Cutaneous Afferents From the Monkeys Fingers: Responses to Tangential and Normal Forces

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Wheat HE, Salo LM, Goodwin AW. Cutaneous afferents from the monkeys fingers: responses to tangential and normal forces. J Neurophysiol 103: 950–961, 2010. First published December 2, 2009; doi:10.1152/jn.00502.2009. Control of tangential force plays a key role in everyday manipulations. In anesthetized monkeys, forces tangential to the skin were applied at a range of magnitudes comparable to those used in routine manipulations and in eight different directions. The paradigm used enabled separation of responses to tangential force from responses to the background normal force. For slowly adapting type I (SAI) afferents, tangential force responses ranged from excitatory through no response to suppression, with both a static and dynamic component. For fast adapting type I (FAI) afferents, responses were dynamic and excitatory only. Responses of both afferent types were scaled by tangential force magnitude, elucidating the neural basis for previous human psychophysical scaling data. Most afferents were direction selective with a range of preferred directions and a range in sharpness of tuning. Both the preferred direction and the degree of tuning were independent of the background normal force. Preferred directions were distributed uniformly over 360° for SAI afferents, but for FAI afferents they were biased toward the proximo-ulnar direction. Afferents from all over the glabrous skin of the distal segment of the finger responded; there was no evident relationship between the position of an afferent’s receptive field on the finger and its preferred direction or its degree of tuning. Nor were preferred directions biased either toward or away from the receptive field center. In response to the relatively large normal forces, some afferents saturated and others did not, regardless of the positions of their receptive fields. Total afferent response matched human psychophysical scaling functions for normal force.

INTRODUCTION

The ability to manipulate objects with precision is a quintessential human attribute. There have been many studies showing that successful manipulation of objects depends critically on sensory signals from cutaneous mechanoreceptors in the hand (Monzée et al. 2003; Nowak et al. 2004; Witney et al. 2004). Routinely these signals are used to monitor progress of the movements and to update representations stored in memory enabling feedforward or predictive strategies that result in rapid and accurate hand movements (Flanagan et al. 2006; Wolpert and Grahramani 2000). Occasionally, when movements are heading to instability, feedback signals may be used to form corrective movements. The importance of feedback is evident from the observation that objects are frequently dropped if the fingers are anesthetized (Augurelle et al. 2003).

A key parameter during manipulation is the force applied by the fingers and thumb to the object. These forces are threedimensional vectors that are commonly viewed in terms of a component normal to the skin and a component tangential to the skin. There have been many behavioral studies of the nature of these forces. Most commonly, subjects grasp and lift an object while the normal force (termed the grip force) and the tangential force (termed the load force) are characterized; the relationship between grip force and load force is crucial in preventing slip and ensuring grasp stability (Johansson 1996; Novak and Hermosdorfer 2003).

Responses of the four classes of mechanoreceptive afferents innervating the glabrous skin of the hand have been studied extensively for a range of stimuli including texture and shape (Goodwin and Wheat 2008; Johansson and Flanagan 2009). There have been surprisingly few studies of their responses to normal forces in the range used in everyday manipulations and even fewer studies of tangential force (Birznieks et al. 2001). An inherent difficulty in studying tangential forces is that they cannot be applied alone, because the object will slip over the skin, and must be combined appropriately with normal forces.

Tangential forces are determined by two components, their magnitude and their direction, both of which play a critical role in motor planning for successful manipulation. Humans are able to scale and discriminate tangential force magnitude (Biggs and Srinivasan 2002; Pare et al. 2002a; Wheat et al. 2004) and can perceive the direction of skin stretch (Srinivasan et al. 1990). It is known that cutaneous mechanoreceptors display direction sensitivity to surfaces scanned over the skin (Edin et al. 1995; Goodwin and Morley 1987; Srinivasan et al. 1990) and to three-dimensional forces applied to the skin (Birznieks et al. 2001), but their direction selectivity to tangential forces is not well understood. Directional responses of sensory neurons play an important role in most sensory systems. The most extensively studied direction sensitive neurons are those in the visual system where the directionality is determined predominantly by cortical circuitry (Livingstone and Conway 2003). The auditory brain stem (Wagner and Takahashi 1992) and somatosensory cortex (Ruiz et al. 1995) contain direction selective units, and neurons in motor cortex also exhibit directional properties (Schwartz et al. 1988). In the somatosensory system it is important to understand the peripheral mechanisms of direction selectivity to tangential forces before cortical mechanisms are tackled; as yet, nothing is known about force direction selectivity in somatosensory cortical neurons.

In the experiments that follow, we used a stimulation paradigm that facilitates characterizing the effects of tangential forces. Tangential forces were presented at a range of magnitudes and in eight different directions. This allowed us to study systematically, the effects of the magnitudes of the forces on
mechanoreceptive afferent responses and their direction selectivity and to compare these results with previous psychophysical data.

METH ODS

Surgery

All experimental procedures were approved by the University of Melbourne Ethics Committee and conformed to the National Health and Medical Research Council of Australia’s Code of Practice for nonhuman primate research. Responses of single mechanoreceptive afferent fibers were recorded from eight Macaca nemestrina monkeys weighing 5.5–12 kg using standard procedures that have been detailed elsewhere (Wheat and Goodwin 2001) and are covered only briefly here. An intramuscular dose of ketamine hydrochloride (15 mg/kg) plus atropine sulfate (60 μg/kg) was given before the induction of surgical anesthesia by intravenous administration of sodium pentobarbital (15 mg/kg). An endotracheal tube was inserted (after the application of topical xylocaine spray) to maintain a patent airway and to enable continuous measurement of end-tidal CO₂ levels. Anesthesia was monitored throughout the experiment and maintained with titrated doses of sodium pentobarbital delivered in isotonic saline (dilution 12 mg/ml) via an intrapitoneal catheter together with additional saline to maintain hydration. Respiration rate, end-tidal CO₂ level, blood pressure, core temperature, heart rate, and oxygen saturation levels were monitored throughout the experiment. Body temperature was maintained at 37°C by a heat pad and blankets. Antibiotic cover was provided throughout the experiment by intra-muscular administration of amoxicillin (18 mg/kg) and at the end of the experiment by a single dose of procaine penicillin (60 mg/kg). Single fibers were isolated by microdissection of the median nerve in the experiment by a single dose of procaine penicillin (60 mg/kg). Antibiotic cover was provided throughout the experiment by intra-muscular administration of sodium pentobarbital (15 mg/kg). An endotracheal tube was inserted after the induction of anesthesia and maintained with additional saline to maintain hydration. Respiration rate, end-tidal CO₂ level, blood pressure, core temperature, heart rate, and oxygen saturation levels were monitored throughout the experiment. Body temperature was maintained at 37°C by a heat pad and blankets. Antibiotic cover was provided throughout the experiment by intra-muscular administration of amoxicillin (18 mg/kg) and at the end of the experiment by a single dose of procaine penicillin (60 mg/kg). Single fibers were isolated by microdissection of the median nerve in the upper arm or lower arm.

Stimulator

The stimulus, which has been described in a previous paper (Wheat et al. 2004), consisted of a probe (24 mm diam) with a flat contact surface covered with fine sandpaper (500 grade; Fig. 1A). A custom-built stimulator, computer-controlled using Labview (Austin, TX) software, allowed simultaneous application of normal and tangential forces to the fingerpad. Tangential force direction was set to one of eight angles. The vertical position of the stimulator was such that when a normal force of 1 N was delivered, the beam came to rest in a horizontal position. The damper was set to ensure that, with all normal forces, contact was smooth. A six-axis force/torque transducer (Nano FT, ATI Industrial Automation, Apex, NC) measured the three-dimensional forces and torques applied to the fingerpad with a resolution of 0.0125 N and 0.0625 N mm, respectively.

General procedure

The finger to be stimulated was immobilized in a customized mold with the fingernail secured by cyanoacrylate. The angle of the finger was such that the relatively flat central part of the distal segment was in the horizontal plane (Fig. 1B). A standard contact point was marked on the skin, and its x, y, and z coordinates were measured. When the stimulus was applied to the finger, the first point of contact on the skin was the marked standard contact point and the surface was tangential to the skin. To facilitate across-fiber comparisons, this stimulus position was comparable for all fingers and for all fibers and corresponded to the location most commonly contacted in everyday human manipulations (Christel et al. 1998).

Fibers were classified by established response criteria (Talbot et al. 1968; Vallbo and Johansson 1984). We recorded predominantly from slowly adapting type I (SA1) afferents (n = 89) and from a smaller number of fast adapting type I (FA1) afferents (n = 14). For each fiber, the most sensitive spot in the receptive field, hereafter referred to as the receptive field center, was located using calibrated von Frey filaments. The x, y, and z coordinates of each receptive field center were measured and marked on a plaster cast of the respective monkey’s hand to facilitate subsequent identification and analysis (Fig. 1C).

Initially, fibers with receptive field centers anywhere on the glabrous skin of the distal segment were selected but, after careful mapping, fibers were rejected if their receptive field centers were in close proximity to the nail, close to the distal interphalangeal crease, or close to the hairy/glabrous skin border.

The stimulus was presented to the skin of the fingerpad with a defined matrix of forces comprising different combinations of normal and tangential force as described in the next section. At the start of each trial, the stimulus surface was positioned just above and tangential to the surface of the skin but there was no contact with the skin before the start of stimulus presentation.

Tangential force

In this series, for 103 fibers, five tangential forces (0, 0.175, 0.25, 0.35, and 0.5 N) were applied at a normal force of 0.7 N and five (0, 0.35, 0.5, 0.6, and 0.85 N) at a normal force of 1.2 N. In addition, for 41 of those fibers, four tangential forces (0, 0.6, 0.85, and 1.2 N) were applied at a normal force of 1.7 N. These combinations were chosen to facilitate comparisons in two respects. First, two tangential forces were common to consecutive levels of normal force. Second, at each normal force, there was a tangential force for which the ratio of tangential to normal force was 0.5. To prevent slip, the largest ratio of tangential to normal force used was 0.7, which was below the measured effective coefficient of friction, which ranged from 0.8 to 1.4 depending on individual fingers and force direction. Force traces were examined off-line to confirm that there was no slip between the

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A computer-controlled stimulator. Torque motor m₂, coupled to damper d, produced a vertical (normal) indenting force on the monkey’s finger f, which was immobilized in plasticine p. Torque motor m₁, attached to m₂ via beam b, produced a tangential force on the finger. The direction of the tangential force in the horizontal plane was set by the hub h, indexed at 15° increments. Left inset: an enlarged view of the flat surface s, covered with 500-grade sandpaper, coupled to the stimulator via a 6-axis force-torque transducer t. The stimulator was mounted on an x-y-z vernier shift to allow accurate positioning in all 3 dimensions. B: the position of the initial contact point of the stimulus was standard on all fingers. Normal (Fₙ) and tangential (Fₜ) forces were orthogonal to each other with tangential force in 1 of 8 directions. C: coordinate system for location on the finger of receptive field (RF) centers and of the standard contact point. x, y, and z positions were measured from the midline of the finger, from the distal interphalangeal crease and from the volar edge of the distal segment, respectively.
stimulus and the finger and also to check for any irregularities in force delivery.

The time sequence is shown in Fig. 2A. First, the normal force was applied and, then, after a delay of 1.2 s, the tangential force was applied for 1.5 s. Successive trials were separated by intervals of 3.5 s. Tangential/normal force complexes were presented in order of increasing magnitude so that tangential forces at a normal force of 0.7 N were presented first, followed by those with normal force of 1.2 N and, finally, those with a normal force of 1.7 N. At each level of normal force, tangential forces were presented in order of increasing magnitude. Each combination of forces was presented at eight directions of tangential force in the order 0, 180, 90, 270, 45, 225, 135, and 315°. This sequence was repeated five times (n = 6 for each direction, for each force combination).

**Normal force**

In this series, for 45 fibers, a sequence of nine normal forces (0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, and 2.0 N) was presented with zero tangential force. For an additional 42 fibers, two larger forces were added giving a sequence of 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 2.0, 2.2, and 2.5 N. For each fiber, forces were presented sequentially from low to high with the entire sequence repeated five times (n = 6). Each trial (Fig. 2B) consisted of the presentation of a single force with a rise time of 0.2 s, a plateau phase of 1.5 s, and a fall time of 0.2 s (1.9 s in total), with 8 s between trials.

**Statistics**

Pearson product-moment coefficients were used for linear correlation analysis and Kolmogorov-Smirnov goodness of fit to compare linear distributions. Circular statistics (Mardia and Jupp 2000) were used for angular data (Rayleigh’s test for uniformity of distributions, angular-angular correlations, and angular-linear correlations). For all tests, the significance level was set at 0.05.

**RESULTS**

We recorded from 103 low-threshold mechanoreceptive afferents with receptive fields located on the glabrous skin of the distal segments of monkey fingers. To facilitate comparison with previous neural data and with psychophysics experiments, we concentrated on SAI afferents but also characterized FAI afferents. Fast adapting type II (FAII) afferent responses to our stimuli were negligible. Receptive field centers of the 89 SAI afferents and 14 FAI afferents were distributed randomly across the entire glabrous surface of the distal segment of the finger (Fig. 3).

**Tangential force**

Applying tangential forces to the fingerpad is inherently more complicated than applying normal force. To prevent the object from slipping on the skin, any tangential force must be accompanied by a normal force of sufficient magnitude; the ratio of tangential to normal force must be less than the effective coefficient of friction between the skin and the surface of the object. Coefficients of friction were estimated in preliminary experiments and were consistent with those ascertained by us for humans in our earlier psychophysics study on tangential force scaling and discrimination (Wheat et al. 2004). The time course chosen for the application of the forces (Fig. 2B) corresponded to that used in the psychophysics study and ensured that tangential force was always preceded by a stable normal force.

The range of responses to tangential force is shown by the impulse ensembles and rate histograms in Fig. 4. For SAI afferents, application of tangential force had a range of effects on the ongoing response to the normal force. It could increase the response (Fig. 4B), decrease the response (Fig. 4D), or have no effect (Fig. 4C). In general, tangential force elicited both a dynamic and a static component of response in SAI afferents as is the case for normal force. For FAI afferents (Fig. 4E), the response to the normal force had decayed to zero before the application of tangential force. Tangential force elicited only a dynamic component of response, consistent with the time course of FAI responses to normal force.

To facilitate further analysis, the response to the normal force and to the superimposed tangential force were quantified by the impulse count during a 1-s window starting at the commencement of the corresponding force. This corresponds to our previous psychophysical measurements of responses to tangential forces in humans (Wheat et al. 2004).
Because the force ramps were always 0.2 s in duration (Fig. 2), increases in force magnitude resulted in a concomitant increase in force rate during the ramps. Thus it is not possible from our data to separate the effects of force magnitude and force rate on the dynamic responses of the afferents. This would require a different experimental paradigm with systematic parametric variation in force magnitude, duration, and rate.

**Sensitivity to increasing tangential force magnitude**

For most of the analysis that follows, responses are shown using a midrange combination of normal and tangential forces: 1.2 and 0.6 N, respectively. Comparisons are made for other forces. SAI and FAI fiber responses are presented in parallel.

In our experiments, responses to the tangential force are potentially affected by three parameters: the magnitude of the tangential force, the direction of the tangential force, and the magnitude of the background normal force. The data in Fig. 5 highlight a feature exhibited by many of the fibers in our sample. Increasing tangential force magnitude was reflected in an increase in response for some directions, but in other directions, there was little change in response or, in the case of a number of SAI afferents, increasing suppression of the response. Because FAI afferents do not respond during the normal force plateau (Fig. 4E), suppression of responses resulting from tangential force could not be shown in FAI afferents. Response variability is shown by representative SD. This low variability was shown by all our fibers for all stimulus conditions and is not shown again. A similar consistency in afferent responses has been reported in other studies for a range of different stimuli (Vega-Bermudez and Johnson 1999a; Wheat and Goodwin 2000).

For a single afferent, the effect of all three parameters (tangential force magnitude, tangential force direction, and normal force) is readily shown by polar plots (Fig. 6). Response to normal force alone (shaded gray region) increased with increasing force but was, of course, nondirectional. For all three normal force magnitudes, the response of this fiber increased with increasing tangential force applied in most directions but was suppressed when tangential force was applied in at least one of the eight directions.

Two questions stem from Fig. 6. First, how does sensitivity to tangential force magnitude vary among afferents? Second, does sensitivity vary with the magnitude of the normal force? To answer these questions, we computed an index of sensitivity to tangential force ($I_s$) for each fiber at each of the eight directions. $I_s$ was calculated at the two normal forces, 0.7 and 1.2 N, that were used for all fibers. At a normal force of 0.7 N, the index was the average slope (impulses N$^{-1}$) of the force-response function for the four tangential forces used: $I_s = (R_5 - R_{3.5})/(0.5 – 0.35) + (R_{3.5} - R_{2.5})/(0.35 – 0.25) + (R_{2.5} - R_{1.5})/(0.25 – 0.175)$, where $R_f$ is the response at tangential force $f$ N. Similarly, for a normal force of 1.2 N, the index was $I_s = (R_{5.5} - R_{3.5})/(0.85 – 0.6) + (R_{3.5} - R_{2.5})/(0.6 – 0.5) + (R_{2.5} - R_{1.5})/(0.5 – 0.35)$. A positive value for $I_s$ indicates that the response was dominated by increasing excitation to increasing tangential force and a negative value indicates that the response was dominated by increasing suppression to increasing tangential force.
For both the SAI afferents and the FAI afferents, the distribution of indices for the two normal forces overlaid each other with no statistically significant difference (Fig. 7). For the SAI afferents, correlation of the 464 \( I_s \) pairs at the two forces was statistically significant with a correlation coefficient of 0.64. Similarly, for the FAI afferents, correlation of the 80 pairs was statistically significant, with a correlation coefficient of 0.57.

**Directional tuning**

Fibers in our sample were not uniformly sensitive to tangential force direction. Some were more sharply tuned than others, and the preferred direction varied among fibers.

SAI afferents fell into three groups, shown by responses of typical afferents in Fig. 8. Some afferents (Fig. 8A) were excited by tangential force in all directions with little direction sensitivity. Others (Fig. 8B) were excited by tangential force in all directions but differentially and were thus sensitive to force direction. Many (Fig. 8C) were excited in some directions and suppressed in other directions, resulting in sharp tuning. The polar plots represent eight vectors (response magnitude in each of the eight directions shown in Fig. 1B) and their vector sum is shown by the resultant vector. The angle of this vector indicates the preferred direction of the afferent. The magnitude of this vector increases with increased tuning sharpness, but it also increases with increasing responsiveness of the afferent. To obtain a measure of tuning, independent of the afferent’s overall responsiveness, we calculated a tuning index \( T_i \) given by the magnitude of the vector sum divided by the average response of the afferent over the eight directions. \( T_i \) ranges in value from 0 (no tuning) to 1 (responds in 1 direction only). The middle panel in Fig. 8 shows the responses as standard direction tuning curves in Cartesian coordinates.

Data described in the preceding paragraph were obtained at a tangential force of 0.6 N with a normal force of 1.2 N. Similar results were obtained with tangential forces of 0.35 and 0.85 N at normal forces of 0.7 and 1.7 N, respectively; in all three cases, the ratio of tangential force to normal force was 0.5. Scatter plots (Fig. 8G) show that the preferred direction was consistent across all three tangential force magnitudes. Angular-angular correlations yielded statistically significant correlation coefficients of 0.65 and 0.79 for the comparison tangential forces of 0.35 and 0.85 N, respectively. Similarly, the scatter plots in Fig. 8H show consistency of the tuning index with statistically significant correlation coefficients (Pearson) of 0.74 and 0.70 for the comparison tangential forces of 0.35 and 0.85 N, respectively.

The results for FAI afferents are comparable (Fig. 9) but should be interpreted with some caution because of the small sample size. The angular-angular correlation coefficients (Fig. 9G) were 0.34 and 0.55 for comparison forces of 0.35 and 0.85 N, respectively, but neither was statistically significant. However, in Fig. 9H, the correlation coefficients of 0.73 and 0.90 for comparison forces of 0.35 and 0.85 N, respectively, were both statistically significant.

**Distribution of tuning properties**

Tuning characteristics for the entire sample of SAI and FAI afferents are shown in Fig. 10, A and D, at the mid-range of tangential and normal forces (0.6 and 1.2 N, respectively). The angle of each vector is the preferred direction of the afferent, and the magnitude of the vector is the tuning index \( T_i \). For the SAI afferents, preferred directions showed no bias toward a particular orientation on the fingertip; angles were uniformly distributed between 0 and 360° (Rayleigh’s test). Preferred
directions for the FAI afferents were biased toward the proximo-ulnar direction (significant Rayleigh’s test). Distributions of the tuning indices (Fig. 10, B and E) show that most afferents were sharply tuned (compare index values with the shown values of $T_i$ in Figs. 8 and 9). Scatter plots (Fig. 10, C and F) show that any relationship between an afferent’s preferred direction and its tuning index was minor. For the SAI afferents, the significant angular-linear correlation coefficient (unsigned) of 0.38 is small. For the FAI afferents, the coefficient of 0.48 is not significant.

Location of receptive fields on the fingertip

We examined (Fig. 11) whether an afferent’s preferred direction or tuning index depended, in a systematic way, on the location of its receptive field on the distal segment of the finger.

Receptive fields were distributed all over the glabrous skin on the distal segment of the finger. Distributions of the afferents’ preferred directions and tuning indices are shown in Fig. 11, A and D, and B and E, respectively. No striking pattern is apparent in these distributions.

One plausible hypothesis is that an afferent might respond preferentially to forces directed toward its receptive field center (or away from its receptive field center). To test this hypothesis, we measured the angle of the receptive field by the angle of the line joining the receptive field center and the point of initial contact with the stimulus. If the hypothesis is correct, scatter plots of the afferents’ preferred directions versus their receptive field angles should lie on the diagonal at 45° (or $-45°$). Scatter plots for the SAI afferents (Fig. 11C; angular-angular correlation coefficient, $-0.17$) show no significant correlation between an afferent’s preferred direction and the direction of its receptive field. For the FAI afferents (Fig. 11F; angular-angular correlation coefficient, $-0.60$), there was a significant tendency for preferred direction to decrease with increasing receptive field angle, but the effect is minor. These scatter plots do not support the hypothesis.

The distance between the initial contact point of the stimulus and the receptive field center of an afferent had no consistent effect on either the preferred direction of the afferent or its tuning index as shown in Fig. 12.
Responses to normal force alone (no tangential force) were recorded in 87 fibers. For 45 SAI afferents, nine forces were used: 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, and 2.0 N. For an additional 30 SAI afferents and 12 FAI afferents, 11 forces were used; the previous 9 forces plus 2.2 and 2.5 N.

Contrary to our expectations, we found that the position of an afferent’s receptive field on the finger had no consistent effect on its response. Responses of two SAI afferents, both with receptive fields on the ventral surface of the fingertip (centers separated by 2.5 mm) and both in contact with the stimulus, are shown in Fig. 13A. For one afferent (filled symbols), the response saturated at $\sim 1$ N, but for the other afferent (open symbols), the response did not saturate. Afferents with receptive fields on the side or end of the finger, not in contact with the stimulus, showed a similar range of responses (Fig. 13B). In addition, afferents with neighboring receptive fields could have different force thresholds and different saturation points (Fig. 13C).

A simple population code that has been proposed for normal force is the total population response (Goodwin and Wheat 1999). The summed responses of the SAI afferents (Fig. 14A) and the summed responses of the FAI afferents (Fig. 14B) increase monotonically with increasing normal force, which is necessary for a total response code. For an analogous stimulus, a vibratory probe, Johnson (1974) showed that a number of population measures, including the total response and the number of active fibers, are monotonically related to the vibratory intensity.

**DISCUSSION**

**Comparison with previous studies**

Force control is a key component of hand movements during manipulation and relies on sensory signals from cutaneous mechanoreceptors in the hand. In addition, force cues contribute to the tactile perception of shape (Robles-De-La-Torre and Hayward 2001). Despite this, there have been surprisingly few studies of mechanoreceptive afferent responses to force. In most experiments, the stimulus parameter that has been varied and controlled is normal skin displacement (Knibestol 1975;
Muniak et al. 2007) and in only a few cases has normal force been controlled directly (Cohen and Vierck 1993; Goodwin et al. 1997). Moreover, with a few notable exceptions (Jenmalm et al. 2003), normal forces have been an order of magnitude lower than those used in everyday manipulations.

SAI latencies seen in Fig. 4 are longer than those shown in many previous studies. There are at least three reasons for this. First, the contact surface used by us was flat, whereas in most other studies, the surface was curved or only 1–2 mm in diameter, leading to greater rates of increase in stress and strain. Second, the ramp of increasing normal force had a duration of 200 ms, which is longer than in most studies. Third, the ramp started at a contact force of zero, whereas in many previous studies, indentation started from a baseline of nonzero contact force.

We used forces typical of those occurring during natural everyday manipulations, scaled to take account of the dif-
ference in size between human and monkey fingers (Goodwin et al. 1997). At these normal force levels, responses occur in afferents from all over the fingerpad and not just from those with receptive fields in contact with the stimulus (Jenmalm et al. 2003). Regardless of the location of their receptive fields, responses of some afferents saturated, with a range of different saturation forces, whereas other afferents did not saturate. It has been postulated that normal force could be encoded by the total SAI afferent population response (Goodwin and Wheat 1999), but before this study, this was not tested for (large) forces comparable to those used in everyday manipulation. Our data confirm that this is indeed the case. An analogous analysis for low-amplitude vibratory stimuli also showed the viability of population codes for stimulus intensity (Muniak et al. 2007).

An even greater lacuna exists for the effect of tangential forces on mechanoreceptor responses, and we know of only one prior study with tangential forces comparable to those used in manipulation. Our experiments extend that study on humans by Birznieks et al. (2001), providing significant new data. In their study, normal and tangential forces were presented concurrently for short durations and with rapid repetition. Only one force magnitude was used, with only four directions for the tangential force component. By using longer-duration stimuli with separable normal and tangential components, we were able to decouple the tangential force responses. A range of tangential force magnitudes was used, allowing us to characterize the magnitude effect, and eight directions were used for more secure characterization of directional effects. Three different normal force values were used, allowing interactions between normal and tangential forces to be studied. Where comparable, our results are in accordance with those of Birznieks et al. (2001).

FIG. 12. Effect of distance between the initial contact point of the stimulus and an afferent’s receptive field center. A and C: effect of distance on preferred direction. Angular-linear correlation coefficients were 0.40 (significant) and 0.45 (not significant) for the SAI and FAI afferents, respectively. B and D: effect of distance on the tuning index. Linear correlation coefficient were 0.29 (significant) and −0.01 (not significant) for the SAI and FAI afferents, respectively.

FIG. 13. Single fiber responses to normal force only (0 tangential force). Responses are compared for fibers innervating overlapping regions of skin on the same finger and with the same von Frey filament thresholds. A: the receptive field centers were located on the volar surface of the finger and were separated by 2.5 mm. B: the receptive field centers were located on the side of the finger and were separated by 3 mm. C: fiber recruitment with increasing force magnitude is apparent from the different response onsets for 3 afferents (maximum distance between receptive field centers was 3.5 mm). Data points are mean responses (±SD, n = 6).

FIG. 14. Total population responses can encode normal force magnitude. A: filled symbols and solid line show summed responses of the 75 SAI afferents. Open symbols and broken line show adjusted summed responses for 30 of the SAI afferents tested at the additional forces of 2.2 and 2.5 N; sum adjusted by multiplying by 75/30. Inset: positions of the receptive field centers of the afferents. B: summed responses of the 12 FAI afferents.
Tangential force magnitude

Behavioral experiments have shown that information about tangential force (termed load force in grasp and lift tasks) must be relayed from the periphery to the somatosensory control system (Johansson and Westling 1984). In a previous psychophysics study, we showed that the cutaneous afferents alone provide sufficient information for precise perception of tangential force (Wheat et al. 2004), supported by data from Pare et al. (2002a). Data from this study showed that responses of both SAI and FAI afferents increased in an ordered way when the magnitude of the tangential force increased, providing the neural basis for peripheral signals of tangential force magnitude.

Nature of direction selectivity

A striking result was the extent of direction selectivity. The majority of afferents were tuned. In some cases, the responses to tangential force were excitatory in all directions but greater in some directions than others, leading to directional tuning. This applied to both SAI and FAI afferents. In other cases, tangential force was excitatory in some directions but suppressive in other (opposite) directions, leading to even sharper tuning curves.

Direction selectivity is not usually associated with primary receptors but rather is a property of more complex circuitry, for example, in the retina or more commonly in the cortex (Clifford and Ibbotson 2003). In the somatosensory system, direction selectivity in primary afferent responses has been reported for stimuli moving over the hairy and glabrous skin (Edin et al. 1995; Goodwin and Morley 1987; Srinivasan et al. 1990), and Birznieks et al. (2001) showed direction selectivity in human primary afferents for three-dimensional forces applied to the fingertip. However, to our knowledge, this is the first demonstration of suppressive components in direction-selective responses of tactile primary afferents. Inhibition in the null direction is well documented in the visual system in the retina (Euler and Hausselt 2008), VI cortex (Livingstone and Conway 2003), and middle temporal cortex (Maunsell and Van Essen 1983). It has also been shown in the somatosensory cortex for stimuli moving over the skin (Gardner and Costanzo 1980; Hyvarinen and Poranen 1978; Ruiz et al. 1995) and in the auditory midbrain of the owl (Wagner and Takahashi 1992). However, suppression in the null direction is not usually associated with receptors or primary afferent fibers. One of the difficulties in showing suppression in primary afferent fibers is the lack of spontaneous activity in SAI, FAI, and FAII afferents. Thus suppression can only be shown in the presence of an additional excitatory stimulus. This technique has been used to show inhibition in the visual cortex (Bishop et al. 1973).

Suppression in primary afferent fibers is different from inhibition seen in higher-level circuitry where the inhibition results from excitation of a second neuron, which in turn inhibits, either postsynaptically or presynaptically, the neuron being characterized. Rather, suppression is a result of skin mechanics and the interaction between two stimuli. In our case, the normal force excites the afferent, and the added tangential force reduces the efficacy of that excitation. An analogous phenomenon was reported by Vega-Bermudez and Johnson (1999b), who showed that the response to an indenting pin was reduced by the presence of adjacent indenting pins, which they termed surround suppression. At a gross level, it is relatively simple to hypothesize mechanisms for suppression in the null direction; for example, the normal force will result in stress and strain at the receptor membrane, and tangential force in the null direction will reduce the stress or strain. However, to test any specific hypothesis requires a detailed model of skin mechanics of the whole fingertip and the transduction mechanism, which as yet does not exist.

It has been suggested that afferents might show a response preference for forces directed toward (or away from) the receptive field center. However, we found no relationship between the position of an afferent’s receptive field center and its preferred direction, which is consistent with the data of Birznieks et al. (2001). This rules out simplistic models of direction selectivity such as compressive (or tensile) strain from forces directed toward (or away from) the receptor. Similarly, there was no relationship between preferred direction and the direction of the skin ridges, despite evidence that fingertip skin is more elastic across ridges than along them (Wang and Hayward 2007). Interestingly, Vega-Bermudez and Johnson (1999a) found no relationship between skin orientation and the orientation of receptive fields mapped with multiple indenting probes (normal force). Apparently, the directional properties of the afferents are determined by the anisotropic nature of the local environment of individual receptors and of their attachments to the skin or anisotropy in the receptor membranes themselves. This is complicated by the fact that each primary afferent terminates on several receptors (Pare et al. 2002b; Quilliam 1978). For specific hypothesis testing, models of skin mechanics and transduction far more detailed than those available are needed (Dandekar et al. 2003; Maeno and Kobayashi 1998; Srinivasan and Dandekar 1996; Sripati et al. 2006).

The tuning index (sharpness of tuning) also varied among afferents in an unpredictable way. Moreover, there was no correlation between an afferent’s tuning index and its preferred direction, suggesting independent components in the transduction mechanisms for these two parameters. We cannot explain these results, which provide a rich opportunity for skin mechanics models with specific hypothesis testing.

Effect of normal force on tangential force responses

During manipulation, normal force and tangential force are independent variables that are coordinated according to the nature of the task. By using three different values of normal force, we showed that the preferred direction, the sharpness of tuning, and the tangential force sensitivity were all largely independent of normal force levels. This is a distinct advantage because it provides a substrate for the brain to extract information about tangential force without cross-talk from normal force.

Multiparameter transduction and coding

An interesting problem is how the multiple parameters of a tactile stimulus interact in determining the response of a particular afferent. For example, an afferent’s response is affected by normal force magnitude, tangential force magnitude, and tangential force direction, as well as object shape,
position of the object on the skin, object motion over the skin, the surface texture, and other parameters of the stimulus. The transduction mechanism must be influenced by each of these parameters, but how is not clear (French 2009). We do not know of any specific hypotheses for multiparameter transduction, but there is clearly a need for them and a need to test them both experimentally and by modeling.

Even more interesting is how four groups of primary afferents (SAI, SAI, FAI, and FAII) at most can provide unambiguous information about the multiple stimulus parameters (including the 7 listed in the previous paragraph). For some of these stimulus parameters, models have been proposed to explain how different measures of the population response might encode different stimulus parameters (Friedman et al. 2002; Goodwin and Wheat 2004). In the case of tangential force magnitude, some sort of total response code (intensive code) could work, but it is not obvious how this could be disarticulated from the total response effect of normal force. For tangential force direction, a vectorial code such as that proposed by Georgopoulos et al. (1988) for the motor cortex is viable but depends on the brain knowing the preferred direction of each afferent.

There are two basic approaches to the coding problem: an analytical approach and a neural network type approach. In the analytical approach, a computational model of the population response is developed in which a measure for each of the stimulus parameters is hypothesized and computed such that the measure corresponds to the stimulus parameter and is independent of other stimulus parameters (Goodwin and Wheat 2004). Currently there is no model that accounts for the more than seven possible parameters of a stimulus. In the neural network approach, the network would be trained to extract the stimulus parameters independently without the need to hypothesize particular measures for particular stimuli (Ghazanfar et al. 2000). One criticism here is that current network models differ in mechanism from real neural networks. Nevertheless, it would be extremely useful to show that a neural network could achieve this impressive extraction.

A complementary view of the coding problem is the extent to which the direction selectivity of afferents is used for the conscious perception of direction or is used by the motor control system during manipulation. Although little is known about the human ability to perceive the direction of tangential force, Srinivasan et al. (1990) showed that subjects can discriminate between medial and lateral directions of stretch of the fingertip skin. Also, it is obvious that tangential force direction information is critical for successful manipulations (Johansson and Flanagan 2009). In both cases, a parsimonious hypothesis is that such behavior results from directionally selective responses of mechanoreceptive afferents processed at a higher stage by mechanisms such as those described in the previous two paragraphs.

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REFERENCES


