The roles and functions of cutaneous mechanoreceptors

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Combined psychophysical and neurophysiological research has resulted in a relatively complete picture of the neural mechanisms of tactile perception. The results support the idea that each of the four mechanoreceptive afferent systems innervating the hand serves a distinctly different perceptual function, and that tactile perception can be understood as the sum of these functions. Furthermore, the receptors in each of those systems seem to be specialized for their assigned perceptual function.

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Abbreviations

PC	Pacinian
RA	rapidly adapting
SA1	slowly adapting type 1
SA2	slowly adapting type 2

Introduction

The four cutaneous mechanoreceptive afferent neuron types that innervate the glabrous skin comprise slowly adapting type 1 (SA1) afferents that end in Merkel cells, rapidly adapting (RA) afferents that end in Meissner corpuscles, Pacinian (PC) afferents that end in PC corpuscles, and slowly adapting type 2 (SA2) afferents that are thought to terminate in Ruffini corpuscles. Each of these neuron types responds to cutaneous motion and deformation in a different way. The mechanosensitive transducers reside in the unmyelinated endings of the afferent fibers. The receptors' selectivity seems to be due as much to the receptor structure that surrounds each of these endings as to the transducer itself.

The Merkel cell has the simplest structure; it is a special cell type in the basal layer of the epidermis that enfolds the unmyelinated ending of the SA1 afferent fiber. The SA1 receptor is selectively sensitive to a particular component of the local stress-strain field, which makes it sensitive to edges, corners, and curvature; it is not known whether this selectivity is due to the Merkel cell or to the transducer mechanism within the afferent terminal. Meissner corpuscles are relatively large cell assemblies in the dermal ridges that lie just beneath the epidermis. They comprise cell layers that cushion and enfold the large leaf-like endings of two to six RA afferent fibers. This pillow-like arrangement appears to act as a filter that protects the velocity-sensitive endings from static skin deformation. PC corpuscles reside in the dermis and deeper tissues. The PC corpuscle is a large, layered onion-like structure with as many as 70 layers, enclosing a single nerve ending that is sensitive to deformation in the nanometer range. The layers function as a series of mechanical filters to protect the extremely sensitive receptor from the very large, low-frequency stresses and strains of ordinary manual labor. The Ruffini corpuscle, which is located in the connective tissue of the dermis, is a relatively large spindle shaped structure tied into the local collagen matrix. It is, in this way, similar to the Golgi tendon organ in muscle. Its association with connective tissue makes it selectively sensitive to skin stretch. Each of these receptor types and its role in perception is discussed below.

During three decades of neurophysiological and combined psychophysical and neurophysiological studies, evidence has accumulated that links each of these afferent types to a distinctly different perceptual function and, furthermore, that shows that the receptors innervated by these afferents are specialized for their assigned functions.

As the combined psychophysical and neurophysiological evidence that supports this view is too extensive to discuss here and has been reviewed recently [1], I will focus on the apparent specialization of each of the mechanoreceptors for its assigned function. Where important references supporting a statement are pre-1990 and have been discussed previously, the reader is referred to the earlier review [1].

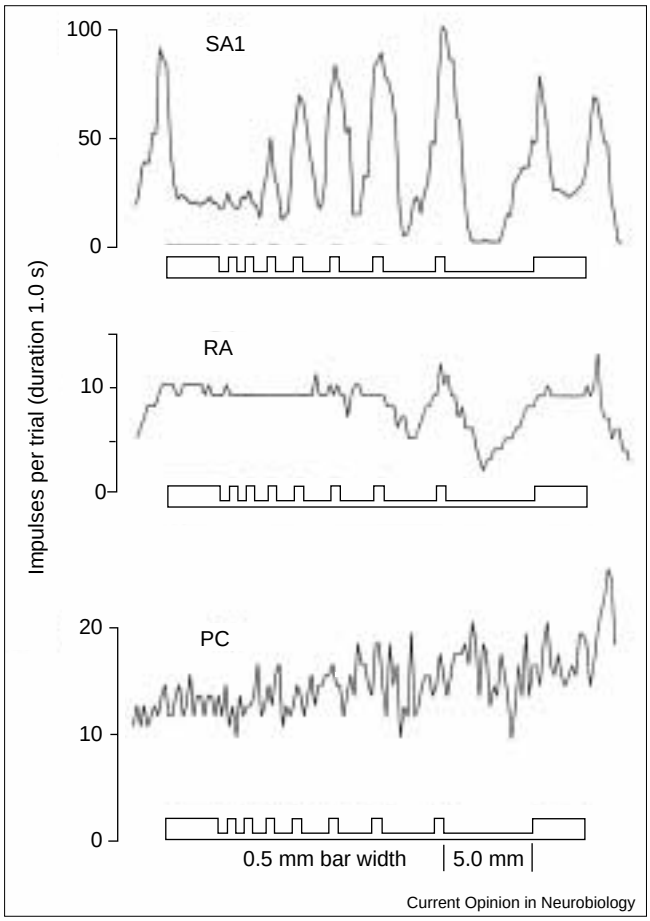
Merkel–SA1 afferents

SA1 afferents innervate the skin densely (about 100 per cm^2 at the fingertip in man and monkey [1]), and they respond to sustained indentation with a sustained, slowly adapting discharge that is linearly related to indentation depth. They have two remarkable response properties. One is their sensitivity to points, edges and curvature, which is a consequence of their selective sensitivity to strain energy density or a closely related strain component (the square of the maximum local compressive strain regardless of its orientation). The other is their spatial resolution: individual SA1 afferents resolve spatial detail of 0.5 mm, although their receptive field diameters are 2–3 mm. Because of these two properties, the SA1 population transmits an acute spatial neural image of a tactile stimulus.

Goodwin and Wheat [2,3•] have analyzed the effects of variation in population parameters such as innervation nonuniformity, and have shown that these parameters have little effect on the acuity of the SA1 neural image and the information conveyed by the population. Combined psychophysical and neurophysiological studies show that the SA1 afferents are, in fact, responsible for form and texture perception [1].

The SA1 receptors are Merkel–neurite complexes involving specialized (Merkel) epidermal cells that enfold the

Figure 1



SA1, RA and PC responses to an aperiodic grating pressed into the skin. The grating is shown in cross-section beneath each response profile. The end bars are 3.0 mm wide; the internal bars are 0.5 mm wide. The grooves are deeper than illustrated (2.0 mm deep) and are 0.5, 0.5, 0.75, 1.0, 1.5, 2.0, 3.0 and 5.0 mm wide. The grating indented the skin by 1 mm for 1 s, was raised and moved laterally 0.2 mm for the next indentation. The ordinate represents the number of action potentials evoked during each 1-s period. RA and PC afferents responded during the indentation phase only, which accounts for their smaller impulse counts. The abscissa for each plot represents the position of the receptive field center relative to the grating; for example, the left peak in the SA1 response profile (95 impulses per s) occurred when the center of the SA1 RF was directly beneath the left edge of the grating. The RA illustrated here was the most sensitive to spatial detail out of all RAs studied. Most RA responses dipped only during the 5 mm gap and some barely registered the presence of the 5 mm gap even though they responded vigorously at all grating positions. Testing progressed from right to left. The progressive decline in PC responses results from adaptation to the repeated indentations. Adapted with permission from [7].

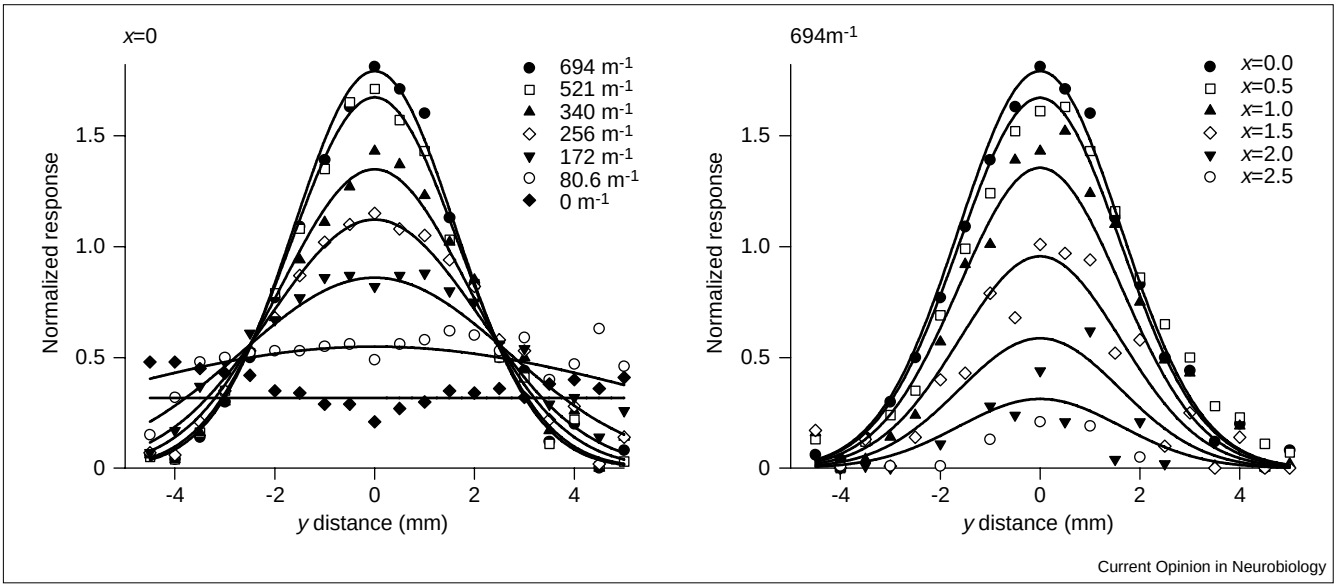
unmyelinated ends of SA1 axons [1]. Although there are synapse-like junctions between the Merkel cells and the axon terminals, action potentials appear to arise as the result of mechanosensitive ion channels in the bare nerve endings [4,5]. As individual SA1 afferent axons approach the epidermis, they branch over an area of about 5 mm^2 [6] and innervate a large but unknown number of Merkel receptors (100 is an estimate of the order of magnitude). The receptive field of an SA1 afferent has hot spots that undoubtedly correspond to individual branches of the afferent axon [7,8]. When the spatial detail becomes finer than the receptive field diameter, a single skin spot (i.e., a single terminal branch) becomes dominant, which accounts for the fact that SA1 afferents resolve spatial detail smaller than their receptive field diameters [7].

Figure 1 illustrates the SA1 afferent's two principal response properties: high spatial resolution, and responsiveness to stimulus features such as edges and bars rather than to indentation *per se*. The modulation of SA1 firing rates beginning at 0.5 mm wide gaps parallels closely the human psychometric function for discriminating grating orientation. Human discrimination begins to rise above chance behavior when gaps and bars are 0.5 mm wide and reaches threshold when they are about 1.0 mm wide [9,10]. The selective sensitivity for edges and bars illustrated in Figure 1 arises from the Merkel receptor's selective sensitivity to strain energy density or a closely related component of tissue strain [11–13].

An additional quality that makes SA1 afferents particularly suited to the representation of surface or object form is its linear response to skin deformation over a very wide range of deformations. SA1 afferents respond to skin indentation to depths of at least 1500 μm with a linear discharge rate [1,6,14]; in contrast, the RA afferent response begins to saturate at about 100 μm [6] and is insensitive to the height of surface features above 300–400 μm [14,15]. Because of the linearity and the SA1 responsiveness to strain energy density, the SA1 afferents represent object curvature very accurately as shown by a number of studies [2,16–19,20•]. For example, Goodwin *et al.* [16] showed that only SA1 afferents provide the brain with a veridical neural image of a curved surface — an image that could be used for the perception of curvature. LaMotte and Srinivasan [17] scanned a series of cylindrical waves with varying curvature across the receptive fields of SA1 and RA afferents. They found that the discharge rates of both afferent types were related to surface curvature, but SA1 firing rates represented the shapes of the cylindrical wave more effectively than did the RA firing rates [17]. Finally, Dodson *et al.* [19] showed that the human threshold for object orientation is 4 to 5 degrees at the fingertip. Only the SA1 population provides a neural image of the stimulus and its orientation that can account for the psychophysical behavior.

Goodwin and colleagues have shown also that humans can discriminate curvature independent of contact force [21] and contact area [22], which implies that subjects rely on the spatial profile of the neural activity evoked by a curved surface rather than some intensive cue like total impulse rate. Figure 2 illustrates the SA1 neural activity evoked by a series of curved surfaces. No other afferent type provides a representation on which curvature discrimination might be based [16,23,24].

Figure 2



Population response of peripheral SA1 afferents to indentation with spheres of varying curvature. The left plot shows the mean responses of SA1 afferents as a function of proximal–distal distance from the center of indentation. Data are shown for seven curved surfaces with radii ranging from 1.4 mm (curvature = 694 m^{-1}) to a flat surface (curvature = 0 m^{-1}). The right plot shows population response profiles in proximal–distal slices at varying distances from the center of indentation. Adapted with permission from [16].

There is other evidence of SA1 specialization for the representation of spatial information:

1. SA1 responses to stimulus elements on a surface are independent of the force of application [25].

2. SA1-receptive fields grow minimally (relative to RA receptive fields) with increasing indentation depth [6].

3. SA1 afferents possess a response property, surround suppression, which confers response properties similar to those produced by surround inhibition in the central nervous system [25]. This response property is a consequence of sensitivity to strain energy density, not a synaptic mechanism.

4. SA1 spatial resolution is affected minimally by changes in scanning velocity at velocities up to at least 80 mm s^{-1} [26,27].

5. SA1 afferents are at least ten times more sensitive to dynamic than to static stimuli [1].

6. SA1 responses to repeated skin indentation are practically invariant: the variability is about one impulse per trial regardless of the number of action potentials evoked [6].

The psychophysical correlate of points 1 and 2 is that tactile pattern recognition is independent of contact force [1]. The psychophysical correlate of point 3 is much greater sensitivity to curvature and surface features than to indentation *per se* [1,7,21,22]. The psychophysical correlate of point 4 is tactile spatial pattern recognition at scanning velocity up to at least 80 mm s^{-1} [28]. The psychophysical correlate of point 5 is much greater sensitivity to form and texture when fingers scan a surface than when they are stationary. David Katz [29] has said that "movement [is] as indispensable for touch as light is for color sensations". The SA1 sensitivity to motion is the basis of this observation. The psychophysical correlate of point 6 is the human ability to discriminate surface form. For example, humans can reliably discriminate surfaces with dots or ridges, even when their spacings differ by as little as 2% [30,31].

Meissner–RA afferents

Meissner afferents innervate the skin even more densely (about 150 per cm^2 at the fingertip in man and monkey [1]) than do the SA1 afferents, they are insensitive to static skin deformation, and they are four time more sensitive to dynamic skin deformation than are SA1 afferents. Unlike SA1 afferents, they respond to stimuli over their entire receptive fields (3–5 mm in diameter) with relative uniformity and therefore resolve spatial detail poorly. A mechanistic interpretation is that, unlike the SA1 afferents, all the terminal branches of an RA afferent contribute equally when multiple endings are stimulated simultaneously by dense spatial detail.

Because of this wide, uniform sensitivity, RA afferents transmit a robust neural image of skin motion. For many years, they have been known to be responsible for the detection and discrimination of low frequency vibration [1]. A more recent observation is that they are responsible for

detecting slip between the skin and an object held in the hand [1,32] and that, of the four afferent types, they are the most effective at signaling sudden forces that act on objects held in the hand [33]. Considering the importance of prehension, the RA's most important function would seem to be the provision of feedback signals for grip control [33,34].

Individual RA afferent nerve fibers end as unmyelinated, disk-like endings within Meissner's corpuscles, which occur in dermal pockets between the sweat ducts and adhesive ridges [1,35]. This position places the RA afferents as close to the surface of the epidermis as is possible within the dermis. This may account, in part, for the greater sensitivity of RA afferents to minute skin deformation relative to SA1 afferents, whose receptors are on the tips of the deepest epidermal ridges.

It is difficult to think of a more important role for the RA afferents than as the essential feedback sensors for grip control. Johansson and colleagues [1,33,34] have shown that as we lift and manipulate an object there are frequent microscopic slips between the object and the skin, and that the skin motion associated with these slips evokes reflexive increases in grip force.

This constant adjustment allows us to manipulate objects with delicacy — with grip forces not far above the forces that result in overt slip. A complication is that the required grip forces depend on factors like surface coefficient of friction as well as the object's weight. The evidence from microneurographic recordings in humans as they lift and manipulate objects and in controlled psychophysical and neurophysiological experiments is that RA afferents provide the signals that are critical for grip control [1,32–34].

The RA afferent responses possess several qualities that appear to be specialized for this function. First, studies using indentation, vibration and scanned raised elements have shown that RA afferents are four times more sensitive to skin motion than SA1 afferents [1]. Second, as illustrated in Figure 1, they are more uniformly sensitive to stimuli within their receptive fields than are SA1 afferents [6,7,36,37]. RAs fail to represent the gaps in a grating until they are 3–5 mm wide because of their uniform responsiveness over receptive fields that are 3–5 mm wide. The result is poor spatial acuity but a robust response to local events such as slip. On the basis of their innervation density at the fingertip (150 per cm^2) and their receptive field sizes (10–30 mm^2) it can be estimated that 15–50 RA afferents signal transient local skin motion. Third, they are insensitive to static force and very low-frequency vibration. If they were not, the response to forces required to grip an object would mask the small signals produced by local microslip. The basis of this insensitivity is probably the fluid-filled corpuscle within which the very sensitive receptors reside (see section on PC corpuscles below).

The RA and SA1 systems are, in some ways like the scotopic and photopic systems in vision. The RA system, like the scotopic system, has greater sensitivity but poorer spatial resolution and limited dynamic range. The SA1 system, like the photopic system, is less sensitive but has higher spatial resolution and operates over a wider dynamic range.

Pacinian afferents

PC afferents terminate in single corpuscles [38] that are distributed throughout the palm and fingers (about 350 per finger and 800 in the palm) [1]. These afferents have three remarkable response properties.

The first is their extreme sensitivity: the most sensitive PC afferents respond to 10 nm of skin motion or less at 200 Hz [39]. Because of their extreme sensitivity and the deep locations of PC receptors, PC afferents have almost no spatial resolution, as can be seen in Figure 1. The receptive field of a PC receptor may include an entire hand. The second is their intense filtering (at nearly 60 dB per decade) of low-frequency stimuli that would otherwise overwhelm the sensitive PC receptors. Third, they respond to stimuli less than 100–150 Hz with a phase-locked, Poisson discharge [40]. The theoretical importance of a Poisson discharge (auditory primary afferents also respond to a sinusoidal stimulus with a phase-locked Poisson discharge) is that no single afferent can accurately represent the waveform of a complex stimulus in the 30–150 Hz range with its instantaneous firing rate. However, a whole population firing randomly but at a rate proportional to the instantaneous stimulus amplitude can represent the stimulus waveform accurately.

Because of these response properties, the PC population produces a high-fidelity neural image of transient and vibratory stimuli transmitted to the hand by objects held in the hand. For many years, they have been known to be responsible for the perception of high frequency stimuli [1]. Combined psychophysical and neurophysiological experiments show that an important consequence of this function is the perception of distant events through transmitted vibrations when we grasp an object in the hand [39]. When we become skilled in the use of a probe or a tool, we perceive events at the working surface of the tool or probe as though our fingers were present. The PC afferents are responsible for this critical perceptual capacity.

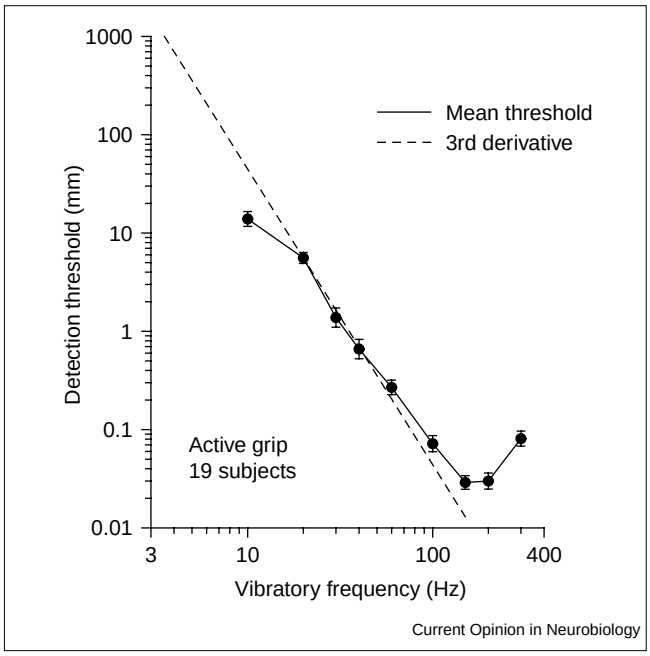
Hunt first showed that PC afferents are sensitive to distant events through transmitted vibrations [1]. He discovered that the spontaneous discharge that he was recording was, in fact, a response to ambient vibrations in the laboratory. The most sensitive PC corpuscles respond to vibratory amplitudes as small as 3 nm applied directly to the corpuscle [41] and 10 nm applied to the skin [39]. Sensitivity thresholds have been shown to be much lower when grasping a large object vibrating parallel to the skin surface as opposed to vibrating normal to the skin surface [39]. When a human subject grasps a rod conveying vibrations from a shaker embedded within the rod, thresholds for individual subjects are as low as 10 nm [39].

In contrast, RA afferents are about two orders of magnitude less sensitive than PC afferents. These observations show that the PC afferents play a principal, if not the exclusive role in the perception of distant events through an object held in the hand.

The most obvious specialization for this function is the extreme sensitivity of the PC receptor, but that sensitivity would be of little use if the receptor were not protected from the intense, low-frequency forces that accompany many manual tasks. Even though we grip a tool, such as a shovel, vigorously, we perceive events at the working surface of the tool, such as the texture of sand at the end of the shovel, as though our fingers were present.

The layered lamellae of the PC corpuscle function as an extremely selective cascade of high-pass filters [42]. Between 20 and 150 Hz, the human threshold for detecting transmitted vibration falls from 5.6 to 0.03 μm, which amounts to a drop of 52 dB per decade (Figure 3). This is close to the filtering characteristic of a mechanism sensitive to the third temporal derivative of tissue displacement (–60 dB per decade, dashed line in Figure 12), which is called 'jerk' because it corresponds to the rate of change of acceleration. Our hands are used constantly in manual tasks that subject the cutaneous and subcutaneous tissues to large, dynamic stresses and strains. If it were not for the steep filtering provided by the multilayered, fluid-filled corpuscles, the sensitive receptor within would be overwhelmed by the deformations produced by these forces. If the extrapolation to low frequencies illustrated in Figure 3 is accurate, a peak-to-peak motion of 1 cm at 2 Hz would not activate the PC system.

Figure 3



Threshold for the detection of transmitted vibration when subjects grasp a 32-mm diameter cylindrical rod. Vibrations were produced by a linear motor mounted at one end of the rod. Vibratory amplitudes were measured with a three-dimensional accelerometer mounted on the rod. The ordinate represents the mean threshold amplitude measured as half the vibratory peak-to-peak excursion. Filled circles and solid lines represent the psychophysical thresholds. The dashed line has the slope of an ideal detector sensitive to the third derivative of stimulus motion (i.e. –60 dB/decade). The human vibratory threshold at 10 Hz is less than the dashed line because the RA afferents are more sensitive at 10 Hz than are the PC afferents. Adapted with permission from [39].

SA2 afferents

SA2 afferents innervate the skin less densely than either SA1 or RA afferents. SA2 receptive fields are about five times larger, they are about six times less sensitive to skin indentation, but they are 2–4 times more sensitive to skin stretch than SA1 afferents [1,43]. They signal skin stretch more effectively than SA1 afferents and with much less interference by stimulus features within their receptive fields. Consequently, the SA2 population transmits a neural image of skin stretch to the central nervous system with relatively little interference from objects held in the hand.

SA2 afferents present a puzzle. They are reported regularly in microneurographic studies of mechanoreceptors in the human hand but have never been observed in neurophysiological studies of mechanoreceptors in the monkey hand. For this reason, they have been studied less extensively than the other afferent types.

Even so, combined psychophysical and neurophysiological studies in the human have identified two important roles for SA2 afferents. The first is perception of the direction of object motion or force when the motion or direction of force produces skin stretch [44•]. SA2 afferents are not, however, exclusively responsible for the perception of motion because motion is clearly perceived when only RA afferents can provide the relevant information [45]. Gardner and Sklar [45] used a device comprising an array of vibrating pins that activate only RA and PC afferents and found that motion and motion direction are discriminated effectively. This demonstrates that motion perception is possible on the basis of RA responses alone (because the PC afferent population response has too little spatial resolution to signal motion detection).

The second is a substantial role, along with muscle spindles and possibly joint afferents, in the perception of hand shape and finger position through the pattern of skin stretch produced by each hand and finger conformation [1,46,47,48•]. Two studies have shown that simply stretching this skin, which activates SA2 afferents strongly (and SA1 afferents more weakly), produces the illusion of finger flexion [46,47], as does tendon vibration [47].

The much greater sensitivity to stretch than to indentation suggests that the SA2 receptor is sensitive to horizontal

tensile strain, which is less sensitive to local indentation than other strain components [11,13]. This and the SA2 receptor's deep location seem to shield SA2 afferents from the confounding effects of the indentation produced by an object, leaving it free to signal the object's direction of motion and hand conformation.

Conclusions

The accumulated evidence suggests that there is a sharp division of function among the four cutaneous afferent systems that innervate the human hand. First, the SA1 system provides a high-quality neural image of the spatial structure of objects and surfaces that is the basis of form and texture perception. Second, the RA system provides a neural image of motion signals from the whole hand. From this, the brain extracts information that is critical for grip control and information about the motion of objects contacting the skin. Third, the PC system provides a neural image of vibrations transmitted to the hand from objects contacting the hand or, more frequently, objects grasped in the hand. This provides the basis for the perception of distant events through probes and tools held in the hand. Fourth, the SA2 system provides a neural image of skin stretch over the whole hand. The evidence for this is less secure but the most likely hypothesis is that the brain extracts information about hand conformation from the dorsal SA2 image (and the ventral image when the hand is empty). When the hand is occupied, the ventral SA2 image signals information about the direction of motion of objects moving across the skin surface and about the direction of forces exerted on the hand.

The distinctively different functions identified for the four cutaneous mechanoreceptive afferent systems suggest the existence of distinct and separate central systems for processing the information provided by each of the primary afferent groups. For example, the computational problems inherent in processing information for form and texture perception (the SA1 system) have little in common with the problems inherent in processing information about motion and motion direction (RA and SA2 functions). A recent study of neurons in area 3b of primary somatosensory cortex shows, for example, that neurons in this region are highly selective for spatial form and have mechanisms that seem designed to preserve spatial information at high scanning velocities [49•]; on the other hand, neurons in area 3b are no more sensitive to motion or motion direction than are primary afferents. This suggests that the very important processes underlying motion perception lie elsewhere.

A major challenge is to map and understand the central pathways processing the information provided by each of the four primary afferent systems. A feature of the four afferent systems that has made the inferences laid out in this paper difficult to come by, is that all four of the afferent systems are very sensitive and almost all suprathreshold stimuli activate all four systems. An important goal for peripheral neurophysiologists is to learn how to selectively stimulate each of the afferent systems with meaningful stimuli so that the central pathways for each of the systems can be identified and studied. The challenge for central neurophysiologists is to understand the operations that underlie the perceptual functions of each of the four systems.

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