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Neuronal activity in somatosensory cortex related to tactile exploration

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Although the cutaneous feedback from the glabrous skin is of critical importance to dexterous object handling and tactile exploration, little is known about how force vectors exerted on the skin of the fingers are represented in somatosensory cortex (S1). Several studies have shown that anesthetizing the fingers results in the misperception of object compliance, excessive grip force, and frequently dropped objects (Augurelle et al. 2003; Johansson and Westling 1984; Monzée et al. 2003; Srinivasan and LaMotte 1995). Similar deficits in manipulative behaviors have been described after reversible S1 inactivation with muscimol, and these include deficits in finger dexterity and excessive grip force (Brochier et al. 1999; Hikosaka et al. 1985). Together, these studies emphasize the important contribution of cutaneous feedback and S1 to the fine motor control of the hand. Further research on this subject would provide useful data for the development of prosthetic systems.

The skin is a viscoelastic material and is readily deformable by light forces in all directions. In lifting objects of different weights and surface textures, Johansson and Westling (1984) first emphasized the importance of the ratio between grip forces normal to the skin and tangential shear forces associated with the inertia of lifting hand-held objects. Goodwin and Wheat (2004) further suggested that force vectors on the fingers, rather than the depth of skin indentation, best describe the components of the skin-object interactions occurring during object handling and tactile exploration. Moreover, models of skin receptor responses show that local strain correlates better with receptor activity than skin indentation (Sripati et al. 2006).

All large fiber, first-order, cutaneous afferents respond to small skin indentations within their receptive fields (Darian-Smith 1984; Iggo and Muir 1969; Mountcastle et al. 1966), and similar responses were described for neurons in S1 (Hyvarinen et al. 1968; Mountcastle et al. 1969). Although initially dismissed as anecdotal, Mountcastle and colleagues (1969) were the first to report that some S1 neurons were also sensitive to the stimuli displaced tangentially over the skin. This sensitivity to tangential forces explains why the cortical spatial resolution is greatly increased if there is lateral movement of the skin relative to a contacting surface (Darian-Smith and Oke 1980; Darian-Smith et al. 1982). However, more recent studies have demonstrated that shear force magnitude and direction are encoded by glabrous skin afferents, even without slip (Birznieks et al. 2001; Wheat et al. 2010).

Both humans and monkeys are skillful at detecting small asperities on a smooth surface, as shown by Johansson and LaMotte (1983) and LaMotte and Whitehouse (1986). Smith et al. (2002b) further suggested that subjects exercise very precise control over normal contact forces during tactile exploration. Similarly, asperities protruding from a flat surface generate transient increases in tangential-resistive force with concomitant skin deformation (Smith et al. 2002a). In addition, resistive force applied during the lateral movement of the finger was shown to be a major factor contributing to roughness estimates of simulated textures (Smith et al. 2010). Beaded surfaces, passively stroked across a monkey’s fingertips, evoke strong responses in both peripheral afferents (Blake et al. 1997) and S1 neurons (Phillips et al. 1988).

A subject performing active tactile exploration controls the normal contact force and exploration speed to optimize the...
sensitivity of the skin for changes in shear. In this respect, tactile exploration and object handling together involve a complex communication of cutaneous feedback and motor commands between the S1 and motor cortical (M1) areas. To exercise the degree of control necessary for tactile exploration, the M1 requires precise cutaneous feedback about the magnitude and direction of normal and tangential forces. The objective of the present study was to demonstrate that monkeys control the finger speeds and normal and tangential forces during exploratory procedures in a manner similar to humans. This behavioral analysis was used to evaluate S1 activity occurring during the tactile exploration task. We hypothesized that tangential force might be represented by a neural population distinct from normal force in S1 based on its demonstrated importance for object manipulation and the strong responses to shear evoked in cutaneous afferents (Johansson and Westling 1984, 1987; Wheat et al. 2010). In addition, we wanted to determine whether surface textures and frictions that affected the exploratory procedure would also affect S1 neuronal activity.

METHODS

Tactile exploration task and apparatus. This study was approved by the Animal Ethics Committee of the Faculty of Medicine of the Université de Montréal. Two female Macaca fascicularis were trained to use the fingertips to explore a circular flat surface, 7.5 cm in diameter, in search of a 2.0-mm square target, slightly raised to a height of 0.280 mm (Fig. 1A). With the exploration surface hidden from view, the monkeys were required to find the asperity and then exert a 3.5-N normal force on the target with a single fingertip. Finally, to obtain a fruit juice reward, the monkey was required to withdraw the hand fully from the exploration surface. The task was relatively easy to perform and required ~1.5 s for the monkey to locate the target. The objective was not to determine the detection threshold but rather, to study the execution of the exploratory procedure itself. The ease of performance was therefore to ensure the monkey’s willingness to execute hundreds of trials to maximize the recording of neuronal activity during active, self-directed exploration. The exploration task was simple enough that the monkeys were willing to execute close to 1,000 trials during the course of a 3- to 4-h daily session, and recording ceased when the animals reached satiety. The task was performed without visual feedback, so the initial or starting position of the hand on the exploration surface was highly variable. If the exploratory surface and the target had been larger, then the monkeys might have adopted a whole-hand exploratory strategy. Instead, the size of the surface relative to the size of the fingertip was such that both animals consistently used the fingertips of digits two and three for scanning the surface. A digital video camera recorded the two-finger exploration continuously at 30 frames/s to monitor the exploratory procedure (Fig. 1A). After each trial, the surface was rotated to one of four randomly selected target locations for the next trial.

A six-axis force and torque sensor (Gamma; ATI Industrial Automation, Apex, NC) recorded the finger forces and paths. The forces and task-related events were recorded continuously in a circular buffer to enable offline sorting. The center of the two-digit pressure position was calculated from the three axes of linear forces and torques, and the displacement of the center of pressure was used to track the finger movement direction and speed on the work space at 250 Hz. For each 4 ms sample, the net force, instantaneous coefficient of friction, direction, and speed were also calculated (Fig. 1, B–D, respectively).

When conditions permitted, cell activity was examined as the monkeys explored four different work surfaces (dry and oil-coated smooth plastic, fine sandpaper with a 12-µm particle diameter, or coarse sandpaper with a 19-µm particle diameter) in search of a raised target. The second monkey also explored a fifth dry plastic surface...
with a recessed target that was more difficult to detect. The order of presentation of the surfaces was almost always the same; beginning with at least 50 trials with the dry plastic surface, followed by 50 trials with the fine and course sandpaper. The oiled plastic was presented last, because it required subsequent careful washing of the monkey’s hand before another surface could be presented. This latter procedure was combined with receptive field determination using a small camel-hair brush and a 1.0-mm blunt probe to identify the cutaneous receptive field of each cell. The receptive field locations and areas were reproduced on standard drawings of the hand. Complete testing of a single neuron required ~1 h.

Data preparation and time alignment. The tactile exploration period used for subsequent analysis was defined as the interval between the first contact with the exploratory surface and the moment, 100 ms before pressing the tactile target. The initial contact was defined as a 0.05-N force increase in normal force. The initial contact and target pressing were used to evaluate neuronal responses to light contact and strong pressure, respectively. All subsequent analyses were based entirely on the tactile exploration phase of the task included between those two events.

Behavioral analyses. An ANOVA was used to compare the normal and tangential forces, kinetic friction, and finger speeds for the five surfaces. When significant, Tukey’s honest significant difference multiple comparison procedures were used to compare pairs of surfaces. Correlation coefficients were used to evaluate the covariance between the parameters.

Recording procedures and histological reconstruction. Under Isoflurane anesthesia and sterile conditions, an 18-mm circular recording chamber was surgically implanted over the central sulcus, 18 mm lateral to the midline and 1 mm anterior to stereotaxic interaural zero. A recording chamber was surgically implanted over the hand region of S1. After postoperative recovery, single-unit recordings were conducted with glass or varnish-insulated tungsten electrodes (~1 MΩ) mounted on a Trent Wells hydraulic microdrive or a modified Crist Instrument screw-driven double microdrive. At the end of the experiment and before perfusion, the recording areas were labeled using India ink. The animals were euthanized with an overdose of pentobarbital sodium, and ventricular perfusion was performed with saline, followed by a 10% solution of phosphate-buffered formalin. The brain region of interest was blocked perpendicular to the central and intraparietal sulci, and 40 μm frozen sections were stained with Cresyl violet.

Cell identification and receptive fields. At the end of each recording session, we used a camel-hair brush to investigate the position and size of the recorded neuron’s receptive field. Very few neurons had propriocceptive fields identified by joint manipulation and muscle tapping, and they were excluded from this study. To establish the location of the electrode in S1, particularly with respect to neurons with cutaneous receptive fields in M1 (Lemon 1981; Picard and Smith 1992; Tanji and Wise 1981), we used microstimulation (300 ms at 300 Hz up to 30 μA) delivered through the recording electrode to evoke hand movements. Microstimulation did not evoke wrist or finger movements from the locations of S1 neurons reported here.

Task parameters and instantaneous firing rate. In view of the fact that the trials had different durations, finger paths, and task kinetics, we elected to compare the instantaneous firing rate at each 4 ms epoch of exploration with the instantaneous velocity, direction, or normal and tangential force magnitudes for the tactile exploration period. The instantaneous firing rate frequency was calculated using a classical sliding Gaussian kernel (Paulin 1992) of 48 ms duration, incremented in 4 ms steps, determined by the force and torque sensor acquisition rate. Although window size can be adapted according to the mean firing rate of each neuron (Richmond et al. 1990), we applied a constant kernel to process all neurons in the same way.

Force analysis. Normal and tangential forces have been reported to affect the activity of both primary cutaneous afferents and S1 neurons (Birznieks et al. 2001; Salimi et al. 1999c; Wheat et al. 2010). As a first step, we calculated linear correlations between the instantaneous firing rate and the normal and tangential forces every 4 ms for the exploration of the dry plastic surface. However, graphic displays showed that the correlations with normal and tangential force were clearly nonlinear. Furthermore, the activity of some neurons appeared to be related to the normal-tangential force ratio. Nonlinear relationships can be described by either quadratic or Gaussian functions, although the latter has the advantage of terminating at zero, whereas quadratic models involve negative values. Although the modulation of many neurons responding to normal or tangential forces could be fitted by a one-dimensional model, this model did not adequately describe the friction-modulated neurons. Our objective in this study was to demonstrate classes of neuronal activity. Consequently, we preferred to use a two-dimensional model that included both types of modulation, allowing a distinction between activity classes, according to the same standard. For these reasons, a two-dimensional Gaussian fit (Eq. 1) was preferred to model the instantaneous firing rate of each neuron with respect to the simultaneous normal and tangential force magnitudes. This model had the advantage of providing an objective means to identify four major modulation patterns without evoking negative firing rates for certain force combinations in the model’s domain.

Equation 1 presents the function used to describe the neural activity related to the two forces, where a is the baseline firing rate, b the predicted maximal firing rate, σ the SD of the model dispersion, and μ the amplitude of both normal (Fn) and tangential shear (Ft) forces for the maximum firing rate. Furthermore, the c factor represents the combined effects of both forces, in other words, the diagonal distortion of the Gaussian shape.

\[
f(F_n, F_t) = a + b \cdot e^{-\left(\frac{(F_n - \mu_{f_n})^2}{\sigma_{f_n}^2} + \left(\frac{(F_t - \mu_{f_t})^2}{\sigma_{f_t}^2}\right)\right)}
\]  

Brincat and Connor (2004, 2006) used a similar equation to describe visual response parameters in posterior inferotemporal cortex. The Gaussian function has the advantage of matching a variety of relationships for a range of force magnitudes. The fit was solved using a least squares curve fit function in Matlab (MathWorks, Natick, MA).

To avoid noise due to high-frequency force transients and outliers, forces above 2.0 N were eliminated. The coefficient of determination \( R^2 \) was calculated using a classical sliding Gaussian kernel (Paulin 1992) of 48 ms duration, incremented in 4 ms steps, determined by the force and torque sensor acquisition rate. Although window size can be adapted according to the mean firing rate of each neuron (Richmond et al. 1990), we applied a constant kernel to process all neurons in the same way.

Since the normal and tangential forces were not uniformly distributed, and the two forces were not independent, we elected to use a randomized permutation method to evaluate the statistical significance of the Gaussian fit. Specifically, we calculated the probability of obtaining a Gaussian fit equal or superior to the real data with the same pairs of normal and tangential forces linked to shuffled firing rates. If the observed modulation was due to the covariance between the two forces, then it would also be evident in the permutations. Similarly, if the modulation arose from the nonuniform distribution of the samples across force magnitudes, then it would also appear obvious in the shuffled firing rates. New Gaussian models were fit to each of 10,000 permutations of firing rates randomly redistributed among the recorded forces. Data fits having a coefficient of determination larger than 0.10 were always statistically significant (P < 0.005).

Stability of neuronal activity. To insure that modulation of the neuronal firing rate remained stable and consistent through time, we calculated a linear regression with the cumulative force error over the temporal course of the recording for each cell. A departure from this
linear relationship would signify an unstable relationship between activity and finger forces. This analysis also insured that the model did not distort the fit to the data as a result of a specific temporal portion of the activity sample. The results indicated that the cumulative error and the time course were significantly correlated for all of the cells included in our analysis, implying a stable and consistent relationship.

**Directional selectivity.** The Rayleigh test for circular tuning and its variations (Mardia 1972; Moore 1980) was used to evaluate the uniformity of the distribution of vector lengths representing firing rates about a circle. In the present study, we wanted to determine how much of the firing rate could be predicted from knowledge of the tangential force direction. To test systematically the activity modulation of each neuron related to the direction of applied force, the Rayleigh test was followed by a correlation of the firing rate with direction using a von Mises function (Fisher 1996; Mardia 1972). This procedure statistically determined the neuronal activity bias for direction by evaluating the correlation between its firing rate and a function of the angles (Eq. 3). The baseline firing rate (a) and the maximum firing rate (b) at the preferred direction (a) were determined by the Rayleigh test for the variance of the distribution (1/k). I₀ corresponds to the modified zero-order Bessel function.

\[
f(\theta) = a + b \frac{\cos(\theta-a)}{2\pi I_0(k)}
\]

This test calculated the extent to which the neural activity was determined by direction of slip on the skin. To evaluate the activity of neurons stimulated by movement in diametrically opposite directions, we halved the phase of the von Mises correlation, such that the neuron needed to present a higher correlation for the half-phase cosine function. A coefficient of \( r = 0.15 \) was statistically significant \( (P < 0.001) \) as a result of the very large data set, which included a minimum of 20,000 samples for each neuron on each surface.

**Finger position and motion derivatives.** Linear correlations were applied to other parameters of tactile exploration, such as finger position, speed, and acceleration. In addition, a fast Fourier transfromation applied to the force traces failed to demonstrate any particular peaks in vibration frequencies below 125 Hz. However, higher frequencies could not be included in this analysis because of the 250-Hz data acquisition rate.

**Influence of surface material.** The effect of surface textures on the global activity of each neuron was first evaluated by calculating the mean firing rate for the exploration period on each trial and applying a one-way ANOVA to the four or five surface textures. Further pairwise Tukey’s comparison tests compared each surface with the others to determine whether the neuronal activity was related to surface friction. A neuron was considered as modulated by the surface texture if the mean firing rate was significantly different among at least three surfaces.

**RESULTS**

**Coefficient of kinetic friction.** Static friction was first defined by Amonton as the ratio of tangential to normal force needed to initiate motion between two surfaces. Coulomb further distinguished kinetic friction from static friction as the force ratio needed to maintain sliding between two surfaces (Comaish and Bottoms 1971). Typically, the coefficient of static friction is higher than the coefficient of kinetic friction, and the greater the difference between static and kinetic friction, the more the sliding movement will be intermittent and jerky, a phenomenon referred to as “stick-slip” motion by Bowden and Tabor (1982). In the present study, we used the kinetic coefficient of friction as the basis for distinguishing among the test surfaces. We computed the mean instantaneous ratio of the tangential to normal forces as the average kinetic coefficient of friction, while the fingers were sliding over the exploratory surface. The five surfaces provided a range of frictions, all significantly different from each other \( (P < 0.05) \) (Fig. 2). The coefficients ranged from 0.48 for the oiled smooth plastic to 1.06 for coarse sandpaper (Table 1). As a result of stick-slip motion, the instantaneous coefficient of kinetic friction over the coarse sandpaper surface varied widely, resulting in the largest SD \( (\pm 0.40) \). Although we did not detect any decreases in friction due to wear for the sandpaper surfaces, the surfaces were changed periodically as a precautionary measure.

**Exploratory movements.** Both monkeys showed exploratory movements composed of circular sweeping movements that occasionally included a combination of back and forth movements along the proximal-distal axis. Since the target location for each surface was approximately half-way between the center and the rim, these circular movements (Table 1) maximized the probability that the fingers would encounter one of the four possible target locations. Monkeys spontaneously performed scanning movements with the fingertips in a manner similar to the exploratory procedures observed in humans (Lederman and Klatzky 1987). It appears that regardless of whether the exploratory objective is the comparison of surface textures or the detection of a tactile target, the exploratory procedures are very similar. The mean finger speed was calculated as the averaged instantaneous velocities over all trials (Table 1). However, no consistent correlation was found between finger speed and total exploration time, even though the finger speed differed significantly among the surfaces \( (P < 0.05) \).

**Force deployment across different surfaces.** The amount of skin deformation due to the normal contact force is an important aspect of the exploratory procedure, since it is a component of the mechanical deformation occurring when the finger encounters a surface asperity (Blake et al. 1997; Smith et al. 2002a). During tactile exploration, the animals deployed very light normal fingertip forces that were maintained within an extremely narrow 16% range (Figs. 2 and 3), which was well below the monkeys’ maximal capacity. At the end of each trial, the monkeys were easily able to apply a 3.0-N normal force when pressing the target with the index finger. Overall, the normal forces exerted on all surfaces were significantly different from each other \( (P < 0.05) \). Globally, the plastic surfaces were explored with greater normal forces \( (\sim 0.69 \text{ N}) \) compared with the rougher sandpaper surfaces, which were scanned with lighter contact forces \( (\sim 0.58 \text{ N}) \). The viscoelastic property of the fingertip is such that it reaches an asymptotic compliance at a normal force of \( \sim 2.0 \text{ N} \) (Andre et al. 2011; Comaish and Bottoms 1971; El-Shimi 1977; Han et al. 1996). The reduction in fingertip compliance also reduced the coefficient of friction between the skin and exploration surfaces. In the present study, the negative correlation between friction and normal force was approximately \( -0.32 \) for all surfaces, despite the restricted range of deployed forces.

The surface resistance opposing lateral finger movement was counterbalanced by the monkeys’ own tangential force. This tangential force was also dependent on both the absolute normal force and the friction between the surface and the finger (Fig. 3). Predictably, the smallest mean tangential force occurred with the surface having the lowest coefficient of friction—the oiled plastic surface \( (0.29 \text{ N}) \). The mean tangential force recorded on the dry plastic surface was 12% greater \( (0.33 \text{ N}) \).
The greatest tangential force was observed for the coarse sandpaper surface with a mean of 0.56 N, almost twice the resistive force deployed on the plastic surfaces. The mean tangential forces were also significantly different for all surfaces (P < 0.05). For the four different surfaces, the tangential forces correlated well (r = -0.53) with normal forces; however, the slope of this relationship was steeper with coarse sandpaper (Fig. 3). Although according the Amonton-Coulomb law, friction between hard solids is the simple ratio of tangential and normal forces, for elastomers like the skin, it is highly variable depending on contact area, moisture, pressure, velocity, and the contact substrate (Andre et al. 2011; Pasumarty et al. 2011). In addition, a stick-slip motion accompanies the motion of the fingertip over high-friction texture surfaces and reflects the fluctuations in the tangential and normal force ratio. Moreover, during active scanning, subjects can voluntarily modulate either the normal or the tangential force or both as a function of friction. However, in general, the normal forces exerted by the monkey decreased as surface friction increased, whereas the tangential force increased with surface friction.

Since both normal and tangential forces affect skin deformation, the total skin deformation can be approximated by calculating the resultant force vector from both tangential and normal forces. The magnitude of the resultant force vector represents the total deformation applied to the skin. The four smoothest surfaces presented very similar resultant forces with variations under 7% (Table 1 and Fig. 2), and only the coarse sandpaper surface presented a resultant vector 12% greater than the dry plastic surface. These results suggest that although the normal and tangential forces vary inversely to one another, the resultant vectors of normal and tangential forces represent the total deforming forces exerted on the fingertip skin for each surface. E: speed of exploration, showing that the modal speed remained approximately constant for all of the surfaces.

### Table 1. Mean values of displacement and forces parameters during tactile exploration

<table>
<thead>
<tr>
<th>Surface</th>
<th>Coefficient of Friction</th>
<th>Displacement</th>
<th>Forces</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Radius, mm</td>
<td>Time, s</td>
</tr>
<tr>
<td>Oiled plastic</td>
<td>0.48 ± 0.24</td>
<td>19 ± 7</td>
<td>1.3 ± 0.7</td>
</tr>
<tr>
<td>Dry plastic</td>
<td>0.52 ± 0.27</td>
<td>22 ± 8</td>
<td>1.2 ± 0.6</td>
</tr>
<tr>
<td>Recessed target</td>
<td>0.54 ± 0.29</td>
<td>18 ± 8</td>
<td>1.8 ± 1.0</td>
</tr>
<tr>
<td>Fine sandpaper</td>
<td>0.76 ± 0.26</td>
<td>22 ± 8</td>
<td>1.4 ± 0.8</td>
</tr>
<tr>
<td>Coarse sandpaper</td>
<td>1.06 ± 0.40</td>
<td>24 ± 9</td>
<td>1.2 ± 0.6</td>
</tr>
</tbody>
</table>

Values are means ± SD except for time, which is trial averaged; all numbers represent 4 ms sample averages.
as friction increases, the resultant force and consequent deformation of the skin remain relatively invariant. In our opinion, all skin mechanoreceptors respond to normal and tangential forces, both of which involve skin strain. The monkeys appeared to adjust their normal contact forces voluntarily, quite possibly, to maintain a maximum compliance and consequently, maximizing sensations arising from changes in skin strain (Hayward et al. 2014; Serina et al. 1997).

Neuron selection. A total of 295 S1 neurons, recorded in areas 1, 2, and 3b in two monkeys, showed activity changes during the tactile exploration task. Of these, 230 (78%) neurons were found to have cutaneous receptive fields located on digits two and three, either entirely or at least partially in contact with the surface during exploration. The receptive fields of the remaining neurons were either on other parts of the hand not in contact with the exploration surface or simply not determined. These 65 neurons were excluded from the data analysis, even though they all showed activity modulation during the task. We know from several studies (Birznieks et al. 2009; Bisley et al. 2000; Wheat et al. 2010) that primary afferents with receptive fields remote from the stimulus contact area can be excited by currents at 30 μA or less evoked finger or wrist movements.

Contact-related activity. S1 neurons are known to discharge at the onset of light contact between the receptive field and a stimulus (Mountcastle et al. 1969). In addition, several investigators have described the strong neuronal responses of S1 neurons occurring when the receptive field encountered a slightly raised surface asperity (LaMotte and Whitehouse 1986; Phillips et al. 1988). Consequently, the initial analysis consisted of aligning the activity rasters on either the first contact with the exploration surface or with the initial operant response of pressing the tactile target. The majority (87%) of neurons responded to the initial contact with the work surface, whereas 29% of neurons attained maximum discharge upon contact with the tactile target (Table 2). In fact, 146 neurons were best aligned with the first contact with the work surface (Fig. 4A), although 56 other neurons responded to both the initial and target contacts (Fig. 4B). Only 12 neurons were activated by contact with the target alone (Fig. 4C). Finally, 16 neurons failed to show a distinct phasic response to either the initial contact or the subsequent target contact, although they were clearly modulated during the exploration phase.

Force magnitude. As a first step in the analysis, the instantaneous firing rate recorded at 4 ms intervals was correlated with the simultaneous normal or tangential force magnitude. As a result, 120 neurons showed significant linear correlations with the normal force and 98 with the tangential force (r > 0.30, P < 0.01). The activity of 54 of these neurons was significantly correlated with both normal and tangential forces, and a multiple regression analysis was used to compare their instantaneous firing rate with both forces. A total of 163 neurons showed significant linear correlations with both forces and their interaction (r > 0.15).

To portray these statistical results graphically, we constructed a three-dimensional display of the mean instantaneous firing rate for each 0.05 by 0.025 N combination of normal and tangential force (see Figs. 5A, 6A, 7A, and 8A). These representations demonstrated significant nonlinearities between firing rate and force magnitude. That is, many neurons appeared to have an activity plateau or a “preferred” force magnitude. Consequently, we elected to use a two-dimensional Gaussian function fitted to all 4 ms samples of forces and firing rates for each neuron (see Figs. 5A, 6A, 7A, and 8A). Overall, 169 neurons (72%) were significantly described by the Gaussian function (r > 0.1, P < 0.01). For neurons modulated only to normal or tangential force, the Gaussian function and linear

Table 2. Neuronal responses to initial contact, target pressing, and force modulation patterns

<table>
<thead>
<tr>
<th></th>
<th>Total</th>
<th>Normal Force</th>
<th>Tangential Force</th>
<th>Friction</th>
<th>Inverse Friction</th>
<th>Not Defined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial contact</td>
<td>146 (63%)</td>
<td>15 (50%)</td>
<td>16 (73%)</td>
<td>21 (72%)</td>
<td>7 (47%)</td>
<td>87 (64%)</td>
</tr>
<tr>
<td>Target press</td>
<td>12 (5%)</td>
<td>2 (7%)</td>
<td>0</td>
<td>0</td>
<td>3 (20%)</td>
<td>7 (5%)</td>
</tr>
<tr>
<td>Both</td>
<td>56 (24%)</td>
<td>11 (37%)</td>
<td>3 (14%)</td>
<td>5 (17%)</td>
<td>5 (33%)</td>
<td>32 (24%)</td>
</tr>
<tr>
<td>No response</td>
<td>16 (7%)</td>
<td>2 (7%)</td>
<td>3 (14%)</td>
<td>3 (10%)</td>
<td>0</td>
<td>8 (6%)</td>
</tr>
<tr>
<td>Total</td>
<td>230</td>
<td>50</td>
<td>22</td>
<td>29</td>
<td>15</td>
<td>134</td>
</tr>
</tbody>
</table>

Percentages are by column.
Regressions had similar performance. However, the Gaussian function was the only one also to fully describe neurons with preferred magnitudes in both forces axes.

**Force modulation patterns.** Of the 169 neurons significantly fitted by the Gaussian function, 101 were associated with one of five modulation categories related to normal and tangential finger forces (Table 2). Neurons that modulated more significantly to one force compared with the other presented a Gaussian fit with a summit peak oriented along that force axis. That is, normal force-related neurons were the 30 neurons with a summit firing rate at an angle below 30° over the normal force axis. Figure 5 shows an example of a neuron that increased its firing rate, with the normal force exerted by the finger during the course of exploration with little or no influence from the simultaneous tangential force magnitude. The neuron had a moderately large receptive field on the index finger and was recorded in area 2. At the opposite extreme of the continuum, the 22 tangential force-related neurons demonstrated a peak in instantaneous firing rate oriented along the tangential force axis with an angle below 30° over the tangential axis. The example shown in Fig. 6 was recorded in area 1. This neuron had a receptive field on the index finger similar to...
the neuron shown in Fig. 5. However, in spite of the similarity of the receptive fields, the activity of the tangential force-related neurons, such as the one shown in Fig. 6, was closely related to the tangential force magnitude, irrespective of the simultaneous normal force.

Other neurons were influenced by the combination of both normal and tangential forces during the exploration. Neurons presenting an activity modulation related to the force magnitude ratio had an activity summit at angles between 30° and 60° from the normal force axis. Figure 7 shows an example of a neuron most active when the normal and tangential forces reached a ratio of ~0.5. This neuron, recorded in area 2, was also strongly tuned to tangential force direction. Together, the 29 neurons of this type were labeled as friction-related neurons.

**Inverse modulation with force.** Although the Gaussian model was initiated with positive values, some neuronal activity appeared to be best fitted with an inverse function. For instance, neurons modulated with overall force magnitude, regardless of the normal and tangential components, would present a low firing rate at small resultant values and increase proportionally to the scalar product of normal and tangential force. Contrary to our expectation, only five neurons demonstrated modulated activity with force magnitude, irrespective of the normal and tangential components. These resultant force-related neurons were best fitted by Gaussian functions with the inverse summit close to zero. Furthermore, activity of these neurons reached a plateau at low resultant forces of ~0.2 N. In contrast, the majority of neurons fitted by the reversed Gaussian function showed an influence from both normal and tangential forces. This latter group of neurons was unexpected and appeared to be an antithesis of friction-related neuronal behavior. Neurons of this type appeared to be specifically unresponsive to tangential and normal force ratios at ~0.50. Instead, the 15 neurons in this category were excited by any combination of normal and tangential force magnitudes, except when those forces approached a ratio near the coefficient of friction. In the example shown in Fig. 8, this is seen as a diagonal depression of activity. Although visually the activity pattern was quite striking, we were unable to establish an objective criterion to describe the Gaussian fit. However, since the reduction in activity appeared to be related to the coefficient of kinetic friction, these neurons were labeled inverse friction-related neurons.
This neuron had discontinuous receptive fields on the tips of digit 1. Neurons of this type were labeled inverse friction related since they appeared to be specifically unresponsive to tangential and normal force ratios approximating the kinetic friction of the smooth plastic. This particular area I neuron displayed strong activity for normal and tangential force magnitudes that deviated from a particular ratio ~0.50 between normal and tangential forces. This neuron had discontinuous receptive fields on the tips of digits 1 and 2.

Finger direction. Gardner and Constanzo (1980) described S1 neurons presenting activity differences when tested in two opposite directions. In the present study, we evaluated the effect of shear direction with slip on the instantaneous firing rate of S1 neurons. Direction of slip affected the firing rate for 48% (110) of the 230 recorded neurons, which was about the same percentage as the neurons that were modulated by normal and tangential forces (46%). However, a χ² test (P < 0.01) demonstrated that the direction-related neurons were not evenly distributed across the different categories of force modulation. Two-thirds of the normal force-related population failed to show significant modulation with slip direction. Somewhat surprisingly, only 68% of the tangential force-related neuron population showed a clear modulation to tangential force direction. In contrast, 77% of friction-related neurons and 73% of inverse friction-related neurons were additionally correlated with slip direction. These complex relationships are displayed as a Venn diagram in Fig. 9A. Figure 9B shows that there was no particular direction preference among the force-related neuron populations, except for the inverse friction-related neurons that showed a significant bias for a particular exploration direction (Rayleigh, P < 0.05). All but two neurons in this group were tuned to finger movement in the proximal-ulnar direction of shear. The most plausible explanation is that tangential force magnitude was slightly larger (12%) in the ulnar-proximal direction, which could have influenced the directional tuning of these neurons. However, this directional bias was not observed for tangential force-related neurons, although they also should have been affected by this same uneven force distribution.

Seven additional neurons were excited by slip in diametrically opposite directions. These neurons showed a better correlation for movement in opposite directions than for a single direction, and four of these neurons were also tangential force related.

Finger speed and acceleration. Sinclair and Burton (1991) reported that finger speed was also able to influence significantly the firing rate of S1 neurons. To relate S1 neural activity to finger-scanning velocity, we correlated the instantaneous firing rate with the instantaneous finger speed. Forty-five neurons showed significant correlations (r > 0.30, P < 0.01) with velocity, with approximately one-half of the neurons positively correlated (25) and one-half negatively correlated (20). However, the activity modulation with speed appeared to be secondary to the primary influence of force on the skin (Fig. 9C), since 32 of these neurons were also modulated with force. That is, 15 neurons positively correlated with speed were also either tangential force related (9) or friction related (6). A further 18 neurons negatively correlated with speed were additionally classified as normal force related (12) and inverse friction related (6) neurons. Finally, 22 neurons were correlated with finger acceleration, although 20 of these were also correlated with finger speed. Eighteen of these neurons were additionally classified as force related. Together, these data suggest that this activity modulation with speed may be fundamentally related to fluctuations in shear force. That is, neurons with positive correlations with speed would be tangential force- or inverse friction-related neurons, and negatively, correlations with speed would be associated with normal force- and friction-related neurons.

Firing rate, surface textures, and target expectation. To determine whether the surface textures had a bearing on neuronal activity, we applied an ANOVA to compare the mean firing rates of 102 neurons as the monkeys explored the 4 different surface textures. Sixty-two neurons (61%) presented significant differences in mean firing rate related to the surface explored. Of these, 17 neurons (27%) progressively increased their discharge rate in relation to the increasing surface friction and presented the highest activity for the coarse sandpaper surface. An example is shown in Fig. 10A. In contrast, eight neurons (13%) had significantly lower firing rates for the sandpaper surfaces and higher activity rates for the lubricated plastic surface; an example is shown in Fig. 10B.

The changes in activity related to different surface textures were also related to force modulation. From the 102 neurons...
tested on different surfaces, 35 were additionally related to force modulation. Only 10 of the 29 friction-related neurons initially tested with the smooth plastic surface were also tested with the other textured and oiled surfaces. All of these neurons increased their mean firing frequency for the higher friction surfaces, and one-half (5/10) of these conserved an invariant response to friction over a wide range of both textures and frictions. Figure 11 shows the similar response patterns of a neuron tested with four different surfaces, ranging in friction from 0.48 for oiled plastic to 1.06 for coarse sandpaper. The overall mean firing rate of 19 other force-related neurons was increased significantly with the higher friction surfaces. Although these changes did not alter the basic pattern of modulation to forces for the majority (62%) of these neurons, we only have data on five neurons that conserved an invariant response to friction over a wide range of both textures and frictions.

Fig. 9. A: a Venn diagram representation of the population of direction and force modulation types. Normal and tangential force-related neurons represent 2 principal sets, as their combinations are divided between the friction and inverse friction-related modulations. On the 230 neurons selected for analysis, 81 were not significantly modulated for forces or direction (not represented), whereas 96 were modulated with forces, and 112 were modulated by tangential force direction. B: the distribution of preferred direction of the different force-related modulations distributed over all directions. Note that the inverse friction-related subpopulation showed a significant concentration over ulnar-proximal direction. C: the 45 neurons correlated with speed were polarized as positively or negatively correlated. Thirty-two of these neurons were also correlated with forces either negatively for normal- and inverse friction-related neurons or positively for tangential- and friction-related neurons. The bottom columns represent the 64 neurons modulated with forces that were not correlated with speed, i.e., inverse friction (I-Fri)-, normal force (Fn)-, tangential force (Ft)-, and friction (Fri)-related neurons. ND, not determined.

Fig. 10. Neuronal activity related to surface texture. Rasters are aligned on target contact with receptive fields shown on the right. A: a neuron from area 1 with increasing firing rate related to the increasing surface friction. B: another area 1 neuron with greater activity for low-friction, slippery surfaces.
We also compared the effect of a tactile search for a raised target with the search for a recessed target on the same smooth plastic surface. Depending on whether the tactile target was a raised or recessed element, 31 of the 49 tested neurons showed significantly different firing rates for the same plastic surface, despite the fact that the exploration speed and finger forces differed by <7%. Only 11 of the neurons sensitive to target change were also modulated according to force.

**Anatomical location of recordings and receptive fields.** The location of recorded neurons was established by histological reconstruction of Cresyl violet-stained sections, cut approximately perpendicular to the central sulcus. The sections were traced with a camera lucida and digitized for graphic reassembly with a computer. Microstimulation through the recording electrode was used to distinguish the S1 from M1 and eliminate the uncertainty about relative electrode depth in this region. Of the 230 neurons with cutaneous receptors in contact with the surface recorded in S1, 53% (123) was in area 1, 21% (49) in area 2, and 25% (58) in area 3b. The various force-modulated discharge patterns were almost proportionally distributed in all three cytoarchitectonic areas of S1 (Table 3), and there was no statistical difference in the distribution of force, speed, or direction modulation across S1 areas (χ², P > 0.15). The receptive fields were located totally (109) or partially (121) on the fingertips of digit two or three. As noted earlier, neurons with remote receptive fields were discarded to avoid misinterpretation about the observed force modulation. As previously described by Iwamura and colleagues (1983), 20 neurons presented 2 discontinuous receptive fields (Figs. 4C, 8, and 10A), most commonly found on the tips of digits two and three. Nevertheless, we were unable to relate the discharge patterns to particular receptive field positions or size.

**DISCUSSION**

Adventages of the unconstrained tactile exploration task. Previous studies of active touch have reported activity related to differences in surface texture, exploration speed, and contact forces in the context of a tactile discrimination task (Sinclair and Burton 1988, 1991). By comparison, the present tactile exploration task was much more unconstrained with respect to finger kinetics. Consequently, we were able to examine a range of forces, speeds, and directions, as selected by the subject, to optimize task performance. By comparing these parameters with the firing rate of S1 neurons every 4 ms, we were able to examine the instantaneous cortical processing involved in active touch during tactile exploration.

The present study demonstrated that activity of S1 neurons during tactile exploration was influenced by several surface-related parameters. First, in agreement with previous studies (Hyvarinen et al. 1968; Sinclair and Burton 1991), the majority of neurons responded to initial contact between the skin and the exploratory surface. We also confirmed the observations of Sinclair and Burton (1991) that the mean firing rate of S1 neurons is strongly influenced by the roughness of the exploratory surface, as well as the contact force and finger speed during tactile exploration.

![Image](https://via.placeholder.com/150)

Fig. 11. Three-dimensional plot of mean neuronal activity as in Fig. 5 of a friction-related area 3b neuron tested on different surfaces. Tangential force range of the sandpaper surfaces were enlarged up to 1.0 N to show the range of the neuron activity on those surfaces. Although the mean firing rate changes in magnitude, the global shape of modulation remained similar across all surfaces. The receptive field is displayed (top right).

| Area 3b | 58 (25%) | 7 (23%) | 4 (18%) | 8 (28%) | 4 (27%) | 35 (26%) |
| Area 1  | 123 (53%)| 15 (50%)| 15 (68%)| 17 (59%)| 10 (67%)| 66 (49%) |
| Area 2  | 49 (21%) | 8 (27%) | 3 (14%) | 4 (14%) | 1 (7%)  | 33 (25%) |
| Total   | 230      | 30      | 22      | 29      | 15      | 134     |

Percentages are by column. S1, somatosensory cortex.
during exploration. In addition, the present study characterized the relationship between the instantaneous firing rate of S1 neurons and the normal and tangential forces acting on the fingers during tactile exploration. Different subpopulations of S1 neurons appear to encode force vectors either normal or tangential to the skin surface in a nonlinear fashion, including preferred magnitude and force ratios. Furthermore, the majority of these neurons also encodes the direction of finger exploration.

Exploratory behavior adapted to surface properties. The lubrication of the plastic surface with oil consistently reduced the coefficient of friction on all trials. In contrast, the coarse and fine sandpapers provided stable high-friction surfaces throughout. In reaction to increased friction, monkeys decreased the normal force by 13% and 16% on the two sandpaper surfaces. In contrast, normal force during human tactile exploration was reported to be unchanged when an adhesive (sucrose) coating was added to a smooth plastic surface (Smith et al. 2002b). This discrepancy implies that the subjective difference between sticky surfaces compared with abrasive surfaces resides in the temporal ratio of stick to slip. Furthermore, as suggested previously by Sinclair and Burton (1991), the very abrasive nature of coarse sandpaper could have encouraged the monkeys to exert lighter normal contact forces, although the monkeys showed no hesitation in exploring the sandpaper surfaces nor was there any apparent irritation of the fingertip skin.

The monkeys did not substantially increase the normal force when exploring for a recessed target, as previously reported for human subjects (Smith et al. 2002a). Although the two dry plastic surfaces represented the shortest and longest average exploration times, both were performed with almost identical trajectories and forces. In our opinion, the similar normal forces are most likely linked to the nearly identical coefficients of friction for the two dry plastic surfaces. It suggests that the explored surface had greater influence than the target saliency in the modulation of finger forces. The increase in tangential force accompanied by a decrease in normal force suggests a strategy that may have served to maintain a relatively constant resultant force vector under 1.0 N to optimize skin compliance (Hayward et al. 2014; Serina et al. 1997) and maximize the sensitivity to changes in skin strain.

As shown in Table 1, the finger-scanning speeds varied widely depending on the composition of the various surfaces. In addition, the average scanning speed for the monkeys (450 mm/s) was three times faster than those used by human subjects (150 mm/s) performing a similar tactile exploration task (Smith et al. 2002b). Despite this difference, finger speeds were negatively correlated with the normal force, as previously described for both human and monkeys (Sinclair and Burton 1991; Smith et al. 2002b). That is, lighter contact forces were deployed at higher exploration speeds. In the present study, finger speeds on the three plastic surfaces were similar, whereas both monkeys used significantly greater exploration speeds when scanning the coarse sandpaper surface. A greater exploration speed would increase the rate of change in tangential force as the moving finger encounters the target asperity. The sandpaper surfaces provided a noisy background of tangential forces, and consequently, we cannot exclude the influence of a more salient target, leading to an exploratory strategy of lighter contact force and higher exploration speed. However, the effect of having a raised or recessed target seemed to have had relatively little effect on the trajectories, forces, and speeds of exploration, despite the fact that the recessed target took longer to detect. In summary, tactile exploration appears to require precise sensorimotor control in both humans and monkeys depending on the surface explored and to a lesser degree, the characteristics of the target.

Exploration with two fingers. In the present study, both monkeys used the fingertips of digits two and three as a single “virtual” finger to explore the surfaces, irrespective of the surface texture or whether the target was raised or recessed. However, the force and torque sensor calculated the finger position as the global center of pressure. As a result, the center of pressure actually represented the mean location of both fingertips. Although this introduces some error with respect to the actual finger position, we feel the comparison of finger forces among surfaces remains valid, since the fingers were always moved together in an identical manner for all conditions. Nevertheless, it is possible that the aggregate forces applied by the two fingers may have varied depending on the direction of movement.

Discharge on initial contact and target contact. Sinclair and Burton (1991) reported that a majority of S1 neurons discharge at initial contact when grasping an object. In the present study, the majority of neurons also discharged on initial contact with the exploratory surface. In contrast, fewer neurons were specifically activated by the 4.0-N force associated with pressing on the tactile target. Not only did these larger normal forces fail to produce increased discharge in many cases, but also, pressing on the target was frequently associated with a complete cessation of activity, implying a significant nonlinearity in the neuronal response to pressure on the receptive field (Fig. 4A). However, all of the neurons reported here continued to show sustained activity throughout the exploration phase of the task.

Influence of surface textures on force-modulated neurons. There is general agreement that most S1 neurons are usually more excited by textured surfaces than smooth surfaces in contact with the skin (Darian-Smith 1984; DiCarlo and Johnson 2000). However, some neurons have been reported to be more active with smooth surfaces (Chapman and Ageranioti-Bélanger 1991; Salimi et al. 1999a; Sinclair and Burton 1988). In agreement with these findings, we also found both positive and negative correlations between mean firing rate and surface friction during tactile exploration. Significantly, five S1 neurons that increased activity with increased surface friction nevertheless maintained a similar force-related discharge pattern regardless of the explored surface texture. That is, despite changes in the mean firing rate, the pattern of modulation with finger forces remained similar for different surfaces. More data are needed to assess fully the importance of this observation.

Influence of target type. Blake et al. (1997) demonstrated that primary cutaneous afferents discharge differently when stimulated by protruding or recessed elements. The present study was unable to detect equivalent responses in S1. However, approximately one-half of the neurons recorded during the search for the recessed square target demonstrated a significantly different mean firing rate compared with an identical dry plastic surface with a raised target. Since the forces recorded with these surfaces were nearly identical, the activity differences are, most likely, linked to anticipating particular target features that affected the exploratory procedure itself.
However, these activity differences were evenly divided between increases and decreases.

**Modulation with direction of shear.** Gardner and Costanzo (1980) reported that when the fingers slide over a surface, the slip direction influenced the discharge frequency of S1 neurons. In the present study, the shear and slip direction was a significant parameter for 47% of the neurons. Interestingly, over one-half of this subpopulation was also modulated by force magnitude. This activity modulation with both shear direction and magnitude suggests that in general, S1 neuronal activity is not a specific response to a single parameter, such as force magnitude or direction. Instead, we would suggest that S1 neurons appear to respond to a specific force vector on the skin, according to the particular orientation of the normal and tangential components.

**Modulation with scanning direction and scanning speed.** Sinclair and Burton (1991) reported S1 neurons with activity related to the scanning speed during active discrimination of the spacing of ridged and grooved gratings. Pei et al. (2011) reported a population of neurons related to scanning direction, which might well be related to the force-direction neurons in the present study. However, Pei et al. (2011) used a tactile stimulator comprised of independently controlled probes that produced successive indentations of the skin to simulate the motion of tactile exploration. The shortcoming of this procedure is that it does not simulate natural shear forces and force directions, whereas the present study does so directly. Consequently, it is only our opinion that these two neuronal populations are similar. In the present study, a majority of the 45 neurons that were correlated with finger speed were correlated with either the normal or tangential force or both. This is also consistent with the observation that as the monkeys scanned faster, their normal contact force decreased, and the variations in tangential force increased. However, less than one-half of the population of force-related neurons correlated well with speed, whereas almost all of the speed-modulated neurons correlated with one force or the other. Based on our results, we suggest that forces on the finger should be considered as the primary parameter reflecting the compliance of the skin and that finger-scanning speed is a secondary parameter that covaries with forces. This conclusion is also supported by studies showing the clear capacity of humans to discriminate tangential forces (Biggs and Srinivasan 2002; Paré et al. 2002) compared with the mixed results for speed estimations (Dépeault et al. 2008; Essick et al. 1988).

**Force-related activity patterns isomorphic with skin receptors.** Although earlier studies of S1 activity focused on responses to minute perpendicular indentations of the skin (Iggo and Muir 1969; Johansson et al. 1980; Talbot et al. 1968; Werner and Mountcastle 1965), it is now generally accepted that natural object manipulation and tactile exploration apply forces to fingertips in every direction (Goodwin and Wheat 2004; Johansson and Flanagan 2009; Levesque and Hayward 2003), stimulating even receptors located remotely from the contact area (Birznieks et al. 2009; Bisley et al. 2000; Wheat et al. 2010). Johansson and Westling (1984) first called attention to the importance of the ratio between grip forces normal to the skin and load forces tangential to the skin in providing cutaneous feedback during object manipulation. Salimi and colleagues (1999b) showed that S1 neurons increased their firing rate, according to the forces generated by lifting or in response to force-pulse perturbations applied to a hand-held object. In tactile exploration, these same normal and tangential force vectors were measured as the fingers scanned the work surface. Our classification focused on what force components evoked particular neuronal responses rather than how each neuron responded to a standard range of forces. The neuronal classification was based on the maximal firing rate for a specific normal:tangential force ratio and ignored the dispersion width of that modulation. The population of normal force-related and tangential force-related neurons observed during active touch is in agreement with the modulation reported for passive stimulation (Sinclair and Burton 1988; Sinclair et al. 1996).

The population of normal force-related neurons provides direct and continuous feedback about the contact force during tactile exploration, whereas the tangential force-related neurons provide essential feedback related to texture discrimination and target identification. Together, the activity of these force-related neurons reproduces the direction and magnitude encoding of receptors in the skin (Birznieks et al. 2001; Olausson et al. 2000; Wheat et al. 2010).

The analysis relating instantaneous S1 neuronal activity to normal and tangential forces assumed a direct and simultaneous relationship between the force events on the digit and S1 neural responses and therefore, failed to take into account the conduction latency of the somatosensory system. The temporal resolution of our analysis was 4 ms, and the minimal delay from skin to our recording area in S1 is ~20 ms. The noisiness of the force-tuning functions (shown in Figs. 5A, 6A, 7A, and 8A) may well be, in part, due to the fact that stimulus and response were not optimally aligned. However, since S1 and M1 are reciprocally interconnected (Caria et al. 1997; Ghosh et al. 1987; Stepniewska et al. 1993), one must consider, in addition to the transmission delays from cutaneous receptors to S1 or M1 to finger movement, the possible excitatory input to S1 from a corollary discharge from the M1. Consequently, there is no simple answer to this question. A more detailed description of the lead and lag times between S1 neurons and similar neurons recorded in the M1 will be treated in a subsequent publication on tactile exploration.

**Force-related activity patterns as cortical emergent properties.** In contrast to the simpler force-related neurons, the friction-related neurons responded to the ratio of normal: tangential forces, irrespective of the outright force magnitude. That is, the discharge frequency of these neurons appears to encode a force-related property resembling the coefficient of friction. It is tempting to suggest that these friction-related discharge patterns reflect an emergent property of cortical processing, because to our knowledge, no cutaneous mechanoreceptors have been shown to encode the dynamic ratio between the two forces—the kinetic friction. Although we suggest that the tangential and normal components of the force vector applied on the fingertip skin are computed together at the cellular level in S1, recent studies of primary afferents suggest that considerable stimulus shaping and processing are conferred by the arborization pattern of cutaneous receptors (Paré et al. 2002; Pruszynski and Johansson 2014). Therefore, the possibility exists that peripheral receptors may be capable of encoding kinetic friction.

The friction-related and inverse friction-related neurons demonstrated activity patterns that were the mirror image of one another. The inverse friction-related neurons discharged
when normal forces were applied at either a lower or greater tangential force than expected from the surface properties. That is, these neurons appear to be inactivated and possibly inhibited by the force ratio associated with the coefficient of friction of the explored surface. Like the friction-related neurons, the inverse friction pattern of discharge cannot be easily explained as a direct product of convergent afferent activity. It is possible that the inverse friction discharge pattern is the product of a network of lateral inhibition between neurons modulated by normal forces and neurons modulated by tangential forces. The complementarity of these opposite responses to friction may enhance the capacity of the cortex to discriminate levels of friction. Certainly, the fact that both the inverse friction-related neurons and the friction-related neurons had clearly defined cutaneous receptive fields indicates that this activity pattern is not the result of an effluent copy signal from motor regions controlling movements of the hand. Conversely, these neurons would be a highly useful source of feedback for the motor system.

Texture-related modulation and friction. It is our bias that the sensation of texture is ultimately related to friction to some extent. However, a simple coefficient of friction interpretation is untenable, because surfaces with identical frictions do not feel the same. Moreover, kinetic friction is a complex velocity-dependent measure, although we believe that the rate of change in tangential force is an important part of the sensation of texture roughness. Even so, high-friction sticky surfaces do not feel the same as high-friction rough textures, although the mean kinetic friction may be identical. We hypothesize that the spatial distribution and number of small regions of skin adhesion and release provide the cortex with a complex spatiotemporal code for roughness. We hypothesize that the activity of friction-related neurons similar to those recorded in the present study is an important component of the sensations of roughness, smoothness, slipperiness, and stickiness. However, much further research is needed to test these ideas.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: P.F-P. and A.M.S. conception and design of research; P.F-P. and A.M.S. performed experiments; P.F-P. and A.M.S. analyzed data; P.F-P. and A.M.S. interpreted results of experiments; P.F-P. and A.M.S. prepared figures; P.F-P. and A.M.S. drafted manuscript; P.F-P. and A.M.S. edited and revised manuscript; P.F-P. and A.M.S. approved final version of manuscript.

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S1 ACTIVITY DURING TACTILE EXPLORATION


