Encodings of Object Curvature by Tactile Afferents From Human Fingers

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Goodwin, A. W., V. G. Macefield, and J. W. Bisley. Encoding of object curvature by tactile afferents from human fingers. J. Neurophysiol. 78: 2881–2888, 1997. Isolated responses were recorded from fibers in the median nerves of human subjects by using microneurography. Mechanoreceptive afferent fibers with receptive fields on the fingerpads were selected. The fibers were immobilized and spherical stimuli were applied passively to the receptive field with a contact force of 40-, 60-, or 80-g weight. The radii of the spheres were 1.92, 2.94, 5.81, or 12.4 mm or \(\infty\) (flat); the corresponding curvatures, given by the reciprocal of the radii, were 694, 340, 172, 80.6, or 0 m\(^{-1}\), respectively. When the spheres were applied to the receptive field center of slowly adapting type I afferents (SAIs), the response increased as the curvature of the sphere increased and also increased as the contact force increased. All SAIs behaved in the same way except for a scaling factor proportional to the sensitivity of the afferent. When a sphere was located at different positions in the receptive field, the shape of the resulting response profile reflected the shape of the sphere; for more curved spheres the profile was higher and narrower (increased peak and decreased width). Slowly adapting type II afferents (SAIIs) showed different response characteristics from the SAIs when spheres were applied to their receptive field centers. As the curvature of the stimulus increased from 80.6 to 172 m\(^{-1}\), the response increased. However, further increases in curvature did not result in further increases in response. An increase in contact force resulted in an increase in the response of SAIIs; this increase was proportionately greater than it was for SAIs. For SAIIs, the shape of the receptive field profile did not change when the curvature of the stimulus changed. For fast-adapting type I afferents (FAIs), the responses were small and did not change systematically with changes in curvature or contact force. Fast-adapting type II afferents (FAIIs) did not respond to our stimuli. Human SAIs, FAIs, and FAIIs behaved like monkey SAIs, FAIs, and FAIIs, respectively. The response of the SAI population contains accurate information about the shape of the sphere and its position of contact on the finger and also indicates contact force. Conversely, whereas SAIIs possess a greater capacity to encode changes in contact force, they provide only coarse information on local shape.

INTRODUCTION

The opposable thumb and fine motor control that are characteristic of the primate hand allow precise manipulation of held objects. Sensory feedback from the hand allows features of the object such as its shape and roughness to be assessed and this information is important for successful operation of the motor control system. Although receptors in the muscles and digital joints provide relevant information to the CNS (Burke et al. 1988; Edin 1990; Edin and Vallbo 1990; Gandevia et al. 1992), specialized receptors in the glabrous skin of the hand are of paramount importance in signaling "small-scale" features of an object such as its surface texture and the fine details of its shape (Goodwin 1997).

There have been many studies of cutaneous afferents innervating the fingers in both humans and monkeys (for review see Darian-Smith 1984; Macefield 1997) but so far studies related specifically to the encoding of the shape of handled objects have been restricted to monkeys. LaMotte and his colleagues have studied the responses of these afferents to a variety of shaped stimuli including shaped steps indented into and scanned across the fingers (LaMotte and Srinivasan 1987a,b; Srinivasan and LaMotte 1987), ellipsoids scanned across the skin (LaMotte et al. 1994) and cylindrical profiles scanned across the skin (LaMotte and Srinivasan 1996). We have examined the responses of cutaneous afferents in monkeys to spheres contacting the fingerpad (Goodwin et al. 1995; Wheat et al. 1995). Such studies in monkeys enabled detailed quantitative descriptions of the responses of the cutaneous mechanoreceptive afferents. Comparison with human psychophysical experiments has pointed to likely neural codes for signaling the stimulus parameters to the brain (Goodwin et al. 1991). This raises, once again, the question of how valid it is to compare such psychophysical measurements in humans with equivalent neural recordings from monkeys.

In human glabrous skin, four types of specialized mechanoreceptor terminals have been identified histologically. Merkel cell-neurite complexes and Meissner corpuscles are located superficially and Ruffini endings and Pacinian corpuscles are located more deeply (Bell et al. 1994; Choukov 1973; Halata 1975; Miller et al. 1958). Microelectrode recordings from the median and ulnar nerves have revealed four distinct functional classes of low-threshold mechanosensitive afferent fibers. Two classes adapt slowly to a sustained indentation of the skin and are termed slowly adapting type I or II afferents (SAI or SAII), respectively; two classes adapt rapidly and are termed fast-adapting type I or II afferents (FAI or FAII), respectively (Vallbo and Johansson 1984). Type I afferents possess small, well-defined receptive fields; type II afferents have larger fields that are less clearly defined. A prominent feature of the SAIIs is their capacity to respond to lateral skin stretch, with many possessing the property of directional sensitivity and with some exhibiting a spontaneous regular discharge at rest (Johansson and Vallbo 1983). The relationship between the morphological classes of receptors and the functional classes of afferents has been established by a variety of largely indirect observations in...
several species, but it is generally accepted that SAIIs, SAIIIs, FAIs, and FAIIIs innervate Merkel complexes, Ruffini endings, Meissner corpuscles, and Pacinian corpuscles, respectively (Darian-Smith 1984).

Although Ruffini endings have been found in monkey hairy skin (Biemesderfer et al. 1978), they have not been found in the glabrous skin of these species. Corresponding to this, the functional class of SAIIIs has been found in hairy skin in monkeys but not in their glabrous skin (Harrington and Merzenich 1970). The remaining three receptor types and afferent classes that are found in humans are also found in monkeys. Moreover, the innervation density of SAIs, FAIs, and FAIIIs on the fingers is similar for humans and monkeys (Darian-Smith and Kenins 1980; Johansson and Vallbo 1979).

In most of the experiments that provide data that allow quantitative comparison of the properties of FAIs, FAIIIs, and SAIs in humans and monkeys, the stimulus was a punctate probe. For these stimuli there is a close correspondence in the properties of the afferents in the different species (for review see Darian-Smith 1984). A more rigorous comparison has been made with braille dots and embossed dot arrays scanned across the fingerpad and here too the correspondence was close (Connor et al. 1990; Johnson and Lamb 1981; Phillips et al. 1990, 1992). There have been no recordings from human afferents responding to stimuli with controlled variation in local shape analogous to the studies in the monkeys described.

The current study was undertaken principally to address two specific questions. First, do SAIs, FAIs, and FAIIIs on the central portion of the human fingerpad respond to local curvature and to contact force in a manner similar to those in the monkey? Second, how do SAIIIs in this region, which are not present in the monkey, respond to the same stimuli? Thus we used the same passively applied spherical stimuli that were employed in the monkey studies, so that direct comparisons could be made (Goodwin et al. 1995; Wheat et al. 1995).

METHODS

Thirty-seven experiments were performed on 22 healthy human volunteers (11 female, 11 male; age 18–49 yr). The procedures were approved by the Committee on Experimental Procedures Involving Human Subjects at the University of New South Wales. Subjects sat in a comfortable chair with the supinated forearm supported and the dorsum of the hand embedded in plasticine. The fingers were held flat by clips affixed to the nails and anchored in the supporting material. Care was taken to ensure that the fingers were mechanically stable but that the glabrous skin was not distorted and that the receptive fields of the units were unencumbered by the plasticine.

Recording procedures

The location of the median nerve at the wrist, ~1-cm proximal to the flexor retinaculum, was determined by external electrical stimulation by using a 1 mm diam probe. Once the optimal site for eliciting paraesthesia in the digits was found, an insulated tungsten microelectrode (type TM33B20, World Precision Instruments) was inserted through the skin. The electrode was directed manually into a cutaneous fascicle of the median nerve while delivering weak negative pulses ( <1 mA, 0.2 ms, 1 Hz ) through the microelectrode via an optically isolated constant-current stimulator (MacLab 8/ s & Isolated Stimulator, ADInstruments, Sydney, Australia). An adjacent subdermal microelectrode, from which 1 mm of insulation had been removed, served as the reference electrode. After entering a fascicle of digital nerve origin (paraesthesia elicited at <0.025 mA), the microelectrode was connected to an amplifier (Gain 10000, band-pass 0.3–5 kHz). A search was then undertaken for large spikes originating from single cutaneous afferent axons while the fascicular innervation territory was manipulated and stroked. Isolated units were studied only if their receptive fields were located on the relatively flat portion of the volar surface of the fingers. Preference was given to receptive fields on the pulp of the index finger or middle finger.

An isolated unit was classified as SAI, SAII, FAI, or FAII according to the established criteria of responses to sustained indentation, sensitivity to rapidly changing stimuli, size of receptive field, and sensitivity to lateral skin stretch. The mechanical threshold was measured by using a set of calibrated von Frey hairs (Simms-Weinstein aesthesiometers, Stoelting, Chicago, IL) and the receptive field was mapped with a hair of ~4 times threshold. The mapping was done as carefully as possible because this procedure was used to determine the receptive field center. Neural activity was sampled at 12.8 kHz by using the SC/ZOOM data acquisition and analysis software (Department of Physiology, University of Umeå, Umeå, Sweden) and stored directly on disk for subsequent analysis.

Stimulating procedures

The primary stimuli consisted of spherical surfaces made from delrin with radii of 1.92, 2.94, 5.81, or 12.4 mm or ~ (flat); the corresponding curvatures, given by the reciprocal of the radii, are 694, 340, 172, 80.6, and 0 m–1, respectively. These surfaces were applied to the skin at the receptive field center by a mechanical stimulator that has been described previously (Goodwin et al. 1995). Briefly, it consisted of a balanced beam that, once released by activating a restraining solenoid, applied the surfaces at a constant static force of 40-, 60-, or 80-g weight (0.392, 0.588, or 0.784 N, respectively) determined by adding or removing weights from the beam. A damper regulated the motion of the beam and set the initial rate of application at 20 mm/s. At contact, the skin surface was orthogonal to the direction of application of the surfaces. Stimuli were presented in blocks of trials. For each trial the stimulus remained in contact with the skin for 1.5 s and was then lifted off the skin for 3 s before the next trial commenced. A block consisted of 15 trials. The contact force was successively 40-, 60-, or 80-g weight and at each force the curvature was successively 80.6, 80.6, 172, 340, and 694 m–1. For each force the first application at 80.6 m–1 served as a lead stimulus to minimize interaction from the previous force and was excluded from the analysis. The complete block was repeated a further five times to allow assessment of reproducibility of the responses. For three units, a curvature of 0 m–1 was used in place of the curvature of 80.6 m–1.

Some units were sufficiently stable to allow field studies as well. In these, an x-y micrometer on the stimulator was used to change the contact point in the receptive field in 1-mm steps, either along the long axis of the finger or at right angles to it. A block of trials consisted of the sequence of curvatures 172, 172, 340, and 694 m–1 applied at a contact force of 60-g weight to successive points, separated by 1 mm, from one end of the receptive field to the other. Again the whole block was repeated five times and at each point the lead stimulus (the 1st application at 172 m–1) was excluded from analysis. Alternatively, the field studies were performed by stepping delrin cylinders with the sequence of curvatures 172, 172, 340, and 694 m–1 along the long axis of the finger in 0.5-mm steps at a contact force of 60-g weight. The axis of the cylinder was orthogonal to the long axis of the finger.
changing the contact force to 40- or 80-g weight had a corresponding instantaneous frequency of discharge. Responses to increase with increases in curvature but the responses are overlaid in Fig. 2D. The two normalized profiles are similar, showing that to a first approximation, the entire waveform is scaled by the change in the stimulus. Thus the form of the stimulus-response functions shown in Fig. 2E for responses measured over 1 s were much the same for responses measured over 0.2, 0.3, 0.5, and 0.8 s and over the last 0.5 s.

All SAIs showed the same characteristic increase in response as the curvature of the stimulus increased and as the contact force increased. However, different fibers had different sensitivities as evident from their different response frequencies. The small standard errors show the variability in responses with the complete stimulus sequence applied six times over a period of ~7 min. Responses of single human afferents were highly consistent.

Increasing the curvature from 80.6 m⁻¹ in Fig. 2B to 172 m⁻¹ in Fig. 2C resulted in an increase in instantaneous frequency throughout the time course of the response. For each of these two responses a normalized instantaneous frequency was calculated by dividing the instantaneous frequency by the mean instantaneous frequency; the normalized responses are shown in Fig. 2E. The two normalized profiles are similar, showing that to a first approximation, the entire waveform is scaled by the change in the stimulus. Thus the form of the stimulus-response functions shown in Fig. 2E for responses measured over 1 s were much the same for responses measured over 0.2, 0.3, 0.5, and 0.8 s and over the last 0.5 s.

All SAIs showed the same characteristic increase in response as the curvature of the stimulus increased and as the contact force increased. However, different fibers had different sensitivities as evident from their different response magnitudes to the same stimulus. In Fig. 3, the 10 SAIs with receptive fields on the fingerpad (Fig. 1) have been combined after normalizing to remove the sensitivity factor (Goodwin et al. 1995). For each afferent the normalizing factor was its average response to the nine stimuli common to all fibers (curvatures 694, 340, and 172 m⁻¹, at forces 40-, 60-, and 80-g weight). The most sensitive fiber was 2.3 times as sensitive as the least sensitive fiber as measured by the ratio of the normalizing factors. The small standard errors in Fig. 3 reflect the high degree of consistency of the curvature-response and force-response functions from fiber to fiber. The five SAIs excluded from the pool (because they were not on the fingerpad or were too close to a crease) also showed increasing responses with increasing curvature and with increasing force, but the shapes of the functions were slightly different, presumably because of the different skin mechanics in these regions.

The 120 data points forming Fig. 3 fit well to the function

\[ y = k[a - b \exp(-cx)] \]

The values of the constants \(a\), \(b\), and \(c\) are 2.04, 1.95, and 0.00236, respectively and for contact forces of 40-, 60- and 80-g weight the values of the constant \(a\) have ratios 1:1.08:1.15, respectively (\(F = 451, P \approx 0.001\)) (see Goodwin et al. 1995 for details of the fitting procedure).

Responses of SAIs and FAIs to stimuli applied to the receptive field center

The first experimental protocol was designed to characterize the responses of SAIs to local curvature. Figure 2 shows experimental records from a typical SAI (Fig. 1, ▲, receptive field location). The degree of signal isolation is illustrated in Fig. 2A by the spike train in response to a sphere of curvature 80.6 m⁻¹ (radius, 12.4 mm) applied to the receptive field center with a contact force of 40-g weight; the corresponding instantaneous frequency of discharge is shown in Fig. 2B. In Fig. 2E the response, measured by the total number of action potentials occurring in the 1st s of the response, is shown for all four curvatures and all three contact forces. The response increased as the curvature of the stimulus increased and also increased as the contact force increased. The standard errors show the variability in responses with the complete stimulus sequence applied six times over a period of ~7 min. Responses of single human afferents were highly consistent.

Responses of FAIs and FAIIIs to stimuli applied to the receptive field center

The FAIs responded with a small number of action potentials during the dynamic phase of the stimulus. Even though the responses were small, they were highly consistent for the six repeated applications. Responses for the seven afferents in Fig. 1 (●) are shown in Fig. 4 for all four curvatures at a contact force of 60-g weight. There was a trend for responses to increase with increases in curvature but the changes were small and not systematic from fiber to fiber. Changing the contact force to 40- or 80-g weight had a negligible effect on responses.
A. W. GOODWIN, V. G. MACEFIELD, AND J. W. BISLEY

FIG. 2. Responses of a typical SAI (Fig. 1, ▲) to spheres of different curvature applied to receptive field center. A and B: spike train and instantaneous frequency, respectively for a sphere of curvature 80.6 m⁻¹ (radius, 12.4 mm) applied with a contact force of 40-g weight. Time 0 is defined by the occurrence of 1st spike. C: instantaneous frequency for a sphere of curvature 172 m⁻¹. D: normalized profiles from B (shaded) and C (open). E: response measured by number of impulses in 1 s (mean ± SE, n = 6). F: same as E except that response is number of impulses in 0.3 s. For E and F the 4 curvatures were 80.6, 172, 340, and 694 m⁻¹ and the 3 contact forces were 40-, 60-, and 80-g weight.

None of the FAIs responded at all to our stimuli, presumably because of the low indentation velocity (see DISCUSSION).

Receptive field profiles of SAIs

For some units the spatial characteristics of the receptive field were defined by comparing the responses of the unit for stimuli applied at several different positions in the field.

FIG. 3. Normalized responses for 10 SAI units (mean ± SE). For the 9 stimuli at curvatures 172, 340, and 694 m⁻¹ (forces 40-, 60-, and 80-g weight), there are 10 data points each; for curvature 80.6 m⁻¹ there are 9 data points each. For each fiber, normalizing factor was average value at the 9 points (3 curvatures × 3 forces) common to all 10 fibers. ●, responses for single fiber at 0 m⁻¹. Typical of all 7 afferents.

In Fig. 5A the responses of a typical SAI (Fig. 1, ▼) are shown for spheres with three different curvatures applied at points in the receptive field separated by 1 mm along a line through the receptive field center and parallel to the long axis of the finger. As the curvature of the surface increased, the profile became sharper, with an increase in the magnitude of the peak and a decrease in the width of the profile. Such profiles were collected for three additional afferents and showed similar behavior. In addition, profiles for cylinders.
Responses of SAIIs

As has been reported by others, we encountered many SAIIs with clearly isolated action potentials that had receptive fields near the nails, on the edges of the fingers, or that had poorly defined receptive fields and were presumably located in deeper tissues. However, in this study we wished to record only from those SAIIs that had receptive fields located on the volar surfaces of the fingers, preferably on the fingertip pads. These afferents responded vigorously to our stimuli.

When spheres with different curvatures were applied at a number of contact forces to the estimated center of the receptive field, there were two striking differences in the responses of SAIIs compared with the responses of SAIIs described above. These are illustrated in Fig. 6A by the responses of the SAII (Fig. 1, ▲), which is typical of our sample. Like the other classes of afferents described, the responses of the SAIIs were highly consistent with repeated stimuli. Comparing Figs. 6A and 2E, the first obvious difference is the effect of the curvature of the stimulus. For SAIIs, the response increased when the curvature increased from 80.6 to 172 m⁻¹, but further increases in curvature had a negligible effect on the responses.

The second difference is the effect of force. For SAIIs, increases in force resulted in relatively larger increases in response than was the case for SAIIs. For example, at a curvature of 694 m⁻¹, increasing the contact force from 40- to 80-g weight resulted in a 40% increase in response for the SAI in Fig. 6A but only a 14% increase for the SAI in Fig. 2E. Responses of the five afferents (Fig. 1, ○) were combined in Fig. 6C after normalizing to remove differences in scale because of differences in sensitivity among the afferents. The small standard errors confirm that all five afferents have similar stimulus-response functions. As was the case for the SAIIs, if a change in the stimulus caused a change in the response of an SAII, then the change was seen throughout the time course of the response. Thus the stimulus-response functions, illustrated in Fig. 6A for the number of impulses in

![Fig. 5](https://example.com/fig5.png) Figure 5. Receptive field profiles contrasted for an SAI and an SAII. A: SAI (Fig. 1, ▲). Responses (mean ± SE; n = 6) are shown at points, separated by 1 mm, along a line through center of receptive field and parallel to long axis of finger. More distal stimuli have greater abscissa values. Contact force was 60-g weight. B: SAII (Fig. 1, ○). Responses (mean ± SE; n = 6) are shown along a line through receptive field center and orthogonal to long axis of the finger. Abscissa values are greater for more ulnar positions. Contact force was 60-g weight.

![Fig. 6](https://example.com/fig6.png) Figure 6. Response characteristics of SAII afferents. A and B: spheres applied to the receptive field center of the SAII (Fig. 1, ▲). Response measure is the number of impulses in the 1st s (A) or 1st 0.3 s (B) of the response (mean ± SE; n = 6). C: combined normalized responses (mean ± SE; n = 5) for spheres applied to receptive field centers of the 5 units shown by solid symbols in Fig. 1. For each fiber, normalizing factor was average value at 9 points (curvatures 694, 340, and 172 m⁻¹ × forces of 40-, 60-, and 80-g weight).
the first second of response, were similar when the response measure was the number of impulses occurring in the first 0.2, 0.3 (illustrated in Fig. 6B), 0.5, or 0.8 s or in the last 0.5 s.

Despite the fact that SAI receptive fields are more diffuse than those of the SAlIs, the receptive field profiles were distinctly defined and highly repeatable. Fig. 5B shows the profile for the unit (Fig. 1, ▼) mapped with spheres positioned along a line at right angles to the long axis of the finger. Responses decreased as the stimulus moved away from the receptive field center but, unlike the SAlIs, the shape of the profile was essentially independent of the curvature of the sphere. These characteristics were common to the four afferents mapped with spheres or cylinders. We do not have sufficient data to make a meaningful comparison of the widths of the profiles in the two classes of slowly adapting afferents.

Comparison of SAI responses in humans and monkeys

It was shown previously that SAlIs in both humans and monkeys are sensitive to edges, which are regions of high curvature (Johansson et al. 1982; Phillips and Johnson 1981a). The experiments reported here show that the entire curvature-response function is similar for human and monkey SAIIs. For spheres applied to the receptive field center of human SAlIs, the response was of the form $k[2.04 - 1.95 \exp(-0.00236x)]$ with the constant $k$ having ratios 1:1:0.8:1.15 for contact forces of 40-, 60-, and 80-g weight respectively. For monkeys, the corresponding function is $k[1.91 - 1.62 \exp(-0.00243x)]$, with the constant $k$ having ratios 1:1.28:1.53 for contact forces of 10-, 15-, and 20-g weight, respectively (Goodwin et al. 1995). The shape of the exponential function is almost identical in the two samples, indicating a close similarity in the way local shape is signaled by the SAI populations in humans and monkeys. The smaller force factor in humans than in monkeys suggests that SAIIs on the center of the fingerpad are not that crucial for indicating contact force in humans where SAIIs may play a role. For both primates there are other sources of information on contact force. The receptor mechanisms operating in Merkel complexes and the nature of the skin mechanics must be similar in the different primate species. These observations boost our confidence in using nonhuman primate data for fundamental mechanisms such as transduction (Looft 1994) and skin mechanics (Srinivasan 1989) when explaining human tactile performance. There are, however, some qualifications. The most obvious relates to the size of the finger that is much larger in humans than in monkeys.

There are at least four ways in which finger size may play an important role. First, larger fingers have larger pads so that contact areas are generally larger and corresponding forces need to be higher. We used a range of 40- to 80-g weight in humans and a range of 10- to 20-g weight in monkeys; the resulting magnitudes of the responses of the afferents in humans and in monkeys were similar. For patterns of dots scanned across the fingers, Connor et al. (1990) argued that a contact force of 100-g weight in the human was equivalent to a contact force of 30-g weight in the monkey. Phillips et al. (1990) scanned braille characters across the skin at a contact force of 60-g weight in humans; Johnson and Lamb (1981) used contact forces of 20-g weight and 60-g weight with monkeys. Second, when objects do contact the more curved parts of the fingers, the greater curvatures in the smaller monkey fingers may lead to a greater sensitivity to features of the stimulus like local gaps or edges. Third, the afferents innervating the curved edges of the fingers may show quantitative differences because the curvatures of the fingers depend on their size. Fourth, particularly with higher forces (for example as used in lifting objects that weigh several hundred g), the mechanics of the finger as a whole may be different. In the experiments here and in our curvature experiments in the monkey we have confirmed our studies to the population of afferents innervating the relatively flat portion of the fingerpad; here the relative size difference is less of an issue.

A critical reason for establishing the similarity of human and monkey afferent responses to spheres was to determine...
the validity of our population response reconstructions, based on monkey data, for explaining human tactile performance (Goodwin 1997). The data here support our hypothesis that the shape of the sphere is represented in the shape of the SAI population response. Its position on the skin is represented in the position of the activity profile within the SAI population and, to a lesser degree, the contact force is represented in the overall magnitude of activity in the SAI population.

Responses of SAIIIs

SAIIIs have not been found in the monkey finger but they occur in large numbers in the human finger (Johansson and Vallbo 1979). Their large receptive fields suggest that sensitivity to local curvature would be minimal; however, this was not certain particularly for afferents supplying the central portion of the fingerpad. The SAIIIs we recorded showed a small increase in response when the curvature of the sphere changed from 80.6 to 172 m⁻¹ (radius, 12.4–5.81 mm) but further increases in curvature had no effect on the response. This contrasts with the properties of SAIIs and adds further information relating to the differences in receptor mechanisms of Merkel complexes and Ruffini organs (Khalsa et al. 1996; Phillips and Johnson 1981b). In terms of human sensation, our data reinforce the notion that SAII responses are unlikely to signal information to the brain about the local shape of an object in contact with the skin.

The SAIIIs show a systematic increase in response with increases in contact force and this increase is proportionately larger than for SAIIs. Thus the SAII population may signal information to the brain about forces between the fingerpads and contacted objects. Because the responses depend on force but not on local shape, the signals could be easily interpreted directly. In contrast with the local shape of an object and its position of contact on the fingerpad, which can only be signaled by the cutaneous afferents, there are a number of sources that can signal contact force in addition to the SAIIs and SAIIIs on the fingerpad. These include responses from the large number of afferents innervating the remaining portion of the digits and, in addition, during active manipulation, responses of Golgi tendon organs and effe-rence copy (Gandevia et al. 1992).

We have intentionally studied the subpopulation of SAIIIs located on the fingerpad. There are a large number of SAIIIs located at some distance from a sphere contacting the fingerpad and these may respond because they are sensitive to lateral stretch (Johansson and Vallbo 1983). The quantitative details of the responses of this subpopulation and the possible role of direction sensitivity are unknown. It is interesting to note that microstimulation of single SAIIIs does not evoke any sensation in awake humans, whereas stimulation of single SAIIs does (Macefield et al. 1990; Torebjörk et al. 1987). The relevance of this observation to the role of whole population responses is not clear. However, it is known that microstimulation of a single muscle spindle afferent does not generate any perceptual response, whereas activation of many such afferents generates a clear illusion of movement (Macefield et al. 1990).

Two intriguing questions remain. What is the role of SAIIIs in humans and what can humans do that monkeys, lacking SAIIIs, cannot do? Although the answers to these questions are not known at present, the properties of SAIIIs, including their sensitivity to lateral stretch, suggest a major role in sensing tangential loads while lifting and manipulating objects. If monkeys were able to perform as well as humans in such tasks they would have to be using different neural processing strategies based only on the SAIIs, FAIs, and FAIIIs. However it is more likely that the evolution of hand function has reached a greater degree of sophistication in humans than in monkeys. Most of the data on monkeys result from simple behavioral observations and, although it is clear that they have considerable manual dexterity, it is not clear that they can do everything that humans can do (Christel 1993). For example, could a monkey execute tasks equivalent to writing with a pen or performing delicate surgical maneuvers?

Responses of FAIs and FAIIIs

As was the case in the monkey, the FAIs in the human responded to the spheres but with small responses that did not change systematically with changes in curvature or contact force. They are unlikely to play a major role in signaling these stimulus parameters to the brain. The FAIIIs did not respond at all to our stimuli, nor did the FAIIIs examined in the monkey with the same stimuli (Goodwin et al. 1995). This may seem surprising because the initial contact with the skin was at a velocity of 20 mm/s and it has been shown that FAIIIs respond at even lower indentation velocities in both humans and monkeys (Knibestol 1973; Lindblom and Lund 1966). However, our spherical stimuli are larger than most of the punctate probes commonly used and do not have changes in curvature that occur at the edges of flat probes. More importantly, the forces used by us were set by gravity so that, although the initial velocity was 20 mm/s, contact with the skin would have resulted in a progressive reduction in velocity during the indentation phase. The velocity thresholds quoted lower were measured with stimulators that produced constant velocities throughout the indentation.

Limitations of our data

The restrictions of human microneurography imposed a number of limitations on our data. It is not possible to search for more than ~4 h to find an afferent with a desired receptive field location, nor is it possible to record from the afferents for many hours routinely. In addition, the human hand and fingers cannot be immobilized for long periods with the same stability as in anesthetized monkeys. Thus our sample of afferents is, of necessity, a compromise. For the SAIIs and FAIs the size of the pool on the fingerpads is large enough for quantitative estimates of population responses to spheres with different curvatures applied to the receptive field center. A detailed analysis of the receptive field profiles of the SAIIs (as was done in the monkey) is not possible. The data (Fig. 5A) suggest a strong similarity for profiles in humans and monkeys but we are not justified in making quantitative comparisons of factors like the widths of the receptive field profiles. Because our aim with the SAIIIs was to study only those afferents with receptive fields clearly on the fingerpad, our population is not large. Never-
theless the data are consistent and valuable in suggesting possible roles for these afferents that have not been found in monkeys. Because of the difficulty of finding receptive fields on the center of a fingerpad, a small number of afferents on the middle or proximal phalanxes or close to an interphalangeal crease were studied. These afferents were of some value in that their properties were consistent with those on the fingerpads; however, they were not used in any pooled data analysis.

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