SOMESTHESIS

James C. Craig

Department of Psychology, Indiana University, Bloomington, Indiana 47405;
e-mail:Craigj@indiana.edu

Gary B. Rollman

Department of Psychology, University of Western Ontario, London, Ontario, N6A
5C2, Canada; e-mail: Rollman@julian.uwo.ca

Abstract

In this review we focus on the perceptual and psychophysical aspects of som-
esthesis, although some information on neurophysiological aspects will be
included as well; we look primarily at studies that have appeared since 1988.
In the section on touch, we cover peripheral sensory mechanisms and several
topics related to spatial and temporal pattern perception, specifically meas-
ures of spatial sensitivity, texture perception with particular emphasis on
perceived roughness, complex spatial-temporal patterns, and the use of
touch as a possible channel of communication. Other topics under this sec-
tion include the effects of attention on processing tactile stimuli, cortical
mechanisms, and the effects of aging on sensitivity. We also deal with ther-
mal sensitivity and some aspects of haptics and kinesthesis. In the section on
pain, we review work on the gate-control theory, sensory fibers, and higher
neural organization. In addition, studies on central neurochemical effects
and psychophysics of pain are examined.

CONTENTS

INTRODUCTION

Workers in somesthesis have often complained of the difficulty of conveying to others the importance of the sense of touch and position. For vision and audition, one can imagine being deprived of sight or hearing, and there are, of course, blind and profoundly deaf individuals who can help us understand the nature of their experiences. A head cold lets us know the information derived from olfaction, but what would it be like to be without somesthesis? In May 1971, Ian Waterman lost all sensation of light touch and kinesthesis below his neck. The probable cause was a viral infection that destroyed the functioning of the large-diameter, peripheral fibers. The book *Pride and a Daily Marathon* (Cole 1995), a popular scientific account of Mr. Waterman's experiences, provides a description of what it is like to lose the sense of touch and position. Mr. Waterman must monitor all movements visually. If the lights go out unexpectedly, he falls down. He still has temperature sensitivity and experiences pain (cf large-diameter) consistent with neurophysiological evidence of the involvement of small diameter fibers in these modalities. The book allows readers to appreciate the importance of somesthesis and the extraordinary lengths to which a person must go to cope with its loss. With regard to the personal experience of pain, a compelling account of a battle with spinal cancer by the acclaimed novelist and poet Reynolds Price (1994) provides valuable insights into the many ways in which pain affects the patient and the enormous psychological challenges that accompany physical afflictions.

Studies of the perceptual aspects of somesthesis have benefitted from a long association with parallel neurophysiological experiments. It has been possible to use the same stimuli with both human subjects (psychophysics) and awake monkeys (neurophysiology). The connection between perceptual and neurophysiological responses is even closer in experiments using percutaneous recording techniques (microneurography) wherein human subjects have microelectrodes inserted into their hands and forearms to permit recordings from single, first-order afferents. Subjects report the sensations elicited by stimuli applied to the receptive field of neurons at the same time the activity in these single units is recorded. Human perceptual responses can also be correlated with records of cortical activity obtained using noninvasive electrophysiological or imaging techniques.

TOUCH

Peripheral Afferents and Mechanoreception

Studies on glabrous (hairless) skin of the hand support the view that there are four different types of mechanoreceptive afferents. These afferents are characterized by the size of their receptive fields, large vs small, and by the rate at which they adapt to a sustained indentation, slowly vs rapidly, resulting in a two-by-two classification system. There are afferents that are slowly adapting, with small receptive fields, SAIs; slowly adapting, large receptive fields, SAIIs; rapidly adapting, small receptive fields, RAs [also known as FAIs (fast adapting)]; and rapidly adapting with large receptive fields. These latter fibers are associated with Pacinian corpuscles and are thus known as PCs (or FAIIs). Some areas of the body, such as the perioral region, may lack Pacinian corpuscles (Hollins et al 1991). A four-channel model of mechanoreception has been developed based on correlations with the likely afferents. A summary of much information about these channels can be found in several sources (Table 2.2, Cholewiak & Collins 1991; Table 2, Greenspan & Bolanowski 1996; see also Greenspan & LaMotte 1993). Work on both the psychophysical and the physiological bases of mechanoreception has recently been reviewed (Greenspan & Bolanowski 1996). The four-channel model of mechanoreception maintains that tactile experience results from combined neural activity in the various mechanoreceptive channels (Bolanowski 1996, Bolanowski et al 1988).

There remain psychophysical results that are not easily explained by the properties of the first-order afferents and the four-channel model. For example, accuracy in localizing stimuli that should activate afferents with large receptive fields (Pacinian corpuscles) may be nearly as good as that in localizing stimuli that should activate afferents with small receptive fields (Sherrick et al 1990). Mechanoreceptive afferents have also been examined in hairy skin (Edin et al 1995), where the number and nature of the receptors are less clear (Greenspan & Bolanowski 1996, Vallbo et al 1994), as is the number of channels (Bolanowski et al 1994).

Spatial and Temporal Patterns

SPATIAL SENSITIVITY   Interest continues in developing and evaluating measures of spatial acuity. There has been a long history of criticism of the two-point threshold as a measure of resolution on the skin. Perhaps like bad theories, suspect measures are driven out not by data, but by better measures. Johnson et al (1994) discuss many of the criticisms of the two-point threshold, chief among them the problem of maintaining a stable criterion for responding "one" or "two." They offer support for a different measure, grating orientation.

In this technique, square-wave gratings are presented to the skin in one of two orthogonal spatial orientations. The subject's task is to indicate the orientation. Performance varies as a function of the width of the grooves (Craig & Kisner 1998; Patel et al 1997; Van Boven & Johnson 1994a,b). The measure shows promise in neurological testing (Van Boven & Johnson 1994a). A second promising approach requires subjects to detect the presence of a gap in an otherwise smooth edge (Stevens & Choo 1996, Stevens & Patterson 1995). Both measures benefit from being able to be tested in a forced-choice procedure. Essick (1992) and Greenspan & LaMotte (1993) discuss measures of spatial acuity and other measures of tactile sensitivity that might be used in a clinical setting.

Sensitivity to spatial features such as curvature, local shape, and orientation of small objects has also been examined in psychophysical and neurophysiological studies (Goodwin et al 1996; Goodwin & Wheat 1992; LaMotte & Srinivasan 1993, 1996; LaMotte et al 1996). In general, it appears that the responses of SAIs are important for encoding these spatial features, with a possible contribution of RAs (Greenspan & Bolanowski 1996).

TEXTURE   The perception of surface texture includes attributes such as roughness, hardness-softness, elasticity, and viscosity (Loomis & Lederman 1986). Work on various aspects of texture, including roughness perception, has been summarized in several articles (Johnson & Hsiao 1992, Loomis & Lederman 1986). Hollins et al (1993) used multidimensional scaling techniques to study the perception of the surface texture of objects. The result was a three-dimensional space. One of the dimensions corresponded to roughness-smoothness and a second dimension to hardness-softness. The third dimension appeared to be related to compressional elasticity. In other studies, subjects attempt to identify or classify an object based on its texture (Klatzky & Lederman 1995, Klatzky et al 1989, Reed 1994) or to match surface texture (Van Doren & Menia 1993). Other researchers have had subjects—both human and nonhuman—attempt to discriminate differences in texture (Burton & Sinclair 1994, Kops & Gardner 1996, Sinclair & Burton 1991, Trembly et al 1996).

Although there have been some recent studies of hardness-softness (Srinivasan & La Motte 1995), roughness continues to be the most widely examined textural dimension, and a number of studies have examined judgments of the perceived roughness of surfaces (Connor et al 1990, Connor & Johnson 1992, Sathien et al 1989). Using surfaces that vary in the spacing between elements, it was found that the function relating roughness judgments to dot spacing is an inverted U, with perceived roughness declining as dot spacing increases beyond 3 mm (Johnson & Hsiao 1994). Based on these human judgments and recordings from first-order afferents in monkeys exposed to similar surfaces, Johnson & Hsiao (1992) offer a model of roughness perception. The model in-

volves spatially structured responses from SAIs, a between-fiber as opposed to a within-fiber code (Johnson & Hsiao 1994). The model accounts for the perception of roughness across a spatially extended surface. As the authors indicate, the model does not account for other situations, such as perceiving the roughness of a surface by touching the surface with a tool. Also relevant to the issue of SAIs encoding roughness is a study by Stevens (1990) in which subjects judged the perceived roughness of surfaces presented to various parts of the body. Although there were differences attributable to different sites, an interesting result was that the variations in spatial acuity, and presumably the distribution of receptors sensitive to spatial variations, did not necessarily correlate with judgments of perceived roughness. For example, in comparing three sites such as the fingerpad, forearm, and back, spatial acuity would be highest on the fingerpad and poorest on the back; however, in judging roughness, the same textured surfaces were judged to be slightly rougher on the forearm than on the fingerpad and less rough on the back. The results suggest that central mechanisms responsible for roughness are sensitive to the density of peripheral innervation.

Phillips & Matthews (1993) used a novel technique to alter peripheral afferent discharge and the perception of roughness. They cooled the ulnar nerve at the elbow on one arm and had subjects scan surfaces with their little fingers, which are innervated by that nerve. Subjects matched the roughness of surfaces scanned by the cooled arm and by the unaffected arm (and hand). Surfaces felt significantly smoother on the cooled side, an effect that was correlated with inhibition of high-frequency discharge patterns in the ulnar nerve.

COMPLEX PATTERNS   Several chapters provide good reviews of the perception of complex spatial patterns (Loomis & Lederman 1986, Sherrick 1991), including braille (Foulke 1991), and neural mechanisms associated with such patterns (Johnson & Hsiao 1992). Loomis (1990) presents a model of pattern recognition that is consistent with neurophysiological data and that postulates that tactile spatial patterns are initially subjected to low-pass spatial filtering. He presents results comparing the recognition of raised letters and braille cells to blurred visual representations of the same patterns.

Studies using arrays of tactors have examined some of the interactions that occur when two spatial patterns are presented in close temporal proximity to the same site. Pattern identification may be interfered with because the target pattern is masked by the nontarget pattern (Craig 1995, Mahar & Mackenzie 1993) or because the subject responds with the nontarget pattern (Craig 1996), an effect referred to as "response competition." Moving the nontarget pattern to a separate location reduces masking but still leaves interference due to response competition (Craig & Evans 1995, Evans et al 1992, Evans & Craig 1992), an apparent failure of selective attention.

Accuracy in judging whether two patterns are similar in shape depends on whether they are presented to the same or different locations. Accuracy declines as the distance between the two locations on the same fingerpad increases (Horner 1995). If subjects are asked to judge the direction of movement across the finger, then the orientation of the hand in space affects the perceived similarity (Rinker & Craig 1994). Heller (1992) reports effects of spatial orientation on the identification of braille cells. Other studies of braille have examined scanning strategies (Davidson et al 1992), the effects of braille reading on spatial acuity (Stevens et al 1996), and the representation of braille characters in first-order afferents in humans using microneurographic techniques (Phillips et al 1990).

Investigators have also studied the ability of subjects to identify raised line drawings of objects (Loomis et al 1991, Shimizu et al 1993) and have compared the performance achieved by blind and sighted subjects (Heller et al 1996a,b, Heller & Kennedy 1990). In addition, investigators have examined the identification of raised line drawings of objects as compared to the identification of the actual objects by means of haptic exploration. The relatively poor performance with raised line drawings may be due to a number of factors, such as the lack of 3-D shape and size information about the real object (Klatzky et al 1993).

Sensitivity to the movement per se of objects across the skin has been studied both psychophysically (Essick et al 1991) and neurophysiologically (Essick & Edin 1995, Edin et al 1995). Judgments of the velocity (Essick et al 1996a) and direction of movement (Essick 1991) have been made in response to a brushing stimulus. Directional sensitivity varies as a function of a number of factors such as skin site, velocity of movement, and the length of movement (Essick et al 1991, 1996b). From testing of sites on the fingerpad, hand, and arm, it was found that directional sensitivity was greater at the more distal sites (Essick et al 1991), similar to the results obtained with other measures of spatial sensitivity. Directional sensitivity is related to velocity by an inverted U-shaped function. For example, on the perioral region, sensitivity is better at velocities of 6 cm/sec than at higher or lower velocities (Essick et al 1996b). Generating the movement with a tactile array produced levels of sensitivity similar to those obtained with the brushing stimulus (Essick et al 1996b).

COMMUNICATION   There continues to be interest in using touch as a channel of communication, particularly for blind and deaf individuals. Braille, discussed below, has long been used to communicate written material to the blind. The Tadoma method of speech reception involves a deaf-blind individual placing his or her hand on the face of a talker (Loomis & Lederman 1986, Reed et al 1992). By means of feeling the articulatory gestures, such as lip and jaw movements, individuals can understand speech at low-normal rates. This

ability has been cited as evidence for the information-processing capabilities of the hand (Weisenberger 1992). To explore this ability and to gain better control of the stimulus, devices have been built that combine both tactile and kinesthetic stimulation (Eberhardt et al 1994, Tan et al 1989). One such device, which provided large-amplitude finger movements and vibratory stimulation for three fingers, achieved impressive rates of information transmission (Tan 1996).

The book *Tactile Aids for the Hearing Impaired* (Summers 1992) has chapters on the sense of touch, electrotactile stimulation, and the design of tactile stimulators. There are also chapters on communicating acoustic information via touch, the use of single- and multichannel systems, the evaluation of tactile aids, and the necessity of training users. Kaczmarek & Bach-y-Rita (1995), in a book on virtual environments, review many of the systems for presenting information tactually and cover such topics as telepresence, transmitting information through gloves, and electrotactile stimulation, as well as practical considerations in using tactile displays.

Attention

Paralleling results with visual stimuli, a number of studies have found that reaction times were faster when subjects were responding to a site at which a vibratory stimulus was expected (80% validly cued trials) as compared to responding to unexpected sites (20% invalidly cued trials). Bradshaw et al (1992) report a 46-msec advantage for validly cued locations. The advantage for validly cued locations extends to cross-modal conditions in which visual stimuli cue tactile locations and the reverse (Butter et al 1989). Post & Chapman (1991) cued subjects to switch between visual and tactile stimuli. They reported that reaction times to detect a vibrotactile stimulus, when the subject had been invalidly cued to the visual modality, increased by more than 100 msec.

Whang et al (1991) developed a task in which subjects were required to detect either the presence of an amplitude change at one of four fingerpads or the absence of a change. They found that valid cuing did not aid the detection of the presence of an amplitude change but did assist detection of the absence of such change. Similarly, Sathian & Burton (1991) found an abrupt change in texture was unaffected by cuing. The authors suggest that the increase in stimulation may be processed preattentively.

Neurophysiological correlates of intramodal attention are also being examined (Hsiao et al 1996). Hsiao et al (1993) trained monkeys to respond to either visual or tactile stimuli depending upon a cue stimulus. Recording from SI and SII cortex, they found that discharge rates evoked by the tactile patterns (raised letters) were altered as a function of whether the visual task or the tactile task was cued. Importantly, tactile spatial patterns were presented continuously. Only the cuing changed.

Cortical Mechanisms

Many of the types of stimuli that have been used in psychophysical experiments and in single-unit studies of peripheral afferents have also been used in single-unit studies of cortical neurons. There have been examinations of the responses of cortical cells to such stimuli as textured surfaces, vibration, spatial patterns, motion, and so forth. These types of studies are discussed by Burton & Sinclair (1996).

Work with brain-injured patients has helped to establish the nature of tactile agnosia, the inability to recognize objects through touch (Caselli 1991, 1993). A case study was conducted with one such patient who had suffered a left, parietal infarction (Reed & Caselli 1994, Reed et al 1996). The patient showed significantly poorer object recognition with the right as compared to the left hand, even though measures of basic touch sensitivity were normal for both hands. The authors conclude that there can be specific interference in shape perception independent of other tactile or spatial abilities.

Issues concerning altered sensory inputs, cortical reorganization in adult animals, and plasticity and its functional significance have been examined from a number of perspectives; neurophysiological (Garraghty et al 1994), perceptual (Benedetti 1991b, Craig 1993), and clinical (Halligan et al 1993). Changes in peripheral input may alter the representation of tactile stimuli in the somatosensory cortex. For example, cutting the nerves from digit D3 (middle finger) in monkeys silences the corresponding region in SI, but over time, stimulating adjacent fingers D2 (index finger) and D4 (ring finger) may activate cortical cells in the D3 cortical region (Jenkins et al 1990, Merzenich & Jenkins 1993). An impressive example of reorganization was demonstrated in a monkey tested 12 years after undergoing deafferentation of an upper limb. In this monkey, stimulating the face evoked activity in the cortical region that is normally evoked by stimulation of the upper limb (Pons et al 1991). Clinical studies have also been carried out with human amputees. In some cases, stimulation of the facial region has elicited reports of sensations in the missing portion of the arm (Ramachandran et al 1992). Training at a particular site on the skin with intact subjects may result in increased cortical representation, results that have been observed with both human (Elbert et al 1995) and nonhuman subjects (Merzenich et al 1988), and may also result in improved discriminability (Recanzone et al 1992).

Cortical reorganization has also been studied using noninvasive techniques with human subjects (Mogilner et al 1993, Sterr et al 1998, Yang et al 1994). As with microneurography, there is an advantage in having subjects with whom one can correlate perceptual and neural responses. In the Mogilner et al (1993) study, two adult patients were examined. The patients were undergoing surgical treatment for syndactyly (webbed fingers). Magnetoencephalo-

graphic images of these patients, prior to surgery, showed a reduced area representing the hand. Following surgery, several effects were observed: The cortical hand area expanded, with a greater distance between the thumb and little finger; the individual digits functioned independently; and one patient reported that the fingers were now perceived as individual entities (Mogilner et al 1993). These results are consistent with data obtained in recording from single units in the cortex of monkeys whose fingers had been surgically joined to produce an artificial syndactyly (Allard et al 1991). Other noninvasive studies have used positron emission tomography (PET) to examine cortical responses to textured surfaces (Burton et al 1997, O'Sullivan et al 1994) and to vibratory stimuli (Burton et al 1993).

Aging

As compared to younger subjects, older subjects have reduced absolute sensitivity to vibratory stimuli (Schmidt & Wahren 1990), particularly high-frequency vibration (Gescheider et al 1994b). They also show greater forward masking (Gescheider et al 1992) and reduced temporal summation (Gescheider et al 1994a). Many of these findings have been reviewed by Verrillo (1993). These effects are more prominent with stimuli that affect Pacinian corpuscles. Difference thresholds for intensity, however, remain relatively unchanged with age, as long as the thresholds are expressed in relative rather than absolute terms (Gescheider et al 1996).

Spatial acuity, as measured by a variety of tasks, also declines with age (Stevens & Cruz 1996, Stevens & Patterson 1995, Stevens et al 1996, Woodward, 1993), although it should be noted that there are large individual differences (Stevens & Patterson 1995, Verrillo 1993). Stevens & Choo (1996) measured spatial acuity at 13 different body sites and found that sensitivity declined with age at some sites much more than at others. The feet and hands showed the greatest drop in sensitivity, a result that may be due to reduced circulation.

THERMAL SENSITIVITY

For many years, textbooks and review chapters (Sherrick & Cholewiak 1986) have been showing a supine figure with vertical lines, the heights of which indicate spatial acuity measured at various locations on the body. A twin, fraternal rather than identical, has now been created showing warm and cold thresholds across the body. Based on the results from 60 subjects, this map shows the facial region to be the most sensitive area of the body and the extremities, particularly the lower ones, to be considerably less sensitive. Subjects were more sensitive to cold stimuli than to warm ones, and as noted for tactile sensitivity, thermal sensitivity declined with age (Stevens & Choo

1998). Thermal testing on the face and in the mouth showed the mouth to be less sensitive to warming than the facial regions. No differences were seen for cooling (Green & Gelhard 1987).

Also widely noted in textbooks is the impressive inaccuracy in localizing warm stimuli unaccompanied by tactile stimulation. Cain (1973) found that subjects were unable to tell whether a radiant heat source was focused on the front or back of the torso on a significant portion of trials (14% error rate). Lee et al (1996) asked subjects to indicate which of two contact thermal stimulators was raised (or lowered) in temperature. Subjects were more accurate in localizing cooling stimuli than warming ones and more accurate when the two thermal probes were positioned to stimulate different dermatomes as compared to the same dermatome.

The heat grill is part of a classic demonstration of thermal interaction. The device consists of alternating warm and cool bars that elicit a sensation of painful heat. A study of this effect combined human and animal work (Craig & Bushnell 1994). The same stimulus conditions that elicited reports of painful heat from human subjects were applied to cats' hindpaws. The analysis of the response of spinal cord neurons to warm, cool, and "grill" stimuli suggested that the illusion may result from a central disinhibition process. More recently, Craig et al (1996) used PET imaging of regional cerebral blood flow in humans to show that the grill produces activation in the anterior cingulate cortex (a region also activated by noxious levels of heat and cold), whereas the component warm and cold stimuli do not. Warm stimuli primarily activated the insula and SI while cool stimuli produced significant activation in the insula and SII, implying differential cortical processing of these submodalities.

Thermal stimulation has also been investigated for the way it interacts with, or the effects that it has on, other types of cutaneous sensitivity such as vibratory (Apkarian et al 1994, Green 1987), chemical (Green 1991, 1992), and spatial (Sherrick & Cholewiak 1986, Stevens 1989).

HAPTICS AND KINESTHESIS

Most of the information that we gain by means of touch comes by way of the hand, which is both a perceptual and manipulative organ. In haptics, which combines tactile and kinesthetic stimulation, there is a long history of distinguishing between active and passive touch and the differences between the two modes of stimulation. In their review, Loomis & Lederman (1986) propose a classification system they refer to as "tactual modes." The five categories of tactual modes incorporate both the idea of subjects' control (active) and no control (passive) over the pickup of information and whether the information is cutaneous, kinesthetic, or both. (Although active touch, which involves efferent control, afferent kinesthetic information, cutaneous stimuli, and an ac-

tive observer, is the most common way of gaining touch information in every-day life, most of the experimental work has involved the presentation of cutaneous stimuli to a passive observer, in large part because that permits greater stimulus control.)

A traditional issue in haptics is the degree to which active exploration increases the accuracy of the perception of objects. This issue is also important in studies of neurophysiological responses to spatial patterns. Most of these studies involve the imposition of a spatial pattern on a passive, nonhuman subject. To answer the question of whether sensitivity to passively imposed spatial patterns is much less than to patterns actively scanned, human subjects were tested in a letter-identification task. The subjects were allowed to move their fingers laterally back and forth a few centimeters over raised letters. This provided no advantage over having the raised letters scanned across the stationary fingerpad (Vega-Bermudez et al 1991). Srinivasan & LaMotte (1995) examined how subjects discriminate the softness of objects under a variety of conditions. For example, reducing tactile sensitivity by anesthetizing the fingertip resulted in judgments of softness dropping to chance for samples of rubber. They also tested active vs passive contact and found that pressing the sample of rubber down onto the passive fingerpad of the subject produced performance nearly as good as allowing the subject to actively contact the sample. Chapman (1994) reviewed work on active and passive touch in light of the intriguing finding of diminished cortical input, referred to as input "gating," that occurs during active touch. Several explanations are offered for the findings that sensitivity is, in fact, not reduced during active as compared to passive touch.

Klatzky, Lederman, and their coworkers have analyzed hand movements when subjects are asked to identify objects and properties of objects. Based on these analyses, they identified a series of relatively stereotyped hand movements they call "exploratory procedures" (EPs). Particular EPs are associated with the extraction of certain properties of objects. For example, an EP such as lateral movement is associated with the extraction of texture, the EP of static contact is associated with the extraction of thermal properties, that of enclosure (molding the hand around an object) with extracting global shape and volume, and so forth (Klatzky & Lederman 1993, Lederman & Klatzky 1993). The use of EPs has been investigated in a variety of tasks, such as in speed of object classification (Lederman et al 1993), in identifying, matching, or classifying objects on the basis of particular properties such as surface texture (Klatzky et al 1987, 1989), and in directed exploration (Lederman & Klatzky 1987), in which subjects are required (constrained) to use a particular EP to explore an object.

Haptic exploration is also involved in a different task, the exploration of the near space around us (Loomis & Lederman 1986). Several studies have investigated distortions of this space such as that produced in the horizontal-vertical illusion (vertical generally judged greater than horizontal) (Heller et al 1993,

Heller & Joyner 1993), which corresponds to judging lengths of objects oriented tangentially vs radially (Marks & Armstrong 1996) and in judging the length of objects. In this latter case, Hollins & Goble (1988) showed that velocity had a large effect on perceived length. As velocity increased from 0.5 to 50 cm/sec, perceived length declined by a factor of 3.

Textbooks in sensation and perception occasionally mention Aristotle's Illusion. In this illusion, two fingers are crossed over one another, such as D3 over D2, and a pencil is placed between the two crossed fingertips. Typically, subjects report a sensation of two objects. The illusion of double sensation, or "tactile diplopia," can also be produced by bringing together nonadjacent fingers (D2 and D4 or D2 and D5) (Benedetti 1986a) or by squeezing adjacent fingers tightly together and bringing together locations on the adjacent fingers that are normally apart from one another (Benedetti 1986b). Benedetti has quantified the crossed-fingers effect by touching each finger with one of two objects, for example, a sharp point and a small ball. The subjects indicated the relative position of the two stimuli (Benedetti 1991a). Benedetti has also used these effects to examine the adaptation of motor and perceptual responses with altered inputs. In one study relevant to the issue of plasticity, subjects kept their fingers crossed (D3 over D2) for as long as six months. The crossed fingers were maintained in position for several subjects by putting screws through the distal ends of the fingernails. Both motor and perceptual responses showed adaptation over a period of several months (Benedetti 1991a). Readers of Frank Geldard's *The Human Senses* (1972) may be reminded that the days of "somewhat Spartan" experiments in somesthesis are not over.

Clark & Horch's (1986) chapter on kinesthesis provides a valuable review of this topic. Particularly noteworthy from the point of view of understanding the perceptual aspects are the explanations that are offered of both the psychophysical testing procedures and the results of such testing. With regard to kinesthetic receptor mechanisms, the consensus continues to be that receptors in muscles play the major role (Jones 1994, Matthews 1988). The contributions of other receptors, such as cutaneous and joint receptors, may depend on the joint being examined (Clark & Horch 1986, Ferrell & Craske 1992). Studies using nerve block (Ferrell & Smith 1987, 1989), microneurography (Edin 1990), and other techniques (Ferrell 1995) have found evidence that nonmuscle receptors may provide kinesthetic information about the hand. The nature and role of kinesthetic feedback are also discussed in an article by Gandevia & Burke (1992) and in associated commentaries.

PAIN

Books and articles about pain often begin with attempts to find a suitable definition for the topic. Many provide the "official" definition offered by the Inter-

national Association for the Study of Pain (IASP) (Merskey & Bogduk 1994), "An unpleasant sensory or emotional experience associated with actual or potential tissue damage, or described in terms of such damage." While that may do justice to the subject matter, it fails to capture the extensive scholarly, clinical, public, and commercial interest in the topic. For that purpose, a definition generally given tongue in cheek may be preferable: "Pain is a growth industry."

There are numerous ways to quantify that interest and that growth and numerous reasons to account for it. In 1973, IASP was formed. By 1975, when the Society held its first World Congress on Pain, there were 1200 members. That number increased to 2100 in 1984 and to nearly 4500 by 1996. The numbers attending the triennial pain congresses mushroomed from 760 in 1975 to 4300 in 1996. Clearly, academic interest in pain comes from many disciplines, but psychology figures very prominently among them. About 550 IASP members list psychology as their main discipline, a number second only to anesthesiology.

Bibliographic databases provide another perspective on the current interest in pain research. A search of PsycLIT for the period 1990–1997 reveals that there were 1025 journal articles on the "exploded terms" of "tactual perception" or "somesthetic perception" if articles related to "pain" are not included. Performing the reverse search, looking for articles devoted solely to "pain," comes up with 4343 references. The medical literature, of course, yields a much larger sum: Entering "pain" into Medline and asking for references over the past five years yields an astonishing count of 47,092.

Research on pain touches on every aspect of psychology presented in a typical introductory psychology course: brain and behavior, psychophysics and perception, learning and motivation, memory and cognition, individual differences, development, personality, psychological disorders, and social behavior. Many of the 81 chapters in the encyclopedic *Textbook of Pain* (Wall & Melzack 1994) deal with psychological issues. Psychologists play major roles in the leadership of the International Association for the Study of Pain and the American and Canadian Pain Societies, and on the editorial boards of the major journals *Pain, Pain Forum, Clinical Journal of Pain,* and *Journal of Pain and Symptom Management.*

Gate-Control Theory

While psychology's involvement in the field of pain has long been recognized, Melzack & Wall's (1965) classic paper on the gate-control theory served as a major catalyst by moving the field of pain research away from the Cartesian model of a direct connection between a source of injury and a pain center in the brain. Their model provided instead for a variable link between injury and

pain, with descending influences from the central nervous system serving to modulate afferent activity in response to noxious inputs. Suddenly, it seemed, pain research and pain management, both of which had largely been the domain of the medical profession, were open to many other disciplines, and, over the years, psychology's value was established.

The gate-control theory has undergone modifications (Melzack & Wall 1996) since its formulation, but the basic conception remains unchanged. Small-diameter fibers respond to noxious inputs and convey information to the dorsal horn of the spinal cord and then to subcortical and cortical structures subserving three dimensions of pain: sensory-discriminative, motivational-affective, and cognitive-evaluative. In addition, descending influences from higher regions act via the midbrain and medulla to exert an inhibitory influence on the spinal cord and to inhibit the response of transmitting cells to injury.

Clearly, this description is farcically simplistic. Wall & Melzack's *Textbook of Pain* (1994) devotes its first dozen chapters and over 250 pages to an elaboration of the neurophysiological and neurochemical mechanisms that might account for pain transmission and modulation. Theoretical developments regarding pain transmission and encoding continue apace. One such is Melzack's (1990) concept of the "neuromatrix," a genetically determined neural network subserving body sensation that can be modified by experience. It has been applied particularly to phantom-limb phenomena. Magnetic source imaging in phantom-limb patients (Flor et al 1995) has disclosed extensive reorganization of the somatosensory cortex, an example of neuronal plasticity that may be revealed repeatedly in future studies of chronic pain conditions.

Sensory Fibers

Considerable interest among neuroscientists has focused on each of the elements in the complex pain-transmission system. The two sets of highly specialized peripheral sensory fibers, one myelinated (A-delta) and one unmyelinated (C), are characterized by high thresholds but differ in other respects. C-fiber nociceptors that respond to both intense mechanical stimulation and high temperatures (<38°C) show a nice monotonic relationship between number of impulses and temperature or pressure, but selective analgesia to heat by the application of capsaicin in humans (Simone & Ochoa 1991) suggests independent transducer mechanisms (Meyer et al 1994).

The neural response of C-fiber nociceptors is intimately linked to the nature of prior stimulation. Presentation of noxious heat 10 sec before a test stimulus reduces the response to the latter by about 65%; even at 5 min there is a measurable suppression. Likewise, response to a heat pulse of, say, 47°C, is markedly less if the previous stimulus was 47° or 49°C than if it was 41° or 43°C (Meyer et al 1994).

Interesting issues about the appropriate neurophysiological measure to use in correlating human and nonhuman data about C-fiber mechano-heat nociceptors arise from the finding by Tillman et al (1995a) that heat pain thresholds decreased as stimulus ramp rate increased, but the threshold for detecting an action potential in the C-fiber of the monkey increased with ramp rate. Tillman et al (1995b) developed a three-layer heat-transfer model to describe temperature distribution after application of heat to the skin, relating threshold to base temperature, ramp rate, and duration of the heat step. Their results suggest that the heat threshold for C-fiber mechano-heat nociceptors is determined by receptor depth.

Schmidt et al (1995) found new classes of C-fiber nociceptors, namely ones responding only to mechanical stimuli, only to heat stimuli, and ones that were unresponsive to pressure or heat. Some of each of these units were sensitized after topical application of the irritants capsaicin or mustard oil, acquiring responsiveness to a stimulus modality to which they were previously nonresponsive. The discovery that previously silent nociceptors can be recruited by local injury suggests that central sensitization may result from spatial summation of a nociceptive barrage, with implications for chronic pain that are discussed below.

A-fiber units have high thresholds to both mechanical pressure and temperature, but since they typically respond to temperatures greater than 50°C, it is more likely that the C-fiber nociceptors signal pain around the human pain threshold ($\sim$ 45°C). As temperature rises, particularly for long-duration stimuli, the A-delta nociceptors begin to respond vigorously (Meyer et al 1994). Moreover, the A-fiber nociceptors display an extraordinary response to burn injury, showing both a sharply reduced threshold and a marked increase in response rate to thermal stimuli after a 30-sec burn to the hand (Meyer et al 1994). This pattern closely matches the hyperalgesia seen in human observers following a similar burn.

Single-fiber recordings from A-delta and C-fibers in awake humans have revealed a great deal about the physiological properties of these units (Torebjork 1994). Curiously, although the A-delta fibers are much larger in diameter than the unmyelinated C-afferents, it is exceedingly difficult to record from the former, perhaps because the electrode tip must be close to the node of Ranvier. Lundberg et al (1992) used small electrodes to stimulate groups of A-delta and C-fibers, with trains of electrical pulses varying regularly in frequency from 1 to 15 Hz or mimicking some of the irregular patterns seen in microneurographic recordings. The data indicated that the subjective magnitude of pain increased monotonically as a function of frequency for the regular patterns, but that even greater peak magnitudes of pain were reported for the irregular but natural patterns.

Many phenomena are seen in parallel when examining neurophysiological data and psychophysical ratings. Often, the correlations are evident in peripheral recordings, as in studies of primary hyperalgesia at the site of an injury, but higher-level influences become apparent in studies of secondary hyperalgesia, an enhanced level of pain to mechanical stimuli seen in a large area surrounding a burn. Baumann et al (1991) and Simone et al (1991) concluded that central rather than peripheral sensitization is responsible for these effects.

Higher Neural Organization

The second-order neural organization of the spinal cord reveals both elegance and complexity, since it is at this level that one finds the interplay between nociceptive and non-nociceptive afferents, excitatory and inhibitory neurotransmitters, and both afferent and descending influences. Nociceptive neurons respond maximally to high intensities, project to higher areas known to be involved in processing pain information, generate pain experiences when stimulated electrically, and reduce pain when their activity is inhibited (Fields 1987). About a quarter of the spinal neurons tend to be "high-threshold" or "nociceptive-specific" but they are outnumbered by "wide-dynamic-range" (WDR) neurons that have large receptive fields, respond weakly to brushing, pressure, and mild touch but vigorously to strong pressure, pinch, or high temperature (Price 1988).

Simone et al (1991) injected capsaicin into the skin of human observers. This produced an immediate burning pain that built over about 15 seconds and declined over the next half hour, increased the perceived intensity of noxious stimulation (hyperalgesia), and caused even gentle strokes to be perceived as painful (allodynia). After a similar treatment in monkeys, both the high-threshold and WDR cells showed increased activity whose time course correlated with magnitude estimates from the human observers, although the correlation was greater for the activity of the WDR cells. More recently, Pertovaara (1998) found that secondary hyperalgesia, the altered responsiveness in the region away from the injury, is submodality-specific; neurogenic inflammation induced by the injection of mustard oil in the rat enhanced the response of WDR cells in the dorsal horn to intense mechanical but not thermal stimuli. Even weak mechanical stimuli produced enhanced spinal activity, suggesting that the injury engaged a descending facilitatory feedback loop that may enforce inactivity and thus promote healing.

Submodality specificity was also seen in an elegant study by Torebjork et al (1992), who demonstrated that the secondary hyperalgesia to mechanical stimuli following capsaicin injections is mediated by input from large myelinated fibers. These fibers normally evoke nonpainful tactile sensations, but nerve compression, which selectively blocked their capacity to respond, also abol-

ished the mechanical hypersensitivity in the wide surrounding area. Hyperalgesia to heat in that region was unaffected, however, indicating that afferent signals from other fibers, presumably the C-polymodal nociceptors, must be responsible for that effect. The mechanical hyperalgesia appears to be due to reversible changes in central processing.

Central Neurochemical Effects

The role of higher-order centers in such inflammation-produced hyperalgesia was supported by the findings of Kolhekar et al (1997), who found that blockade of receptors for N-methyl-D-aspartate (NMDA) in the rat thalamus significantly reduced both thermal and mechanical hyperalgesia induced by injection of carrageenin in the contralateral hindpaw of the rat. NMDA is an excitatory amino acid whose receptor, when unmasked, permits previously weak inputs to be expressed and produces much larger than normal responses in postsynaptic cells (McMahon 1994). NMDA is seen to play a role in many chronic pain states, since it markedly influences central excitability [even more in the neonate (Fitzgerald 1994) than the adult].

NMDA antagonists, then, ought to be helpful in blocking and reversing central sensitization (Coderre et al 1997, Dubner & Basbaum 1994) and thus preventing and reducing pain. Stubhaug et al (1997) showed that ketamine, a selective blocker of the NMDA receptor, when administered postoperatively in humans, markedly reduced hyperalgesia in the region surrounding the surgical incision. A recent study used ketamine to enhance the effects of preemptive analgesia. In this procedure, a local anesthetic or an opiate is administered prior to general anesthesia in surgery. It is based on the notion, which has received considerable support, that it is prudent to block nociceptive inputs from the site of the operation, even if the pain they would produce is not consciously experienced. Otherwise, the thinking goes, a strong afferent barrage may alter the activity of central neurons and lead to extended pain. Barbieri et al (1997) divided patients into three groups, all of whom received the potent synthetic opiate, fentanyl, on arrival in the operating room and then a general anesthetic. One group of patients received ketamine 30 min before this preemptive analgesia treatment. Their visual analog scale ratings of postoperative pain were sharply reduced compared to those of patients who had the standard procedure or who received ketamine in the recovery room. Ketamine or fentanyl, given as an adjuvant to general anesthesia, altered electrocutaneous detection and pain thresholds for up to 5 days in patients who underwent abdominal surgery (Wilder-Smith et al 1998).

Psychophysical studies of central sensitization have often focused on the phenomenon of second pain, seeing it as a correlate of the neurophysiological "wind-up effect" that occurs after repeated application of an electrical or thermal stimulus. A single application of an intense pulse can elicit both a local-

ized pricking sensation and, a second or so later, a diffuse throbbing or burning experience. After repeated applications of thermal pulses, each a second or two apart, the perceived intensity of the first pain declines to about one third of its original level while that of the second pain doubles (Price 1994). This differential effect has been linked to suppression of the A-delta heat nociceptive afferents and central summation of activity initiated by C-fiber polymodal nociceptive afferents. Price et al (1994) have shown that the cough suppressant dextromethorphan, which is an NMDA antagonist, attenuated the level of second pain, leaving first pain unaffected. Arendt-Nielsen et al (1995), in a related study, found that ketamine inhibited temporal summation for trains of electrical pulses in human observers, although ratings of a single stimulus were unaffected. These data reinforce the notion that central mechanisms, involving NMDA-receptors, are involved in temporal summation studies in the laboratory and secondary hyperalgesia phenomena in the pain clinic.

Pain Psychophysics

There is a growing interest in combining the elegance of laboratory research with the relevance of clinical studies. While such traditional measures as pain threshold and pain tolerance still provide many useful insights into the pain experience, the tools for studying pain responsiveness have expanded enormously in recent years. The applicability of signal-detection theory methods to studying noxious signals remains contentious, with both adherents (Clark 1994) and critics (Rollman 1977) debating whether the discrimination of two intense stimuli provides insights into possible changes in their painfulness. Irwin & Whitehead (1991), using category scaling and identification tasks with electrocutaneous stimuli, have attempted some resolution of the conflicting views.

Technological advances have strongly influenced pain investigations, at both the stimulus and response end, in recent years. It is comforting to see that good research can still be accomplished on a meager budget. Koltzenburg et al (1993), who wanted to measure localization ability for noxious stimuli as compared to innocuous ones, asked subjects to localize pin pricks, noxious heat (using small copper probes heated to 50°C), and chemical irritants (mustard oil applied to a small cotton ball). The mean mislocalization was about 9 mm, with no difference among the submodalities and no effects of blocking the large fibers. Localization of tactile sensations induced by von Frey hairs, signaled by the large fibers, was only marginally better (a mean error of about 6 mm), suggesting that somatotopic representation in the brain for noxious inputs is similar to that found for tactile ones.

There has been considerable interest in the scaling of both the intensity and unpleasantness of pain, using visual analog scales or scaled verbal descriptors (Gracely 1994), multidimensional scaling (Clark et al 1989), measures of re-

flex activity (DeBroucker et al 1989), studies of pupil diameter (Chapman et al 1997), somatosensory evoked potentials (Chen & Bromm 1995), and a number of other methods (Chapman & Loeser 1989, Rollman 1992) designed to elicit information about the sensory, affective, and to a much smaller extent, cognitive components of pain experiences. These behavioral and physiological instruments have helped to address fundamental issues such as gender differences in pain responsiveness (Berkley 1997) and the assessment of pediatric pain (McGrath & Unruh 1994). Neuroimaging studies have begun to appear in abundance (Casey et al 1995, Casey & Minoshima 1997), but technical, interpretational, and philosophical issues will remain with us for many years.

Attempts to bridge the laboratory-clinical gap come from studies of pain perception among pain patients. Naliboff et al (1981) contrasted Chapman's (1978) model of hypervigilance with Rollman's (1979) model of adaptation level in examining the threshold for noxious input in pain patients. Chapman's model suggests that pain patients have diminished pain threshold and tolerance levels, hyper-responding to both internal and external stimuli. In contrast, the adaptation-level model suggests that pain patients compare external stimuli to their endogenous pain, rating the stimuli as less intense than they would if they did not have a high level of pain as an internal anchor or comparison point. Both models have received support (Naliboff & Cohen 1989, Rollman 1992), but for different populations of pain patients.

For example, fibromyalgia patients who have exquisite sensitivity at a number of tender points also show much lower pain threshold and pain tolerance to pressure applied at control sites (Scudds et al 1987). Lautenbacher et al (1994) showed that fibromyalgia patients had significantly lower pain thresholds when the noxious stimulus was heat or a train of electrical pulses, and McDermid et al (1996) demonstrated that they have an extremely low discomfort threshold for white noise. At the least, fibromyalgia patients generally show a considerable degree of responsiveness to noxious stimuli, whatever the origin.

More recent studies have employed psychophysical methods to look at possible deficiencies of pain modulation in these patients. Using the diffuse noxious inhibitory control paradigm, in which a tonic noxious stimulus (such as a tourniquet or a long-lasting intense heat stimulus) at one site on the body, such as the arm, suppresses the pain threshold or rated painfulness of a noxious phasic stimulus (such as electrical shock) applied to a distant body part, both Kosek & Hansson (1997) and Lautenbacher & Rollman (1997) found less suppression of pain in patients than in controls. It remains to be determined whether this reflects a dysfunction of physiological inhibition or an attentional disorder in which the fibromyalgia sufferers concentrate on all noxious inputs while pain-free individuals channel their attentional capacity to the more lasting and noxious input.

This examination of recent findings on touch, haptics, and pain indicates that both biological and psychological perspectives are necessary to uncover the phenomena that make up these areas. The future direction of work on somesthesis will be enormously exciting, but it is unlikely that we will see a unified theory emerging that covers the complexities of the separate modalities and their interactions, just as it is unlikely that we will see a unified theory that covers the complexities of vision or hearing. We do expect continued close cooperation between the psychophysical approach and the neurophysiological approach, particularly as the latter continues to put increasing emphasis on central mechanisms. The improved resolution in both the spatial and temporal dimensions of brain imaging, coupled with increased emphasis on multidimensional behavioral assessment, will enable us to better understand the sensory, affective, and cognitive components of normal and abnormal states. Basic scientists and clinicians will seek to integrate their models, investigative tools, and findings in dealing with a wide range of disorders, with behavioral medicine increasing in scope and influence. Finally, we expect to see an increased emphasis on the complex interactions between modalities as investigators capture the richness of somesthetic experience.

> Visit the *Annual Reviews home page* at
> http://www.AnnualReviews.org.

Literature Cited

Allard T, Clark SA, Jenkins WM, Merzenich MM. 1991. Reorganization of somatosensory area 3b representations in adult owl monkeys after digital syndactyly. *J. Neurophysiol.* 66:1048–58

Apkarian AV, Stea RA, Bolanowski SJ. 1994. Heat-induced pain diminishes vibrotactile perception: a touch gate. *Somatosens. Mot. Res.* 11:259–67

Arendt-Nielsen L, Petersen-Felix S, Fischer M, Bak P, Bjerring P, Zbinden AM. 1995. The effect of N-methyl-D-aspartate antagonist (ketamine) on single and repeated nociceptive stimuli: a placebo-controlled experimental human study. *Anesth. Analg.* 81:63–68

Barbieri M, Colnaghi S, Tommasino C, Zangrillo A, Galli L, Torri G. 1997. Efficacy of the NMDA antagonist ketamine in preemptive analgesia. See Jensen et al 1997, pp. 343–49

Baumann TK, Simone DA, Shain CN, LaMotte RH. 1991. Neurogenic hyperalgesia: the search for the primary cutaneous afferent fibers that contribute to capsaicin-induced pain and hyperalgesia. *J. Neurophysiol.* 66:212–27

Benedetti F. 1986a. Spatial organization of the

diplesthetic and nondiplesthetic areas of the fingers. *Perception* 15:285–301

Benedetti F. 1986b. Tactile diplopia (diplesthesia) on the human fingers. *Perception* 15:83–91

Benedetti F. 1991a. Perceptual learning following a long-lasting tactile reversal. *J. Exp. Psychol.: Hum. Percept. Perform.* 17: 267–77

Benedetti F. 1991b. Reorganization of tactile perception following the simulated amputation of one finger. *Perception* 20:687–92

Berkley KJ. 1997. Sex differences in pain. *Behav. Brain Sci.* 20:371–80

Boff KR, Kaufman L, Thomas JP, eds. 1986. *Handbook of Perception and Human Performance. Sensory Processes and Perception,* Vol. 1. New York: Wiley & Sons. 2 Vols.

Boivie J, Hansson P, Ludblom U, eds. 1994. *Touch, Temperature, and Pain in Health and Disease: Mechanisms and Assessments,* Vol 3. Seattle, WA: IASP

Bolanowski SJ. 1996. Information processing channels in the sense of touch. See Franzen et al 1996, pp. 49–58

Bolanowski SJ, Gescheider GA, Verrillo RT. 1994. Hairy skin: psychophysical channels and their physiological substrates. *Somatosens. Mot. Res.* 11:279–90

Bolanowski SJ, Gescheider GA, Verrillo RT, Checkosky CM. 1988. Four channels mediate the mechanical aspects of touch. *J. Acoust. Soc. Am.* 84:1680–94

Bradshaw JL, Howard MJ, Pierson JM, Phillips J, Bradshaw JA. 1992. Effects of expectancy and attention in vibrotactile choice reaction time tasks. *Q. J. Exp. Psychol.* 44A:509–28

Bromm B, Desmedt JS, eds. 1995. *Pain and The Brain: From Nociception to Cognition.* New York: Raven

Burton H, MacLeod AK, Videen TO, Raichle ME. 1997. Multiple foci in parietal and frontal cortex activated by rubbing embossed grating patterns across fingerpads: a positron emission tomography study in humans. *Cereb. Cortex* 7:3–17

Burton H, Sinclair R. 1996. Somatosensory cortex and tactile perceptions. See Kruger 1996, pp. 105–77

Burton H, Sinclair RJ. 1994. Representation of tactile roughness in thalamus and somatosensory cortex. *Can. J. Physiol. Pharmacol.* 72:546–57

Burton H, Videen TO, Raichle ME. 1993. Tactile-vibration-activated foci in insular and parietal-opercular cortex studied with positron emission tomography: mapping the second somatosensory area in humans. *Somatosens. Mot. Res.* 10:297–308

Butter CM, Buchtel HA, Santucci R. 1989. Spatial attentional shifts: further evidence for the role of polysensory mechanisms using visual and tactile stimuli. *Neuropsychologia* 27:1231–40

Cain WS. 1973. Spatial discrimination of cutaneous warmth. *Am. J. Psychol.* 86:169–81

Caselli RJ. 1991. Bilateral impairment of somesthetically mediated object recognition in humans. *Mayo Clin. Proc.* 66:357–64

Caselli RJ. 1993. Ventrolateral and dorsomedial somatosensory association cortex damage produces distinct somesthetic syndromes in humans. *Neurology* 43:762–71

Casey KL, Minoshima S. 1997. Can pain be imaged? See Jensen et al 1997, pp. 855–66

Casey KL, Minoshima S, Morrow TJ, Koeppe RA, Frey KA. 1995. Imaging the brain in pain: potentials, limitations, and implications. See Bromm & Desmedt 1995, pp. 201–11

Chapman CE. 1994. Active versus passive touch: factors influencing the transmission of somatosensory signals to primary somatosensory cortex. *Can. J. Physiol. Pharmacol.* 72:558–70

Chapman CR. 1978. The perception of noxious events. In *The Psychology of Pain*, ed. RA Sternbach, pp. 169–203. New York: Raven

Chapman CR, Loeser JD, eds. 1989. *Issues in Pain Measurement. Advances in Pain Research and Therapy,* Vol. 12. New York: Raven

Chapman CR, Oka S, Jackson RC. 1997. Phasic pupil dilation response to noxious stimulation in humans. See Jensen et al 1997, pp. 449–58

Chen ACN, Bromm B. 1995. Pain-related generators of laser-evoked brain potentials: brain mapping and dipole modelling. See Bromm & Desmedt 1995, pp. 245–66

Cholewiak RW, Collins AA. 1991. Sensory and physiological bases of touch. See Heller & Schiff 1991, pp. 23–60

Clark FJ, Horch KW. 1986. Kinesthesia. See Boff et al 1986, pp. 1–62

Clark WC. 1994. The psyche in the psychophysics of pain: an introduction to sensory decision theory. See Boivie et al 1994, pp. 41–62

Clark WC, Janal MN, Carroll JD. 1989. Multidimensional pain requires multidimensional scaling. See Chapman & Loeser 1989, pp. 285–325

Coderre TJ, Fisher K, Fundytus ME. 1997. The role of ionotropic and metabotropic glutamate receptors in persistent nociception. See Jensen et al 1997, pp. 259–75

Cole JD. 1995. *Pride and a Daily Marathon*. Cambridge, MA: MIT Press. 1st ed.

Connor CE, Hsiao SS, Phillips JR, Johnson KO. 1990. Tactile roughness: neural codes that account for psychophysical magnitude estimates. *J. Neurosci.* 10:3823–36

Connor CE, Johnson KO. 1992. Neural coding of tactile texture: comparison of spatial and temporal mechanisms for roughness perception. *J. Neurosci.* 12:3414–26

Craig AD, Bushnell MC. 1994. The thermal grill illusion: unmasking the burn of cold pain. *Science* 265:252–55

Craig AD, Reiman EM, Evans A, Bushnell MC. 1996. Functional imaging of an illusion of pain. *Nature* 384:258–60

Craig JC. 1993. Anomalous sensations following prolonged tactile stimulation. *Neuropsychologia* 31:277–91

Craig JC. 1995. Vibrotactile masking: the role of response competition. *Percept. Psychophys.* 57:1190–200

Craig JC. 1996. Interference in identifying tactile patterns: response competition and temporal integration. *Somatosens. Mot. Res.* 13:199–213

Craig JC, Evans PM. 1995. Tactile selective attention and temporal masking. *Percept. Psychophys.* 57:511–18

Craig JC, Kisner JM. 1998. Factors affecting tactile spatial acuity. *Somatosens. Mot. Res.* 15:29–45

Davidson PW, Appelle S, Haber RN. 1992. Haptic scanning of braille cells by low- and high-proficiency blind readers. *Res. Dev. Disabil.* 13:99–111

DeBroucker T, Willer JC, Bergeret S. 1989. The nociceptive flexion reflex in humans: a specific and objective correlate of experimental pain. See Chapman & Loeser 1989, pp. 337–52

Dubner R, Basbaum AI. 1994. Spinal dorsal horn plasticity following tissue or nerve injury. See Wall & Melzack 1994, pp. 225–41

Eberhardt SP, Bernstein LE, Barac-Cikoja D, Coulter DC, Jordan J. 1994. Inducing dynamic haptic perception by the hand: system description and some results. *Proc. Am. Soc. Mech. Eng.* 55:345–51

Edin BB. 1990. Finger joint movement sensitivity of non-cutaneous mechanoreceptor afferents in the human radial nerve. *Exp. Brain Res.* 82:417–22

Edin BB, Essick GK, Trulsson M, Olsson KA. 1995. Receptor encoding of moving tactile stimuli in humans. 1. Temporal pattern of discharge of individual low-threshold mechanoreceptors. *J. Neurosci.* 15:830–47

Elbert T, Pantev C, Wienbruch C, Rockstroh B, Taub E. 1995. Increased cortical representation of the fingers of the left hand in string players. *Science* 270:305–7

Essick GK. 1991. Human capacity to process directional information provided by tactile stimuli which move across the skin: characterization and potential neural mechanisms. In *Wenner-Gren International Symposium Series: Information Processing in the Somatosensory System*, ed. O Franzen, J Westman, 57:329–39. London: Macmillan

Essick GK. 1992. Comprehensive clinical evaluation of perioral sensory function. *Oral Maxillofac. Surg. Clin. NA* 4:503–26

Essick GK, Bredehoeft KR, McLaughlin DF, Szaniszlo JA. 1991. Directional sensitivity along the upper limb in humans. *Somatosens. Mot. Res.* 8:13–22

Essick GK, Edin BB. 1995. Receptor encoding of moving tactile stimuli in humans. II. The mean response of individual low-threshold mechanoreceptors to motion across the receptive field. *J. Neurosci.* 15:848–64

Essick GK, Franzen O, Nguyen TA, Jowers K, Shores JW, et al. 1996a. Experimental assessment of the temporal hypothesis of velocity scaling. See Franzen et al 1996, pp. 83–99

Essick GK, Rath EM, Kelly DG, James A, Murray RA. 1996b. A novel approach for studying direction discrimination. See Franzen et al 1996, pp. 59–72

Evans PM, Craig JC. 1992. Response competition: a major source of interference in a tactile identification task. *Percept. Psychophys.* 51:199–206

Evans PM, Craig JC, Rinker MA. 1992. Perceptual processing of adjacent and nonadjacent tactile nontargets. *Percept. Psychophys.* 52:571–81

Ferrell WR. 1995. Contribution of joint afferents to proprioception and motor control. In *Neural Control of Movement*, ed. WR Ferrell, U Proske, pp. 61–66. New York: Plenum

Ferrell WR, Craske B. 1992. Contribution of joint and muscle afferents to position sense at the human proximal interphalangeal joint. *Exp. Physiol.* 77:331–42

Ferrell WR, Smith A. 1987. The effect of digital nerve block on position sense at the proximal interphalangeal joint of the human index finger. *Brain Res.* 425:369–71

Ferrell WR, Smith A. 1989. The effect of loading on position sense at the proximal interphalangeal joint of the human index finger. *J. Physiol.* 418:145–61

Fields HL, ed. 1987. *Pain.* New York: McGraw-Hill

Fitzgerald M. 1994. Neurobiology of fetal and neonatal pain. See Wall & Melzack 1994, pp. 153–63

Flor H, Elbert T, Knecht S, Wienbruch C, Pantev C, et al. 1995. Phantom-limb pain as a perceptual correlate of cortical reorganization following arm amputation. *Nature* 375:482–84

Foulke E. 1991. Braille. See Heller & Schiff 1991, pp. 219–33

Franzen O, Johansson R, Terenius L, eds. 1996. *Somesthesis and the Neurobiology of the Somatosensory Cortex.* Basel, Switz. Birkhauser

Gandevia SC, Burke D. 1992. Does the nervous-system depend on kinesthetic information to control natural limb movements? *Behav. Brain. Sci.* 15:614–32

Garraghty PE, Kaas JH, Florence SL. 1994. Plasticity of sensory and motor maps in adult and developing mammals. In *Advances in Neural and Behavioral Development*, ed. VA Casagrande, PG Shinkman, 4:1–36. Norwood, NJ: Ablex

Geldard FA. 1972. *The Human Senses*. New York: Wiley & Sons. 2nd ed.

Gescheider GA, Beiles EJ, Checkosky CM, Bolanowski SJ, Verrillo RT. 1994a. The effects of aging on information-processing channels in the sense of touch: II. Temporal summation in the P channel. *Somatosens. Mot. Res.* 11:359–65

Gescheider GA, Bolanowski SJ, Hall KL, Hoffman KE, Verrillo RT. 1994b. The effects of aging on information-processing channels in the sense of touch: I. Absolute sensitivity. *Somatosens. Mot. Res.* 11: 345–57

Gescheider GA, Edwards RR, Lackner EA, Bolanowski SJ, Verrillo RT. 1996. The effects of aging on information-processing channels in the sense of touch: III. Differential sensitivity to changes in stimulus intensity. *Somatosens. Mot. Res.* 13:73–80

Gescheider GA, Valetutti AA Jr, Padula MC, Verrillo RT. 1992. Vibrotactile forward masking as a function of age. *J. Acoust. Soc. Am.* 91:1690–96

Goodwin AW, Browning AS, Wheat HE. 1996. Representation of the shape and contact force of handled objects in populations of cutaneous afferents. See Franzen et al 1996, pp. 137–45

Goodwin AW, Wheat HE. 1992. Human tactile discrimination of curvature when contact area with the skin remains constant. *Exp. Brain Res.* 88:447–50

Gracely RH. 1994. Studies of pain in normal man. See Wall & Melzack 1994, pp. 315–36

Green BG. 1987. The effect of cooling on the vibrotactile sensitivity of the tongue. *Percept. Psychophys.* 42:423–30

Green BG. 1991. Interactions between chemical and thermal cutaneous stimuli: inhibition (counterirritation) and integration. *Somatosens. Mot. Res.* 8:301–12

Green BG. 1992. The sensory effects of l-menthol on human skin. *Somatosens. Mot. Res.* 9:235–44

Green BG, Gelhard B. 1987. Perception of temperature on oral and facial skin. *Somatosens. Res.* 4:191–200

Greenspan JD, Bolanowski SJ. 1996. The psychophysics of tactile perception and its peripheral physiological basis. See Kruger 1996, pp. 25–103

Greenspan JD, LaMotte RH. 1993. Cutaneous mechanoreceptors of the hand: experimental studies and their implications for clinical testing of tactile sensation. *J. Hand Ther.* 6:75–82

Halligan PW, Marshall JC, Wade DT, Davey J, Morrison D. 1993. Thumb in cheek? Sensory reorganization and perceptual plasticity after limb amputation. *NeuroReport* 4:233–36

Heller MA. 1992. The effect of orientation on tactual braille recognition: optimal touching positions. *Percept. Psychophys.* 51: 549–56

Heller MA, Calcaterra JA, Burson LL, Tyler LA. 1996a. Tactual picture identification by blind and sighted people: effects of providing categorical information. *Percept. Psychophys.* 58:310–23

Heller MA, Calcaterra JA, Tyler LA, Burson LL. 1996b. Production and interpretation of perspective drawings by blind and sighted people. *Perception* 25:321–34

Heller MA, Joyner TD. 1993. Mechanisms in the haptic horizontal-vertical illusion: evidence from sighted and blind subjects. *Percept. Psychophys.* 53:422–28

Heller MA, Joyner TD, Dan-Fodio H. 1993. Laterality effects in the haptic horizontal-vertical illusion. *Bull. Psychon. Soc.* 31: 440–42

Heller MA, Kennedy JM. 1990. Perspective taking, pictures, and the blind. *Percept. Psychophys.* 48:459–66

Heller MA, Schiff W, eds. 1991. *The Psychology of Touch*. Hillsdale, NJ: Erlbaum

Hollins M, Delemos KA, Goble AK. 1991. Vibrotactile adaptation on the face. *Percept. Psychophys.* 49:21–30

Hollins M, Faldowski R, Rao S, Young F. 1993. Perceptual dimensions of tactile surface texture: a multidimensional scaling analysis. *Percept. Psychophys.* 54:697–705

Hollins M, Goble AK. 1988. Perception of the length of voluntary movements. *Somatosens. Res.* 5:335–48

Horner DT. 1995. The effect of location on the discrimination of spatial vibrotactile patterns. *Percept. Psychophys.* 57:463–74

Hsiao SS, Johnson KO, Twonbly A, DiCarlo J. 1996. Form processing and attention effects in the somatosensory system. See Franzen et al 1996, pp. 229–47

Hsiao SS, O'Shaughnessy DM, Johnson KO. 1993. Effects of selective attention on spatial form processing in monkey primary and secondary somatosensory cortex. *J. Neurophysiol.* 70:444–47

Irwin RJ, Whitehead PR. 1991. Towards an objective psychophysics of pain. *Psychol. Sci.* 2:230–35

Jenkins WM, Merzenich MM, Ochs MT, Allard T, Guic-Robles E. 1990. Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *J. Neurophysiol.* 63:82–104

Jensen TS, Turner JA, Wiesenfeld-Hallin Z, eds. 1997. *Proc. 8th World Congr. Pain.* Seattle, WA: IASP

Johnson KO, Hsiao SS. 1992. Neural mechanisms of tactual form and texture perception. *Annu. Rev. Neurosci.* 15:227–50

Johnson KO, Hsiao SS. 1994. Evaluation of the relative roles of slowly and rapidly adapting afferent fibers in roughness perception. *Can. J. Physiol. Pharmacol.* 72:488–97

Johnson KO, Van Boven RW, Hsiao SS. 1994. The perception of two points is not the spatial resolution threshold. See Boivie et al 1994, 3:389–404

Jones LA. 1994. Peripheral mechanisms of touch and proprioception. *Can. J. Physiol. Pharmacol.* 72:484–87

Kaczmarek KA, Bach-y-Rita P. 1995. Tactile displays. In *Virtual Environments and Advanced Interface Design*, ed. W Barfield, TA Furness, pp. 349–414. New York: Oxford Univ. Press

Klatzky RL, Lederman SJ. 1993. Toward a computational model of constraint-driven exploration and haptic object identification. *Perception* 22:597–621

Klatzky RL, Lederman SJ. 1995. Identifying objects from a haptic glance. *Percept. Psychophys.* 57:1111–23

Klatzky RL, Lederman SJ, Reed C. 1987. There's more to touch than meets the eye: the salience of object attributes for haptics with and without vision. *J. Exp. Psychol. Gen.* 116:356–69

Klatzky RL, Lederman SJ, Reed C. 1989. Haptic integration of object properties: texture, hardness, and planar contour. *J. Exp. Psychol. Hum. Percept. Perform.* 15:45–57

Klatzky RL, Loomis JM, Lederman S, Wake H, Fujita N. 1993. Haptic identification of objects and their depictions. *Percept. Psychophys.* 54:170–78

Kolhekar R, Murphy S, Gebhart GF. 1997. Thalamic NMDA receptors modulate inflammation-produced hyperalgesia in the rat. *Pain* 71:31–40

Koltzenburg M, Handwerker HO, Torebjork HE. 1993. The ability of humans to localise noxious stimuli. *Neurosci. Lett.* 150:219–22

Kops CE, Gardner EP. 1996. Discrimination of simulated texture patterns on the human hand. *J. Neurophysiol.* 76:1145–65

Kosek E, Hansson P. 1997. Modulatory influence on somatosensory perception from vibration and heterotopic noxious conditioning stimulation (HNCS) in fibromyalgia patients and healthy subjects. *Pain* 70:41–51

Kruger L, ed. 1996. *Pain and Touch.* San Diego, CA: Academic. 2nd ed.

LaMotte RH, Lu C, Srinivasan MA. 1996. Tactile neural codes for the shapes and orientations of objects. See Franzen et al 1996, pp. 113–22

LaMotte RH, Srinivasan MA. 1993. Responses of cutaneous mechanoreceptors to the shape of objects applied to the primate fingerpad. *Acta Psychol.* 84:41–51

LaMotte RH, Srinivasan MA. 1996. Neural encoding of shape: responses of cutaneous mechanoreceptors to a wavy surface stroked across the monkey fingerpad. *J. Neurophysiol.* 76:3787–97

Lautenbacher S, Rollman GB. 1997. Possible deficiencies of pain modulation in fibromyalgia. *Clin. J. Pain* 13:189–96

Lautenbacher S, Rollman GB, McCain GA. 1994. Multi-method assessment of experimental and clinical pain in patients with fibromyalgia. *Pain* 59:45–53

Lederman SJ, Klatzky RL. 1987. Hand movements: a window into haptic object recognition. *Cogn. Psychol.* 19:342–68

Lederman SJ, Klatzky RL. 1993. Extracting object properties through haptic exploration. *Acta Psychol.* 84:29–40

Lederman SJ, Klatzky RL, Reed CL. 1993. Constraints on haptic integration of spatially shared object dimensions. *Perception* 22:723–43

Lee DK, McGillis SLB, Greenspan JD. 1996. Somatotopic localization of thermal stimuli: I. A comparison of within- versus across-dermatomal separation of innocuous thermal stimuli. *Somatosens. Mot. Res.* 13:67–71

Loomis JM. 1990. A model of character recognition and legibility. *J. Exp. Psychol.: Hum. Percept. Perform.* 16:106–20

Loomis JM, Klatzky RL, Lederman SJ. 1991. Similarity of tactual and visual picture recognition with limited field of view. *Perception* 20:167–77

Loomis JM, Lederman SJ. 1986. Tactual perception. In *Handbook of Perception and Human Performance. Cognitive Processes and Performance*, ed. KR Boff, L Kaufman, JP Thomas, pp. 1–41. New York: Wiley & Sons. 2 Vols.

Lundberg LE, Jorum E, Holm E, Torebjork HE. 1992. Intra-neural electrical stimulation of cutaneous nociceptive fibres in humans: effects of different pulse patterns on magnitude of pain. *Acta Physiol. Scand.* 146:41–48

Mahar DP, Mackenzie BD. 1993. Masking, information integration, and tactile pattern perception: a comparison of the isolation and integration hypotheses. *Perception* 22: 483–96

Marks LE, Armstrong L. 1996. Haptic and visual representations of space. In *Attention and Performance*, ed. T Inui, JL McClelland, 16:263–87. Cambridge, MA: MIT Press

Matthews PB. 1988. Proprioceptors and their contribution to somatosensory mapping: complex messages require complex processing. *Can. J. Physiol. Pharmacol.* 66: 430–38

McDermid AJ, Rollman GB, McCain GA. 1996. Generalized hypervigilance in fibromyalgia: evidence of perceptual amplification. *Pain* 66:133–44

McGrath PJ, Unruh AM. 1994. Measurement and assessment of paediatric pain. See Wall & Melzack 1994, pp. 303–13

McMahon SB. 1994. Mechanisms of cutaneous, deep and visceral pain. See Wall & Melzack 1994, pp. 129–51

Melzack R. 1990. Phantom limbs and the concept of a neuromatrix. *Trends Neurosci.* 13:88–92

Melzack R, Wall PD. 1965. Pain mechanisms: a new theory. *Science* 150:971–79

Melzack R, Wall PD. 1996. *The Challenge of Pain*. Harmondsworth, UK: Penguin. 2nd ed.

Merskey H, Bodguk N. 1994. *Classification of Chronic Pain: Descriptions of Chronic Pain Syndromes and Definitions of Pain Terms*. Seattle, WA: IASP. 2nd ed.

Merzenich MM, Jenkins WM. 1993. Reorganization of cortical representations of the hand following alterations of skin inputs induced by nerve injury, skin island transfers, and experience. *J. Hand Ther.* 6:89–104

Merzenich MM, Recanzone GH, Jenkins WM, Allard TT, Nudo RJ. 1988. Cortical representational plasticity. In *Neurobiology of Neocortex*, ed. P Rakic, W Singer, pp. 41–67. Chichester, UK: Wiley & Sons

Meyer RA, Campbell JN, Raja SN. 1994. Peripheral neural mechanisms of nociception. See Wall & Melzack 1994, pp. 13–44

Mogilner A, Grossman JAI, Ribary U, Joliot M, Volkmann J, et al. 1993. Somatosensory cortical plasticity in adult humans revealed by magnetoencephalography. *Proc. Natl. Acad. Sci. USA* 90:3593–97

Naliboff BD, Cohen MJ. 1989. Psychophysical laboratory methods applied to clinical pain patients. See Chapman & Loeser 1989, pp. 365–86

Naliboff BD, Cohen MJ, Schandler SL, Heinrich RL. 1981. Signal detection and threshold measures for chronic back pain patients, chronic illness patients, and cohort controls to radiant heat stimuli. *J. Abnorm. Psychol.* 3:271–74

O'Sullivan BT, Roland PE, Kawashima R. 1994. A PET study of somatosensory discrimination in man. Microgeometry versus macrogeometry. *Eur. J. Neurosci.* 6: 137–48

Patel J, Essick GK, Kelly DG. 1997. Utility of square-wave gratings to assess perioral spatial acuity. *J. Oral Maxillofac. Surg.* 55:593–601

Pertovaara A. 1998. A neuronal correlate of secondary hyperalgesia in the rat spinal dorsal horn is submodality selective and facilitated by supraspinal influence. *Exp. Neurol.* 149:193–202

Phillips JR, Johansson RS, Johnson KO. 1990. Representation of braille characters in human nerve fibres. *Exp. Brain Res.* 81: 589–92

Phillips JR, Matthews PBC. 1993. Texture perception and afferent coding distorted by cooling the human ulnar nerve. *J. Neurosci.* 13:2332–41

Pons TP, Garraghty PE, Ommaya AK, Kaas JH, Taub E, Mishkin M. 1991. Massive cortical reorganization after sensory deafferentation in adult macaques. *Science* 252:1857–60

Post LJ, Chapman CE. 1991. The effects of cross-modal manipulations of attention on the detection of vibrotactile stimuli in humans. *Somatosens. Mot. Res.* 8:149–57

Price DD. 1988. *Psychological and Neural Mechanisms of Pain*. New York: Raven

Price DD. 1994. Psychophysical measurement of normal and abnormal pain processing. See Boivie et al 1994, pp. 3–25

Price DD, Mao J, Frenk H, Mayer DJ. 1994. The N-methyl-D-aspartate receptor antagonist dextromethorphan selectively re-

duces temporal summation of second pain in man. *Pain* 59:165–74

Price R. 1994. *A Whole New Life*. New York: Scribner

Ramachandran VS, Rogers-Ramachandran DC, Stewart M. 1992. Perceptual correlates of massive cortical reorganization. *Science* 258:1159–60

Recanzone GH, Merzenich MM, Jenkins WM. 1992. Frequency discrimination training engaging a restricted skin surface results in an emergence of a cutaneous response zone in cortical area 3a. *J. Neurophysiol.* 67:1057–70

Reed CL. 1994. Perceptual dependence for shape and texture during haptic processing. *Perception* 23:349–66

Reed CL, Caselli RJ. 1994. The nature of tactile agnosia: a case study. *Neuropsychologia* 32:527–39

Reed CL, Caselli RJ, Farah MJ. 1996. Tactile agnosia: underlying impairment and implications for normal tactile object recognition. *Brain* 119:875–88

Reed CM, Durlach NI, Delhorne LA. 1992. Natural methods of tactual communication. See Summers 1992, pp. 218–30

Rinker MA, Craig JC. 1994. The effect of spatial orientation on the perception of moving tactile stimuli. *Percept. Psychophys.* 56:356–62

Rollman GB. 1977. Signal detection theory measurement of pain: a review and critique. *Pain* 3:187–211

Rollman GB. 1979. Signal detection theory pain measures: empirical validation studies and adaptation-level effects. *Pain* 6: 9–21

Rollman GB. 1992. Cognitive variables in pain and pain judgments. In *Psychophysical Approaches to Cognition*, ed. D Algom, pp. 515–74. Amsterdam: North Holland

Sathian K, Burton H. 1991. The role of spatially selective attention in the tactile perception of texture. *Percept. Psychophys.* 50:237–48

Sathian K, Goodwin AW, John KT, Darian-Smith I. 1989. Perceived roughness of a grating: correlation with responses of mechanoreceptive afferents innervating the monkey's fingerpad. *J. Neurosci.* 9: 1273–79

Schmidt R, Schmelz M, Forster C, Ringkamp M, Torebjork E, Handwerker H. 1995. Novel classes of responsive and unresponsive C nociceptors in human skin. *J. Neurosci.* 15:333–41

Schmidt RF, Wahren LK. 1990. Multiunit neural responses to strong finger pulp vibration. II. Comparison with tactile sensory thresholds. *Acta Physiol. Scand.* 140: 11–16

Scudds RA, Rollman GB, Harth M, McCain GA. 1987. Pain perception and personality measures as discriminators in the classification of fibrositis. *J. Rheumatol.* 14: 563–69

Sherrick CE. 1991. Vibrotactile pattern perception: some findings and applications. See Heller & Schiff 1991, pp. 189–217

Sherrick CE, Cholewiak RW. 1986. Cutaneous sensitivity. See Boff et al 1986, pp. 1–58

Sherrick CE, Cholewiak RW, Collins AA. 1990. The localization of low- and high-frequency vibrotactile stimuli. *J. Acoust. Soc. Am.* 88:169–79

Shimizu Y, Saida S, Shimura H. 1993. Tactile pattern recognition by graphic display: importance of 3-D information for haptic perception of familiar objects. *Percept. Psychophys.* 53:43–48

Simone DA, Ochoa J. 1991. Early and late effects of prolonged topical capsaicin on cutaneous sensibility and neurogenic vasodilatation in humans. *Pain* 47:285–94

Simone DA, Sorkin LS, Oh U, Chung JM, Owens C, et al. 1991. Neurogenic hyperalgesia: central neural correlates in responses of spinothalmic tract neurons. *J. Neurophysiol.* 66:228–46

Sinclair RJ, Burton H. 1991. Tactile discrimination of gratings: psychophysical and neural correlates in human and monkey. *Somatosens. Mot. Res.* 8:241–48

Srinivasan MA, LaMotte RH. 1995. Tactual discrimination of softness. *J. Neurophysiol.* 73:88–101

Sterr A, Muller MM, Elbert T, Rockstroh B, Pantev C, Taub E. 1998. Changed perceptions in braille readers. *Nature* 391:134–35

Stevens JC. 1989. Temperature and the two-point threshold. *Somatosens. Mot. Res.* 6: 275–84

Stevens JC. 1990. Perceived roughness as a function of body locus. *Percept. Psychophys.* 47:298–304

Stevens JC, Choo KK. 1996. Spatial acuity of the body surface over the life span. *Somatosens. Mot. Res.* 13:153–66

Stevens JC, Choo KK. 1998. Temperature sensitivity of the body surface over the life span. *Somatosens. Mot. Res.* 15:13–28

Stevens JC, Cruz LA. 1996. Spatial acuity of touch: ubiquitous decline with aging revealed by repeated threshold testing. *Somatosens. Mot. Res.* 13:1–10

Stevens JC, Foulke E, Patterson MQ. 1996. Tactile acuity, aging, and braille reading in long-term blindness. *J. Exp. Psychol.: Appl.* 2:91–106

Stevens JC, Patterson MQ. 1995. Dimensions of spatial acuity in the touch sense: changes over the life span. *Somatosens. Mot. Res.* 12:29–47

Stubhaug A, Breivik H, Eide PK, Kreunen M, Foss A. 1997. Mapping of punctuate hyperalgesia around a surgical incision demonstrates that ketamine is a powerful suppressor of central sensitization to pain following surgery. *Acta Anaesthesiol. Scand.* 41:1124–32

Summers IR, ed. 1992. *Tactile Aids for the Hearing Impaired.* London: Whurr

Tan HZ. 1996. *Information transmission with a multi-finger tactual display*. PhD thesis. MIT, Cambridge, MA

Tan HZ, Rabinowitz WM, Durlach NI. 1989. Analysis of a synthetic Tadoma system as a multidimensional tactile display. *J. Acoust. Soc. Am.* 86:981–88

Tillman DB, Treede RD, Meyer RA, Campbell JN. 1995a. Response of C fibre nociceptors in the anaesthetized monkey to heat stimuli: correlation with pain threshold in humans. *J. Physiol.* 485:767–74

Tillman DB, Treede RD, Meyer RA, Campbell JN. 1995b. Response of C fibre nociceptors in the anaesthetized monkey to heat stimuli: estimates of receptor depth and threshold. *J. Physiol.* 485:753–65

Torebjork E. 1994. Nociceptor dynamics in humans. In *Proc. 7th World Congr. on Pain*, ed. GF Gebhart, DL Hammond, TS Jensen, pp. 277–84. Seattle, WA: IASP

Torebjork HE, Lundberg LE, LaMotte RH. 1992. Central changes in processing of mechanoreceptive input in capsaicin-induced secondary hyperalgesia in humans. *J. Physiol.* 448:765–80

Tremblay F, Ageranioti-Belanger SA, Chapman CE. 1996. Cortical mechanisms underlying tactile discrimination in the monkey. 1. Role of primary somatosensory cortex in passive texture discrimination. *J. Neurophysiol.* 76:3382–403

Vallbo AB, Olausson H, Wessberg J, Kakuda N. 1994. Receptive field characteristics of tactile units with myelinated afferents in hairy skin of human subjects. *J. Physiol.* 483:783–95

Van Boven RW, Johnson KO. 1994a. The limit of tactile spatial resolution in humans: grating orientation discrimination at the lip, tongue, and finger. *Neurology* 44: 2361–66

Van Boven RW, Johnson KO. 1994b. A psychophysical study of the mechanisms of sensory recovery following nerve injury in humans. *Brain* 117:149–67

Van Doren CL, Menia LL. 1993. Representing the surface texture of grooved plates using single-channel, electrocutaneous stimulation. See Verrillo 1993, pp. 177–97

Vega-Bermudez F, Johnson KO, Hsiao SS. 1991. Human tactile pattern recognition: active versus passive touch, velocity effects, and patterns of confusion. *J. Neurophysiol.* 65:531–46

Verrillo RT. 1993. The effects of aging on the sense of touch. In *Sensory Research: Multimodal Perspectives*, ed. RT Verrillo, pp. 285–98. Hillsdale, NJ: Erlbaum

Wall PD, Melzack R. 1994. *Textbook of Pain*. Edinburgh, UK: Churchill Livingstone. 3rd ed.

Weisenberger JM. 1992. Communication of the acoustic environment via tactile stimuli. See Summers 1992, pp. 83–109

Whang KC, Burton H, Shulman GL. 1991. Selective attention in vibrotactile tasks: detecting the presence and absence of amplitude change. *Percept. Psychophys.* 50: 157–65

Wilder-Smith OH, Arendt-Nielsen L, Gaumann D, Tassonyi E, Rifat KR. 1998. Sensory changes and pain after abdominal hysterectomy: a comparison of anesthetic supplementation with fentanyl versus magnesium or ketamine. *Anesth. Analg.* 86:95–101

Woodward KL. 1993. The relationship between skin compliance, age, gender, and tactile discriminative thresholds in humans. *Somatosens. Mot. Res.* 10:63–67

Yang TT, Gallen CC, Ramachandran VS, Cobb S, Schwartz BJ, Bloom FE. 1994. Noninvasive detection of cerebral plasticity in adult human somatosensory cortex. *NeuroReport* 5:701–4