Preface

The term "somatosensory system" covers the wide array of specialized receptors, peripheral nerves, and central processing stages underlying the transduction and processing of somatosensory signals. Collectively, these are engaged in sensing, perceiving, and acting—upon stimulation of the body surface or during muscle activity. Cutaneous (skin) sensations are essentially multimodal and are classically described as the senses of touch, temperature, itch, and pain. Afferent types belonging to the class of small-diameter, unmyelinated C fibers have been implicated in each of these functions. Yet so far, the functional neurophysiology and contribution of non-nociceptive mechanoreceptive C afferents to somatosensory signaling have not been researched comprehensively. This volume, therefore, represents an effort to encompass the breadth and depth of our current knowledge of the physiology and function of C-tactile (CT) afferents (or C low-threshold mechanoreceptors, CLTMs). The focus of the chapters ranges from the skin to the brain and from behavior to psychology. The chapters also identify the issues that need to be resolved and point the way toward the future of research in this relatively young, but growing, field of inquiry. This book thus offers the bulk of currently available evidence, knowledge, and insight on CT afferent physiology.

The first eight chapters deal with *Peripheral Low-Threshold Mechanoreceptors and Psychophysical Observations* and provide the essential backdrop for CT neurophysiology: the afferent receptors and nerves in the skin and their sensory and perceptual impact. In their chapter, Åke Vallbo et al. outline the history of the discovery of C-mechanosensitive afferents, which began with Yngve Zotterman's observations in cats in the 1930s. These experiments were the first to identify C low-threshold mechanoreceptors (CLTMs). Vallbo et al. highlight the importance of the microneurography technique in the development of single-unit afferent recordings in healthy humans, which ultimately led to the discovery of CTs in the late 1980s and early 1990s. Until then, CLTMs had been characterized in experimental mammals without much overriding concern about how to interpret their general function. As Vallbo's chapter points out, Zotterman's original speculation that CTs may be involved in tickle sensations is generally regarded as an insufficient proposition for CT function, not well-supported by subsequent evidence. However, more recent

evidence has raised this possibility again (Fukuoka et al. 2013). While the discovery in humans might have surprised some who considered CLTMs to be a phylogenetically older afferent type, which was also expected to be absent in humans, it also prompted the need to build a stronger interpretive framework for the growing body of observations, allowing more directed experimentation. As Vallbo describes, the currently prevailing framework puts CTs at the center of a "second system" of tactile transduction which ultimately plays roles in emotionally and socially relevant touch interactions between individuals.

The chapters by Pitcher et al., Seal and Lumpkin, Donadio, and Vrontou summarize evidence, primarily from animal research, characterizing the functional properties of CLTMs from a neurophysiological and molecular neurobiological basis. The translational power of this approach is yet to be realized with respect to CTs (the human equivalent of CLTMs), and it seems likely that there are at least two groups of CLTMs that differ in membrane properties such as receptor expression. There may also be subgroups of CT afferents waiting to be discovered, as has proved to be the case with C-nociceptors. The chapter by Ackerley et al. provides background on the theoretical issues raised by the central idea of a "second system" for tactile information processing, in particular the contrast between CT's proposed role in "affective touch" as opposed to "discriminative touch." Norrsell's chapter rounds off the peripheral physiology perspective with a historical overview that encompasses the neuroscience and psychophysics approaches that have been brought to bear on CT research. This section closes with Guest and Essick bringing us up to date with more current psychophysical approaches to understanding the complexity of human touch and in particular the separate function of active touch with the hands compared with affective touch from the body.

Chapters 9–13 deal with *Central Processing of Low-Threshold Mechanoreceptor Input* and follow the CT afferent from the skin to the spinal cord and onward to the cortex of the brain. Andrew and Craig's chapter summarizes evidence that CLTM afferents project to the dorsal horn of the spinal cord in mammals in anatomical association with other classes of thinly myelinated and unmyelinated afferents, reinforcing their function within an interoceptive network. This anatomical, and thereby functional, separation of CTs from A-LTMs is further underscored by human patient evidence, summarized in the chapter by Cole et al., where patients with a complete loss of A-LTMs, but survival of CTs, provide further evidence for an affective touch system in human skin. The chapters by Björnsdotter and Morrison present evidence of cortical projections to insular cortex and wider cortical networks that process CT input. It is here we begin to see how CTs may be well positioned to play a fundamental role in social behavior. Finally, the chapter by Rolls provides further supporting evidence for reward-associated and top-down properties of CT function with respect to representations in the orbitofrontal cortex, relevant to both observed and received touch.

The "social touch" hypothesis described by Vallbo and others comes into its own in chaps. 14–19, *Low-Threshold Mechanoreceptor Signaling in Social and Sexual Behavior.* Gallace and Spence's chapter discusses evidence from cognitive psychology and social psychology, supporting the view that touch plays a central role in

human social interactions, with a specific link to affective touch and well-being. This theme is picked up in McGlone et al.'s chapter which focuses on a more neuroethological approach to grooming behaviors. Here, a case is made for CTs providing the necessary reward valence to promote grooming and nurturing touch, which in human primates sees its expression in sustaining a global cosmetic industry. The chapter by Löseth and Leknes explores the neurochemistry of social touch, in particular how the brain's mu-opioid signaling is mediated by touch to give rise to specific behaviors in social situations. Schirmer et al.'s chapter takes the so-called "Midas touch" effect—the contribution of touch to positive feelings and prosocial behaviors—as its starting point. They explore the consequences and potential mechanisms underlying casual forms of touch, such as those occurring in many social situations, where they can induce a positive effect on the recipients of such touches. Giorgiadis and Kringelbach's chapter looks at the influences of pleasant touch from a sexual intercourse perspective, making a case for genital touch to act as a "proximal master" in the perception of pleasurable sexual touch. The section ends with Fulkerson offering a critical philosophical examination of recent discourse on affective touch, in which a note of caution is sounded about the types of inferences we can draw about CT function, as well as to what extent, and how, affective touch can be regarded as a natural kind of touch distinct from other kinds.

Chapters 20–24, *Clinical Implications of Low-Threshold Mechanoreceptor Signaling*, presents several chapters that focus on patient populations and therapeutic approaches involving CT afferents and affective touch. In one way or another, the chapters in this section all explore the wider clinical implications of the "social touch" framework—as well as circumstances under which CT-mediated touch may interact with nociceptive signaling. CT-mediated touch may be relevant in specific disorders, such as chronic pain, psychiatric disorders, and developmental disorders such as autism spectrum disorders (ASD). Thompson's chapter makes a case for a more concerted effort in recognizing the potential for affective touch to be deployed in clinical contexts by building an argument with the recent advances in our understanding of the functional properties of CTs. Gentsch et al., also focusing on interpersonal touch, make a case for how affective touch shapes our sense of self and impacts fundamental aspects of body awareness, such as embodiment. Field's chapter reviews the multiple effects of massage therapies that specifically use gentle touch, describing evidence of how such touch affects weight gain in preterm infants; meanwhile, gentle touch may also have positive effects on depression in adults. Cascio's chapter provides an overview of the role of touch in ASD and other closely related disorders, such as obsessive-compulsive disorder, for which there is a growing body of evidence that such conditions may have their genesis in a developmental failure of the CT system—peripherally and/or centrally. The final chapter by Liljencrantz et al. explores the possible mechanisms of CT-mediated effects on pain in human experimental models of tactile allodynia. This provides an important departure from the emphasis on CTs as pleasure related and raises critical questions about the potential role of CTs in modulatory interactions with other afferent types.

The various discourses on CLTM/CT affective touch nerves and their central projections described in this book serve to demonstrate that the sensory modality we

call “touch” is far richer than a solely mechanical detection sense. It has been long recognized by somatosensory researchers that discrimination is a fundamental property of tactile sensing. However, a sensory system for affective touch is an often-overlooked submodality that we need to include when talking about the skin senses. We now need to incorporate and recognize the central role of affective touch in human emotion. Affective touch is typically associated with slowly moving, low-force mechanical stimulation of the skin and often gives rise to pleasant sensations. As evidenced in this book, cutaneous unmyelinated low-threshold (C-tactile, CT) afferents seem to be particularly important for affective touch behavior and perception. Operating alongside the fast myelinated detection system, there is the slow CLTM/CT system that predominately projects not to primary somatosensory cortices but instead to the posterior insular cortex—part of the limbic system and a first step in the processing of “feelings” in orbitofrontal cortical areas. Gentle touch reduces stress and lowers blood pressure; it elevates pain thresholds, increases tips if you are a waiter (Crusco 1984), can communicate up to eight emotions (Hertenstein et al. 2009), is of fundamental importance in sexual and nurturing behavior, and shapes the destiny of the social brain. Although there are still enormous gaps in our knowledge of the mechanisms by which the rewarding nature of affective touch is encoded and processed, we hope this collection of papers will provide an overview of the current understanding of this novel class of cutaneous low-threshold C-mechanoreceptive afferents.

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