.1 Cortical targets of the CT-spinothalamic pathway. Schematic coronal section of the human brain showing pathway from the dorsal horn of the spinal cord, continuing to thalamic nuclei via the spinothalamic tract (STT), and onward to posterior insular and parietal opercular cortices. *Green* indicates the predominant STT projections to posterior insula via posterior suprageniculate complex (Po-Sg). *Blue* indicates the predominant STT projections to parietal opercular areas OP1 and OP3 via ventroposterior inferior nucleus (VPI). *Note*: *for simplicity of illustration*, *OP1 and OP3 are pictured in the same plane*, *though OP1 lies posterior to OP3 on the human parietal operculum*. For a discussion of the cortical networks in which these targets participate, see the section "Cortical networks"

areas are closely adjacent and highly interconnected—as well as being frequently interchangeably labeled—their receptive fields and cytological characteristics are distinct (Evrard et al. 2014).

Like granular insular cortex, primate opercular somatosensory areas have cytoarchitectonic subregions (Krubitzer and Kaas 1992). Within the parietal operculum, four relatively distinct somatosensory regions have been probabilistically mapped, using evidence from histologically stained postmortem human brains, alongside functional imaging evidence (Eickhoff et al. 2006; Baumgärtner et al. 2010; Kurth et al. 2010). The subregions OP1 and OP3 are particularly relevant here because they are commonly activated across both affective touch paradigms as well as in tasks which involve tactile stimulus detection and/or discrimination (Morrison).

Region OP1 lies posterior to OP3 and is the likely human homologue of "classical" secondary somatosensory (SII) cortex in the monkey (Eickhoff et al. 2006). OP1 responds to noxious tactile stimuli as well as tactile, nociceptive, and vestibular stimulation (zu Eulenburg et al. 2013). OP3 lies deeper in the Sylvian fissure and is

the likely homologue of the primate "ventral somatosensory" area VS, which is not functionally well-characterized (Eickhoff et al. 2006; Krubitzer and Kaas 1992). In nonhuman primates such as the macaque (*Macaca mulatta*) and the marmoset (*Callithrix jacchus*), both SII and PV receive major projections from VPI (Qi et al. 2002), whereas this is not clearly the case for VS. It has been speculated that thalamic inputs to S2 and PV are modulatory rather than relaying strictly sensory response properties (Krubitzer and Kaas 1992; Qi et al. 2002).

Primary somatosensory (SI) areas associated with the discriminative aspect of touch may also contribute to the processing of affective or social touch stimuli in humans. Although the CT pathway may privilege certain information based on specific ranges of speed (Löken et al. 2009) and temperature (Ackerley et al. 2014) variables, any tactile stimulation anywhere on the body will also activate the large myelinated Aβ afferents that project predominantly to somatosensory cortices. The potential involvement of SI is suggested by its ability to use visual cues to distinguish between videos of male and female strokers during tactile stimulation of the leg (Gazzola et al. 2012). Similarly, transcranial magnetic stimulation (TMS) over right SI selectively slowed reaction times on a go–no go task following affective touch (Bolognini et al. 2011). SI has also been activated alongside SII and posterior insula for palm (glabrous skin) stroking, whereas arm (hairy skin) stroking was limited to posterior insula (Perini et al. 2015; see also McGlone et al. 2012). Together with the palm-specific activation in SI, this incomplete overlap between arm and palm stroking activation suggests a general bias toward hairy skin (CT+Aβ input) in posterior insula and a bias toward glabrous skin (Aβ input) in somatosensory cortices.

Other areas implicated in affective touch networks include the superior temporal gyrus and sulcus (STG and STS; Gordon et al. 2011; Bennett et al. 2014). Neurotypical individuals who nonetheless score high on some measures associated with autism spectrum disorder (ASD) show reduced activation in STS during skin stroking (Voos et al. 2013), as do children and adolescents diagnosed with ASD (Kaiser et al. 2015). The role of superior temporal areas may lie in the integration of tactile information with sensory and spatial information from other modalities. A role in processing socially relevant stimuli was first revealed by neurons in the macaque STS, which responded to the eye gaze direction of other primates, especially in conjunction with congruent head orientation (Perrett et al. 1985). This area is also involved in processing convergent auditory and visual facial information (Ghazanfar et al. 2008). In addition to an involvement in processing movement-direction information and in polymodal integration (Beauchamp et al. 2008), STS/STG plays a role in sensory imagery (Berger and Ehrsson 2014). These functional properties are consistent with the fact that during a standard fMRI experiment, participants can feel but not see the tactile stimulation. STS may thus contribute to structuring a coherent representation of the touch by working to "fill in" missing visual and spatial information via imagery (e.g., Kilintari et al. 2014).

Since CT-associated touch can be experienced as pleasant, it may have intrinsic reward value. That is, people might not only *like* social touch but *want* it for its own sake, resulting in active seeking behavior (Berridge and Robinson 2003). Perini et al. (2015) used a feedback-based experimental paradigm in which the subjects

could determine which stroking speed they would receive in a given trial. The speeds that subjects preferred and actively sought above chance level were CT-optimal speeds, which activated both posterior insula and dorsolateral prefrontal cortex. The idea that affective touch networks interact with reward- and decision-related networks is consistent with several findings that implicate orbitofrontal cortex in affective touch processing (Francis et al. 1999; Disbrow et al. 2000; Rolls et al. 2003; McCabe et al. 2008; McGlone et al. 2014). The orbitofrontal cortex is associated with reward-related behavior (Rolls and Grabenhorst 2008; Padoa-Schioppa and Cai 2011) and may work together with posterior insula to evaluate affective touch in ways that guide such behavior. Studies involving tactile massage have implicated another important limbic region, the perigenual ACC, associated with emotional processing (Lindgren et al. 2012; Sliz et al. 2012).

Hypotheses of Role and Origin

Presumably, the wider function of CT signaling is not merely to indicate the presence of a certain stimulus type (for example, "warmish, medium-speed movement"), but to enable certain behaviors instigated by that stimulus. Such processes must take place at the level of cortical networks simply because this is where integration of tactile information with crucial higher-level factors—such as memory, context, and intention—occurs. Integration at this level underpins the complex affective dispositions which translate into behavior. This section therefore discusses and evaluates three hypotheses regarding wider functional roles for the CT pathway. Each revolves around the distinct physiological and functional properties of the afferent pathways followed by CTs, and each is likely to enlist cortical-level integration of various types of information. These hypotheses are (1) the "social touch" hypothesis, (2) the related "interoceptive" hypothesis, and (3) the "thermoregulatory" hypothesis.

These hypotheses have arisen because the functional neuroanatomy of CT-mediated touch invites conjecture as to its wider evolutionary role, and even its origin, in mammalian species. This necessarily involves a degree of speculation, and it is worth emphasizing that direct empirical tests of these hypotheses are lacking. However, they do tend to orbit around a distinct cluster of plausible and testable ideas. The most salient of these is efferent *regulation*, especially brain-level regulation of bodily processes (e.g., cardiac, respiratory, visceral, etc). More specifically, hypotheses of CT function postulate that CTs are part of a segregated afferent–efferent pathway influencing physiological regulation in the face of external perturbation. An implication of this view is that such regulatory mechanisms can extend beyond the individual organism to include social interactions.

The central pillar of the "social touch" hypothesis is the idea that affective touch operates mainly in the domain of social interactions and has an impact on behavior (Olausson et al. 2010; Morrison et al. 2010; McGlone et al. 2014). It proposes that human touch is a specific, distinct category of tactile experience that is inherently hedonic and rewarding, with possible functional roles in fostering and maintaining

social relationships. Such affective touch may thus constitute a domain of touch that draws on a qualitatively different category of information than that coded by Aβ afferents. This may even involve specialized functional organization in both the periphery and the central nervous system.

CT response properties appear to square very nicely with the proposition that they are tuned to stimulus features that typically occur in social interactions, such as caressing. First, the intermediate, caress-like speeds that give rise to the highest mean CT firing frequency are the most hedonically potent (Löken et al. 2009). Second, more recent findings suggest that the unique profile of CT responses to different stroking speeds can interact with temperature (Ackerley et al. 2014). Namely, their mean firing increases most to 3 cm/s stroking by a skin-temperature (32 °C) probe, compared to stroking at other speeds and by warmer or colder probes. This suggests that CT afferents prefer caress-speed stroking at a "creature" temperature, which is also rated as most pleasant. Less directly, the slow conduction velocity of CTs (around 1 m/s) and their diffuse perceptual correlates (e.g., Olausson et al. 2002) point away from a role in fast, high-acuity discriminative processing. On the "social touch" view, signaling in the CT afferent pathway flags tactile stimulation that is likely to signal close, affiliative body contact with others, making it available for further affective evaluation in the brain networks discussed in foregoing sections.

The "interoception" hypothesis dovetails with the social touch hypothesis, but places its emphasis on the physiological effects of affective touch on bodily processes. Historically, the classical view of interoception hinged on a distinction between "interoceptive" tissues within the body, for example, those involving visceral innervation, and "exteroceptive" tissues on the body surface, such as those involving cutaneous innervation. This view has recently undergone a paradigm shift away from a literal "in–out" distinction in favor of one based more on the physiological properties of the relevant nerve pathways. The currently prevailing view of interoception involves the coding and perception of physiological state changes in body tissues (Craig 2002; Migliorini et al. 2013). Craig has redefined interoceptive pathways as those of unmyelinated and thinly myelinated afferents synapsing in lamina I of the dorsal horn and ascending via the STT to medial thalamic nuclei (Craig 2003, 2009; see also Andrew, this volume). In this respect, CTs have more in common with "interoceptive" pathways, both physiologically and functionally, than "exteroceptive" tactile pathways, despite innervating the skin (Björnsdotter et al. 2010, see also Björnsdotter, this volume).

Importantly, Craig classed this pathway as an "afferent limb" of the sympathetic nervous system (Craig 2003). This implies a relationship with efferent autonomic regulation of bodily states via sympathetic and parasympathetic channels, for example, those which influence heartbeat, breathing, and muscle readiness (e.g., Seth and Critchley 2013). However, any such physiological relationships need to be further illuminated by experimental findings, especially in the case of CT-mediated touch in humans. Nonetheless, the plausible idea that small-diameter afferent traffic influences sympathetic outflow can be viewed from the perspective of homeostatic regulation. Homeostasis refers to a set of regulatory processes that defend a system from

deviations from a certain set point. The classic analogy for this is a thermostat, which turns on only when the ambient temperature falls outside a fixed limit.

But the problem with this is that very few complex regulatory loops are likely to involve a thermostat-like set point (Schulkin 2011). Moreover, multiple regulatory systems must operate together throughout the body to achieve and maintain a stable overall dynamic. To complicate matters further, many of these regulatory processes act in an anticipatory manner, especially those which rely on cortically mediated predictions involving context, memory, conditional learning, and so forth. A more accommodating model, then, is "allostasis" (e.g., Sterling 2012; Schulkin 2011). In contrast to strictly homeostatic models, allostatic models emphasize the requirement for energy efficiency in the operation of regulatory systems, and supply a role for predictive modulation as well as flexible input–output ranges among multiple interacting systems. Here, stable dynamics reflect optimized balances among energetic costs, not necessarily defense against deviations from a given set point. This allostatic view has generated a specific model of "interoceptive inference" implicating anterior insular cortex (Seth 2013).

A third, "thermoregulatory," hypothesis is proposed here (see also Morrison, in press). Its focal point is the somatosensory correlates of warmth-seeking behavior in mammals. The thermoregulatory hypothesis does not assume that affective, social touch confers survival benefits that have been directly selected for in our phylogenetic past. Rather, it postulates that CT coding may be an outcome (or "exaptation," Gould and Vrba 1982) of thermoregulatory-related traits that have themselves been more directly shaped by selection pressures. In this scenario, the present functions of mechanoreceptive C afferents have been scaffolded in phylogenetic history by thermosensitive C-mediated mechanisms of thermoregulatory behavior in young mammals, in the context of huddling (e.g., in litters) and counterparts to huddling in dyadic interactions (e.g., parent–offspring "snuggling").

Cold-sensitive subtypes of cutaneous C afferents signal decreases in temperature. This signaling can ultimately result in shivering or nonshivering thermogenesis, or changes in behavior to seek external heat sources. For example, in newborn mammals, nonshivering thermogenesis is mediated by sympathetic vagal efferents which can instigate the burning of brown adipose fat (BAT; Ryu et al. 2015). Though the physiology is less well understood, skin temperature decreases can also drive huddling behavior, a means of social thermoregulation that allows reduction of heat loss as well as lowering energetic metabolic costs of endothermoregulation (Gilbert et al. 2012; Morrison et al. 2008). Huddling in newborn porcupines (*Hystrix africaeaustralis*), for example, lowers the critical temperature at which they can effectively thermoregulate by endogenous means (Haim et al. 1992). Importantly, these decreases enable gains in energy allocation for other important processes, such as growth and repair (vital from an allostatic perspective, as discussed above).

Huddling involves active behavior to maximize its effects, which results in continual movement patterns as individuals nuzzle their way to the center, displacing and being displaced by littermates (Gilbert et al. 2012). It also generates predictable, stable signatures of somatosensory stimulation on hairy skin surfaces: gentle, moving

touch at skin temperature. This opens up an opportunity for mechanoreceptive coding to stand in for thermoreceptive coding in the allostatic regulatory loops, perhaps especially those most relevant to the efficient driving of specific, proximity-seeking behaviors. This is evolutionarily plausible because cutaneous sensory afferents show relatively wide scope for adjusting molecular receptor profiles according to species-level environmental pressures (Gracheva and Bagriantsev 2015). Both in development and phylogeny, genetic regulatory mechanisms determine specific response profiles of C afferent subtypes by differential expression of receptor channels (Lou et al. 2015; Ma 2010, 2012). Such genetic regulation could produce tuning shifts in afferent phenotype and function without requiring large genetic changes. Thus turning "on" or "off" the expression of certain receptor channels (such as MrgprB4; Lou et al. 2015) could result in modality-selective sensory neurons, or even response properties signaling in a combinatorial fashion with other subtypes (Lou et al. 2015; Ma 2010, 2012; Prescott et al. 2014). Importantly, such shifts could also provide energy efficiency gains in allostatic terms, potentially making tactile input energetically "cheaper" than thermoregulatory processing in this context. Via such phylogenetic and developmental mechanisms, the stable temporal coincidence of somatosensory and thermosensory processing in young mammals might thus favor a shift from a general thermoregulatory function to one more tuned to somatosensory aspects of close social contact. This in turn would create a platform for wider possibilities in the domain of social interaction.

Whatever the phylogenetic relationship between C afferent subtypes, though, both thermosensation and somatosensation during close proximity essentially signals that the organism is in a "safety zone." On this basis, these sensory processes can ultimately serve to signal other benefits of social proximity beyond the thermoregulatory realm, such as reduced risk for predation exposure. Social touch then becomes a parsimonious way to sound the "all clear" to the central nervous system with respect to metabolically expensive sympathetic arousal (see also Porges 2007). Conversely, it provides the neural means by which acute stress or anxiety can trigger a motivation to seek proximity in order to dampen arousal, just as being cold can drive behavior to huddle close to others to restore warmth. There is growing evidence that social and C-mechanoreceptor-mediated touch can buffer autonomic and behavioral signs of stress and anxiety (Coan et al. 2006; Vrontou et al. 2013; Schirmer et al. 2013). In this way, thin-fiber-mediated systems may have expanded into further aspects of social interaction and its multiple benefits in social animals.

The ultimate outcome of the "social touch," "interoceptive," and "thermoregulatory" scenarios of CT function is that social factors and events become incorporated into systems for physiological regulation of individual bodily economy. This is brokered by the brain's generation of motivated, adaptive behavioral changes. Future research will follow these various leads to arrive at more direct tests of CT afferent function (Fig. 12.2). In the end, these leads are likely to take us from the body to the brain, and back again.

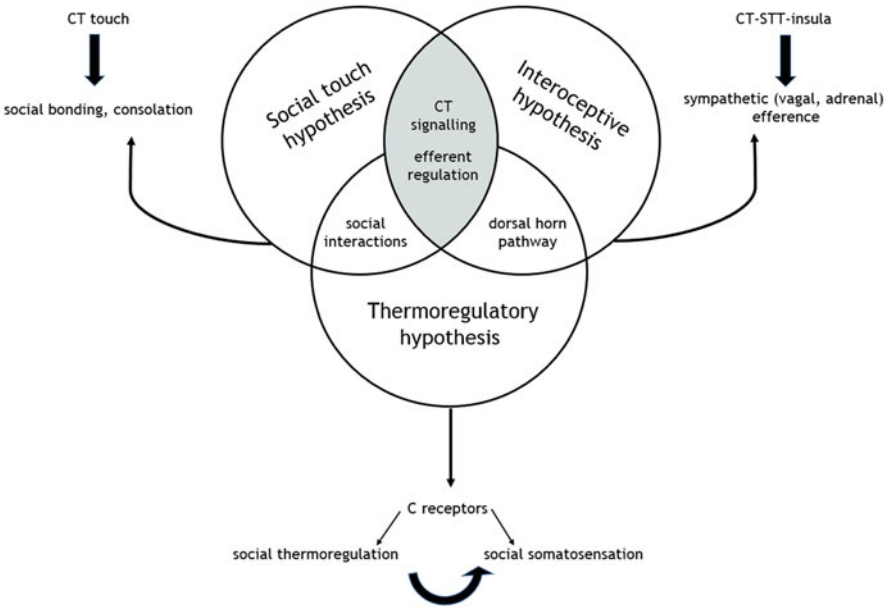

Fig. 12.2 Three hypotheses of CT afferent function. *Left top circle*: the "social touch hypothesis" postulates a relationship between CT-mediated touch and roles in interpersonal bonding, consolation, and other social phenomena (e.g., Morrison et al. 2010; McGlone et al. 2014). *Right top circle*: the "interoceptive hypothesis" postulates a physiological influence of CT afferents on physiological regulation via relationships between STT pathways and the sympathetic nervous system (e.g., Craig 2003). *Bottom circle*: the "thermoregulatory hypothesis" (proposed in this chapter) raises the possibility that a role for C-afferent-mediated circuits in social thermoregulatory behavior (e.g., huddling) may have scaffolded a role for mechanoreceptive C-afferent-mediated circuits in social tactile interactions, via changes in C receptor profiles. These three hypothesis variously share the general features of CT signaling and efferent regulation (*shaded area*), as well as dorsal horn pathways and social interactions

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