Exp Brain Res (2002) 147:209–218
DOI 10.1007/s00221-002-1240-4

RESEARCH ARTICLE

Allan M. Smith · Geneviève Gosselin · Bryan Houde

Deployment of fingertip forces in tactile exploration

Received: 28 March 2002 / Accepted: 29 July 2002 / Published online: 20 September 2002

Abstract The purpose of this study was to examine how contact forces normal to the skin surface and shear forces tangential to the skin surface are deployed during tactile exploration of a smooth surface in search of a tactile target. Six naive subjects participated in two experiments. In the first experiment, the subjects were asked to explore a series of unseen smooth plastic surfaces by using the index finger to search for either a raised or recessed target. The raised targets were squares with a height of 280 μm above the background surface and that varied in side lengths from 0.2 mm to 8.0 mm. A second series of smooth plastic surfaces consisted of small recessed squares (side lengths: 2.0, 3.0, 4.0 and 8.0 mm) that were etched to a depth of 620 μm. Although made of an identical material, the plastic substrate had a lower coefficient of friction against the skin because only the recessed square had been subjected to the electrolytic etching process. The surfaces were mounted on a six-axes force and torque sensor connected to a laboratory computer. From the three axes of linear force, the computer was able to calculate the instantaneous position of the index finger and the instantaneous tangential force throughout the exploratory period. When exploring for the raised squares, the subjects maintained a relatively constant, average normal force of about 0.49 N with an average exploration speed of 8.6 cm/s. In contrast, all subjects used a significantly higher average normal force (0.64 N) and slightly slower mean exploration speed (7.67 cm/s) when searching for the small recessed squares. This appeared to be an attempt to maximize the amount of skin penetrating the recessed squares to improve the probability of target detection. In a second experiment, subjects were requested to search for an identical set of raised squares but with the fingertip having been coated with sucrose to impede the scanning movement by increasing the friction. Overall, the subjects maintained the same constant normal force that they used on the uncoated surface. However, they increased the tangential force significantly. The similarity of the search strategy employed by all subjects supports the hypothesis that shear forces on the skin provide a significant stimulus to mechanoreceptors in the skin during tactile exploration. Taken together, these data suggest that, in active tactile exploration with the fingertip, the tangential finger speed, the normal contact force, and the tangential shear force are adjusted optimally depending on the surface friction and whether the target is a raised asperity or a recessed indentation.

Keywords Finger speed · Active tactile exploration · Normal contact force · Tangential force variation · Cutaneous receptors

A.M. Smith (✉) · G. Gosselin · B. Houde
Centre de Recherche en Sciences Neurologiques,
Département de Physiologie, Université de Montréal,
C.P. 6128 Succursale Centre Ville, Montréal, Québec H3C 3T8, Canada
e-mail: allan.smith@umontreal.ca

Introduction

The human hand serves a variety of both sensory and motor functions and these functions are highly interdependent. From the standpoint of motor control, the contribution of cutaneous receptors for controlling prehensile force during object manipulation has been studied extensively (Cadoret and Smith 1996; Flanagan and Wing 1993; Johansson and Westling 1984; Westling and Johansson 1984). In grip force control, object slip is an error signal requiring a corrective increase in force to achieve the motor objective, which is secure grasping and manipulation by eliminating slip.

In contrast, with tactile exploration, scanning or searching movements are organized to allow slip in the search for a tactile target. Unimpeded slip is therefore a desirable objective of tactile scanning movements but an error signal for grasping. Moreover, slip or relative movement between a surface and the skin has long been recognized as an important enhancement for the perception of roughness (Johnson and Hsaio 1992; Meftah et al. 2000; Morley et al. 1983; Smith et al. 2002), hardness (Srinivasan and LaMotte 1995) and shape (Binkofski et al. 2001; Bodegård et al. 2000; Hikosaka et al. 1985; LaMotte and Srinivasan 1996; Lederman and Klatsky 1987).

Lederman and Klatsky (1987) studied the exploratory movements of the hand used by subjects who were asked to evaluate certain physical features of hand-held objects. They found that depending on what quality the subject was asked to assess, they used different stereotyped exploratory procedures to assist their judgement, i.e. the exploratory procedures differed depending on what stimulus features were to be evaluated. For example, subjects scanned the fingertip tangentially over a surface to assess roughness, they prodded the object for softness, they used whole-hand grasping for shape and they maximized the skin contact area for temperature.

Since the 1960s, the study of tactile exploration has been frequently embroiled in the controversy over whether there is an inherent superiority of self-initiated movement versus passive stimulation with moving stimuli; this issue is however beyond the scope of the present paper. Nevertheless, the exploratory behaviours described by Lederman and Klatsky (1987) indicate that movement is the means by which skin bearing the highest density of receptors (e.g. fingertips, lips, etc.) is brought in contact with a surface to be explored in a particular way. Furthermore, creating motion with respect to a receptor surface such as the hand allows for the active control of either the normal or the tangential force during scanning and also provides proprioceptive feedback. The study of exploratory movements clearly points to a cooperative relationship between tactile feedback and the motor control of the hand. Just as cutaneous feedback enables grip force to be optimally adjusted to the weight and friction of an object (Johansson and Westling 1984; Cadoret and Smith 1996), the exploratory procedures are purposeful acts intended to provide the receptor-bearing skin with optimal stimulation. Kunesch et al. (1989) examined tactile exploratory movements of small objects held between the thumb and index finger while the subjects were asked to make judgements about texture or shape. In general, these movements were slower than the more rapid finger movements generated during handwriting or pencil shading. A subsequent study from the same laboratory (Binkofski et al. 2001) showed that patients with both anterior and posterior parietal cortex lesions were significantly impaired with respect to texture or shape discrimination tasks, whereas patients with focal lesions of motor and premotor cortex were not.

In an attempt to provide a more detailed description of exploratory movements, Smith and Scott (1996) examined the deployment of fingertip forces while subjects rated the stickiness or slipperiness of a variety of smooth surfaces made of various materials. They found that subjects using a single scan with the index finger could accurately scale smooth surface friction by maintaining a constant contact force on the explored surface and by varying the amount of tangential force needed to displace the fingertip. From this study, it was thought that the subjects made their scaling judgements solely on the basis of kinetic friction. However, this conclusion was subsequently reinterpreted in a more recent study (Smith et al. 2002), which investigated the subjective scaling of the roughness of textured surfaces. Although once again significant correlations were found between friction and subjective roughness, a much stronger correlation was found with the variations in the tangential force. Interestingly, in both these studies, the subjects employed a contact force normal to the surface of the skin that varied very little and was generally about 0.50 N. To scan the surfaces with higher friction, the subjects increased the tangential force while keeping the normal force constant. The finding that subjects chose to maintain a steady normal force rather than reducing it in order to allow the tangential force to initiate and maintain sliding suggests that specific sensory information is imparted by the variations in tangential force imposed on a steady and modest normal force. To date, the natural deployment of normal and tangential forces in a relatively unconstrained tactile search task has not been examined in detail. The objective of the present study has been to observe the way in which normal and tangential forces are applied when a subject performs relatively unrestricted tactile exploratory movements by using the tip of a single index finger. This study has focused on three parameters; target form (raised or recessed squares), target size and surface friction.

Materials and methods

Targets and surfaces

In order to maintain a constant contact force of 1.0 N, Blake et al. (1997) used a series of raised and recessed squares passively stroked across the fingertips to test the responses of single rapidly adapting type I (RAI) and slowly adapting type I (SAI) receptors in monkeys. They found that SAI afferents were more sensitive to the raised squares, whereas the recessed squares stimulated RAI afferents preferentially. The tactile stimuli used in our study were similar to those used by Blake et al. (1997) and consisted of the same photo-sensitive flexographic plastic (Toyoba Printight EF series) sheets that were etched according to our specifications by North American Graphics (Detroit, Mich.). The first series of stimuli consisted of various sizes of squares raised 280 μm above the background surface. The lateral dimensions of the squares were 0.2, 1.0, 2.0, 4.0 and 8.0 mm and were chosen to cover the range explored by Blake et al. (1997). The second series of stimuli consisted of four sizes of squares recessed to a depth of 620 μm with lateral dimensions of 2.0, 3.0, 4.0 and 8.0 mm. Initially, much smaller recessed squares (e.g. 0.2 mm) closer to those used by Blake et al. (1997) were evaluated but the smallest dimensions proved to be undetectable by our subjects, although they were apparently sufficient to evoke activity in RAI afferents in monkeys. Each target and surrounding plastic was cut into 7.5 cm diameter circles and glued to a supporting disk made of aluminium. All the targets were located about 1.6 cm from the centre of the disk, which was midway between the centre and the outer rim of the disk. However, once the disks were inserted into the receptacle, each target occupied a different position relative to the subject.

Although the recessed squares were constructed from the same Toyoba Printight EF series plastic as the surface supporting the raised squares, the un-etched background surface had a significantly lower coefficient of friction against the fingertip as shown in Table 1. The effect of friction on tactile exploration will be presented later.

Table 1 Mean friction and speed recorded for subjects seeking the various types of squares

Target character	Mean friction	Mean speed (cm/s)
Recessed squares	0.50±0.13	7.67±3.75
Raised squares	0.89±0.32	8.63±3.24
Sucrose raised squares	1.61±0.41	11.63±2.97

Force measurement

The nine rigid target disks were inserted snugly into a receptacle mounted on a Gamma-6-axis force/torque sensor (ATI Industrial Automation, Garner, N.C.) shown in Fig. 1. The receptacle was similar to that used by Smith et al. (2002), except for a slightly raised rim about the circumference of the receptacle; this helped the subjects to feel the boundary of the exploratory field. The force sensor produced analog voltages corresponding to the linear forces in three dimensions. Fz was the force perpendicular or normal to the exploration plane, whereas Fx and Fy were the two axes tangential to the explored surface. The Fx and Fy forces were measured as either positive or negative deviations from the centre of the disk depending on the force direction. These independently measured forces were fed to an analog-to-digital-converter with 16-bit precision and set for a conversion rate of 250 Hz.

Subjects and the tactile exploration task

Six naive right-handed subjects (5 women and 1 man) aged between 22 and 39 volunteered to participate in the experiment. The study was approved by the Université de Montréal Medical Faculty Ethics Committee and all subjects provided written informed consent regarding their participation.

Before beginning, the subjects were requested to wash and thoroughly dry their hands. The subject was seated at a table facing the experimenter, with the forearm resting on a polystyrene support. The subject introduced his or her hand through an opening in an enclosure housing the target surface and force sensor, which were hidden from the subject's view. The subjects were instructed to explore the test surface by using the tip of the index finger in order to detect either a raised or recessed stimulus depending on which condition was tested.

The experimenter then placed the subject's index finger over the surface to be searched at the point most distal from the subject. At a signal from the experimenter, the subject lowered the finger until it made contact with the surface and tactile searching began. The subjects were instructed that once contact had been made with the exploratory surface, they were to keep the finger in contact with the surface until either the tactile target was sensed with the index finger or they were told to stop by the experimenter. They were further instructed that only the index finger should contact the surface and that the finger should remain within the circumferential boundary of the disk. When the subjects made contact with the tactile target, they were asked to indicate this by pushing down on the target as if it were a button.

Fig. 1 The ATI six-axes force and torque sensor with the receptacle holding a 1.0-mm raised square target. Disk diameter: 7.5 cm. The size and position of the four other raised targets are shown *below*. The recessed squares are not shown

Each of the tactile targets had a different location on the exploration disk (as shown in Fig. 1), the disk was randomly changed on every trial so the subjects had no *a priori* knowledge of the target location. In experiment 1, the two series of stimuli were presented six times in pseudo-random order. The first series consisted of five raised squares of various dimensions, whereas the second series consisted of four recessed squares again of various dimensions. The raised and recessed targets were never presented in the same series of trials and so it may be assumed that the subjects expected either the raised or recessed squares. In the second experiment, five raised squares identical to those used in experiment 1 were presented but the subjects applied sucrose to the fingertip before each trial. Subjects were given three practice trials to familiarize themselves with the task before each testing began. In experiment 2, the subjects were asked to dip the tip of the index finger in a 30% solution (30 g in 100 ml water) of sucrose and pat dry the finger on a paper towel before each trial. After every trial, both the finger and the target surface were rinsed with warm water and dried.

Data acquisition and analysis

The acquisition and computerized storage of the data began as soon as the index finger made contact with the force sensor and the normal force (Fz) exceeded 0.05 N. When the subject felt the tactile target, he or she indicated this by applying a 1.0 N force over the target for 0.5 s. In order to eliminate the transients associated with the finger contacting and breaking contact with the force sensor, we routinely removed the first and last 100 ms from the force traces. However, all the traces were inspected and the start and stop limits were adjusted to eliminate unwanted initial or terminal transients before the force and speed averages were calculated. The computer used to record the three-dimensional linear forces (Fx, Fy and Fz) was also used to calculate the resultant tangential force (F_{rtan}) according to the following formula:

$$F_{rtan} = \sqrt{Fx^2 + Fy^2}$$

In addition, the computer calculated the mean coefficient of kinetic friction (μ) as:

$$(\mu = F_{rtan}/Fz).$$

An estimate of the X and Y position of the centre of finger pressure could be calculated as:

$$\text{X Position} = \text{Torque X}/\text{Force Z}$$

$$\text{Y Position} = \text{Torque Y}/\text{Force Z}$$

These values were plotted by the computer every 4 ms. It was further assumed that the centre of pressure included a radius of 4.0 mm representing the approximately circular contact area of the fingertip. Plotting the change of position of the centre of pressure allowed the computer to track the path of the fingertip. By dividing the total finger travel distance by the time required to reach the target, we had a rough estimate of finger speed. However, this average speed included both reversals in direction and any other accelerations and decelerations incurred during the exploration. A maximum duration of 15 s was arbitrarily determined for each trial and if, as rarely happened, a subject failed to detect the stimulus within that period, the trial was rejected and the condition repeated at the end of the pseudo-random sequence. The statistical significance of the results was evaluated where necessary with *t*-tests or analyses of variance with a probability criterion of less than 0.05.

Results

Experiment 1: detection of raised and recessed squares

Tactile exploration strategy

There was a surprising consistency in the tactile exploration strategy employed by the subjects. After the initial practice trials, the majority of subjects began their search by first touching the outer rim of the disk, apparently to start exploration from an established tactile reference point. Next, the subjects performed right-left sweeping movements (back and forth) of the index finger to scan the field. These features can be seen in the search path of a single trial shown lower right in Fig. 2 illustrating the sweeping strategy adopted by most subjects. These back and forth movements of the index finger were similar to the tactile exploration strategies first described by Lederman and Klatzky (1987). None of the subjects attempted to make sweeping movements in a proximal-distal direction along the long axis of the finger, although one subject occasionally used a more spiral-shaped search path.

Calculation of the finger paths was subject to some error if the contact force exerted by the subject was not perfectly perpendicular or normal to the plane of exploration. This occasionally caused the finger path to appear to exceed the circumferential boundary of the exploratory disk.

The linear forces in three dimensions exerted by the finger during tactile exploration are shown left in Figs. 2, 3 and 4. On average, the normal force (Fz) was 0.49 N for the six subjects and remained constant until the target was contact. The y-axis force aligned with the long axis of the fingers also showed only minor variations, whereas the x-axis force was modulated from positive to negative as the finger swept over the origins of the x- and y-axes in the centre of the disk. The resultant tangential force (see above), compared with the simultaneous normal contact force, and the rate of change in the resultant tangential force are all also shown upper right in Figs. 2, 3 and 5. The brief peaks and valleys in the resultant tangential force occurred at the points where the finger changed scanning direction.

The small changes in the resultant tangential force caused by the fingertip encountering the tactile target were not always clearly distinguishable in our force traces, although they were clearly sensed by the subject's finger. In retrospect, an asperity higher than the 280 μm used here may have provided a more measurable change in tangential force when contacted by the finger.

The mean finger speed (Table 1) was 8.63 cm/s for the raised squares and 7.67 cm/s for the recessed targets and, although this difference was small, it was statistically significant ($P<0.05$) according to a *post hoc* comparison

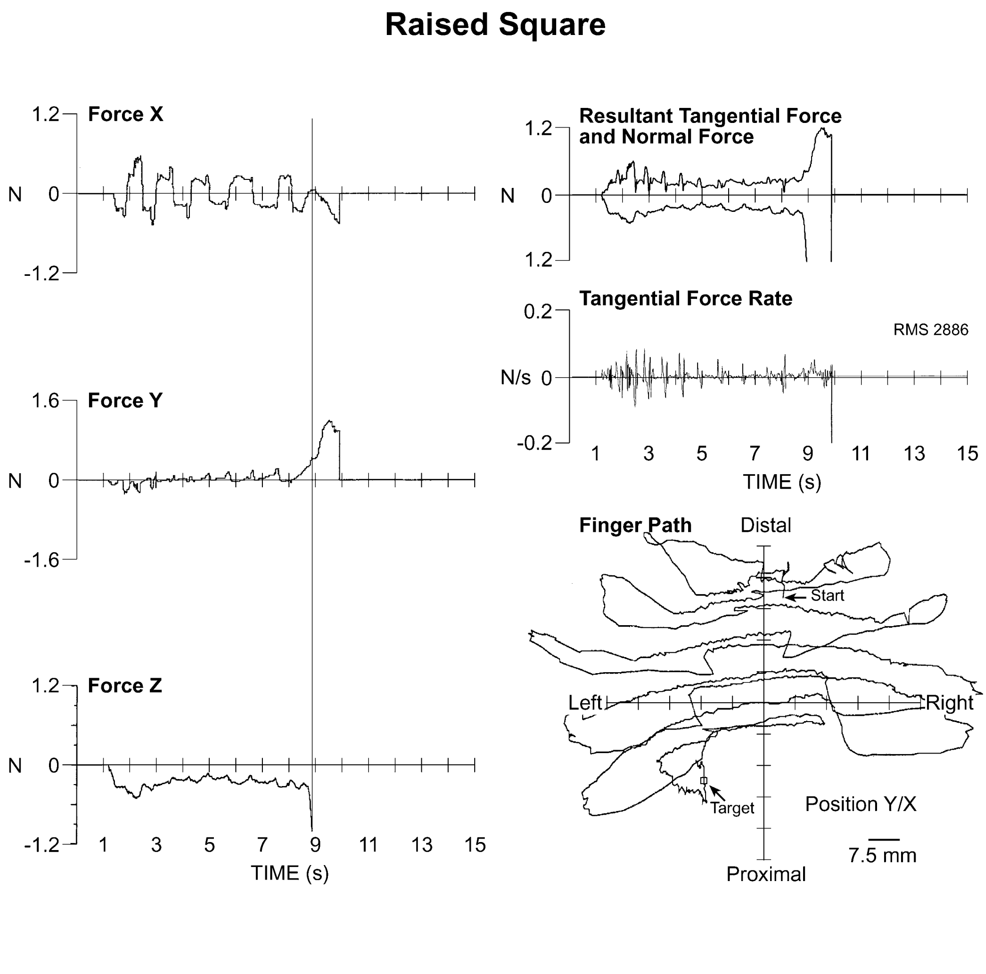

Fig. 2 Data obtained from a single trial from a subject searching the uncoated plastic surface for the smallest (0.2 mm) raised square. *Left* The three linear forces: *Force X, Force Y, Force Z. Upper right* The resultant tangential force is shown *above* and the normal force is shown *below* on a common time base. The increase in normal force is the subject's indication that the target had been found. The rate of force change in the resultant tangential force is shown on the same time scale *below* (*RMS* root mean square of tangential force variation). *Lower right* The exploratory finger path (*upper arrow* start of the exploration path for the raised square, *lower arrow* end of the exploration path for the raised square)

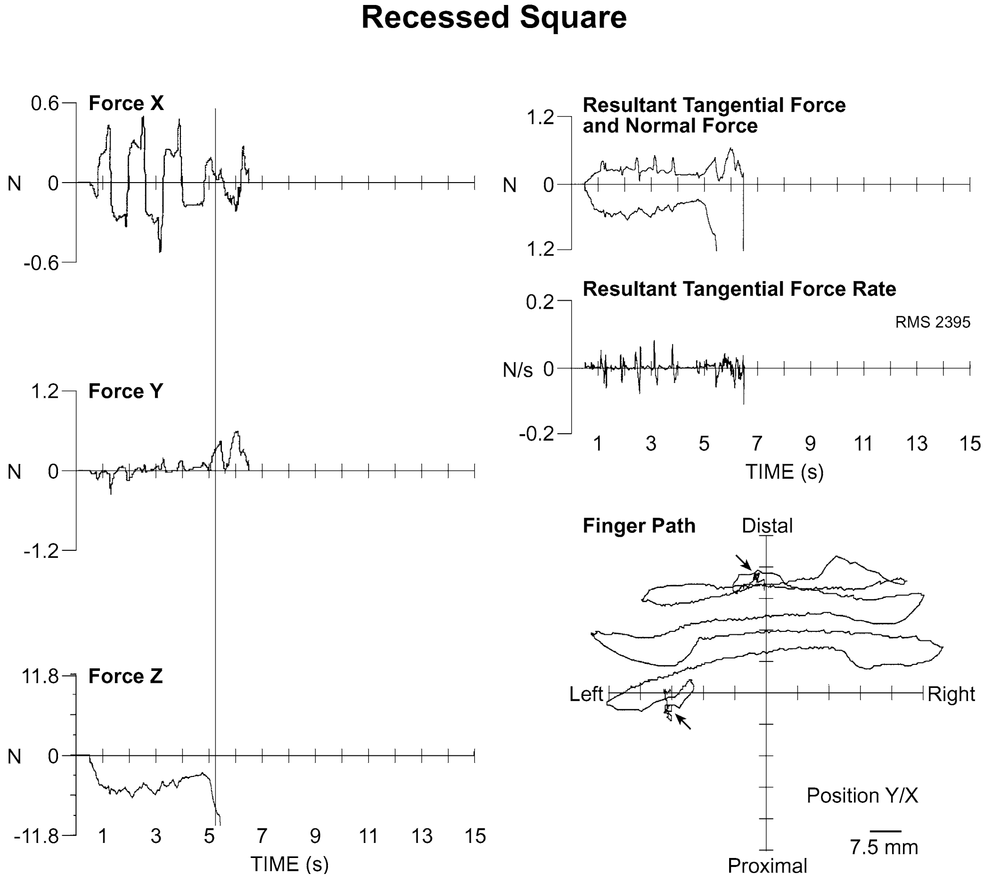

Fig. 3 Data obtained from a single trial from the same subject as in Figs. 2 and 5 searching the uncoated plastic surface for the smallest (2.0 mm) recessed square. *Left* The three linear forces: *Force X, Force Y, Force Z. Upper right* The resultant tangential force is shown *above* and the normal force is shown *below* a common time base. The increase in normal force is the subject's indication that the target had been found. The rate of force change in the resultant tangential force is shown on the same time scale *below* (*RMS* root mean square of tangential force variation). *Lower right* The exploratory finger path (*upper arrow* start of the exploration path for the recessed square, *lower arrow* end of the exploration path for the recessed square)

made by using Tukey's HSD test after an analysis of variance. Since the mean speed was calculated as the total distance divided by the total time, it included both changes in direction and acceleration other than the initial starts and stops.

Search strategies for raised and recessed squares

An objective of this first experiment was to determine whether similar tactile search strategies were used when the target squares were recessed rather than raised. It was immediately apparent that finding the recessed stimuli was much more difficult than detecting the raised squares. The smallest raised square (0.2 mm side, 280 µm high) was much more salient and easily detected that a recessed square of mirror dimensions, which proved to be undetectable (data not shown). Squares of 2.0 mm, 3.0 mm, 4.0 mm and 8.0 mm side lengths were etched to a depth of 620 µm; the 2.0 mm dimensions of the smallest target used was only barely noticeable by the subjects. As previously mentioned, the background surface for the recessed squares had a significantly lower coefficient of friction than the surface supporting the raised squares. Table 1 shows the mean kinetic friction of the surface surrounding the recessed squares was 0.50 (±0.13) compared with 0.89 (±0.32) for the surface surrounding the raised squares. The exploratory movements made by the subjects searching for the recessed squares resembled greatly those used for the raised squares. These features can be seen in the search path from a single trial shown in Fig. 3, which again illustrates the back and forth sweeping strategy. Figure 3 also shows the force profiles exerted by the finger during tactile exploration on a single trial and the resultant tangential force and rate of force change. Figures 2, 3 and 5 are single trials taken from the same subject.

Normal and tangential forces

In contrast to the similarity of the exploratory finger movements for raised and recessed squares, the force deployment differed markedly. Figure 4 shows the distributions of normal and tangential forces for all subjects searching for raised and recessed squares. The distribution is skewed to the left. On average the normal force increased from 0.49 N to 0.64 N (Wilcoxan matched pairs signed ranks test, P<0.001). At the same time, the mean resultant tangential force decreased from a mean of 0*Top* Two histograms comparing the mean normal forces for six subjects searching for raised (*left*) or recessed (*right*) squares. *Bottom* Two histograms comparing the mean resultant tangential forces for the six subjects searching for raised (*left*) or recessed (*right*) squares.41 N to a mean of 0.33 N, although this difference was not

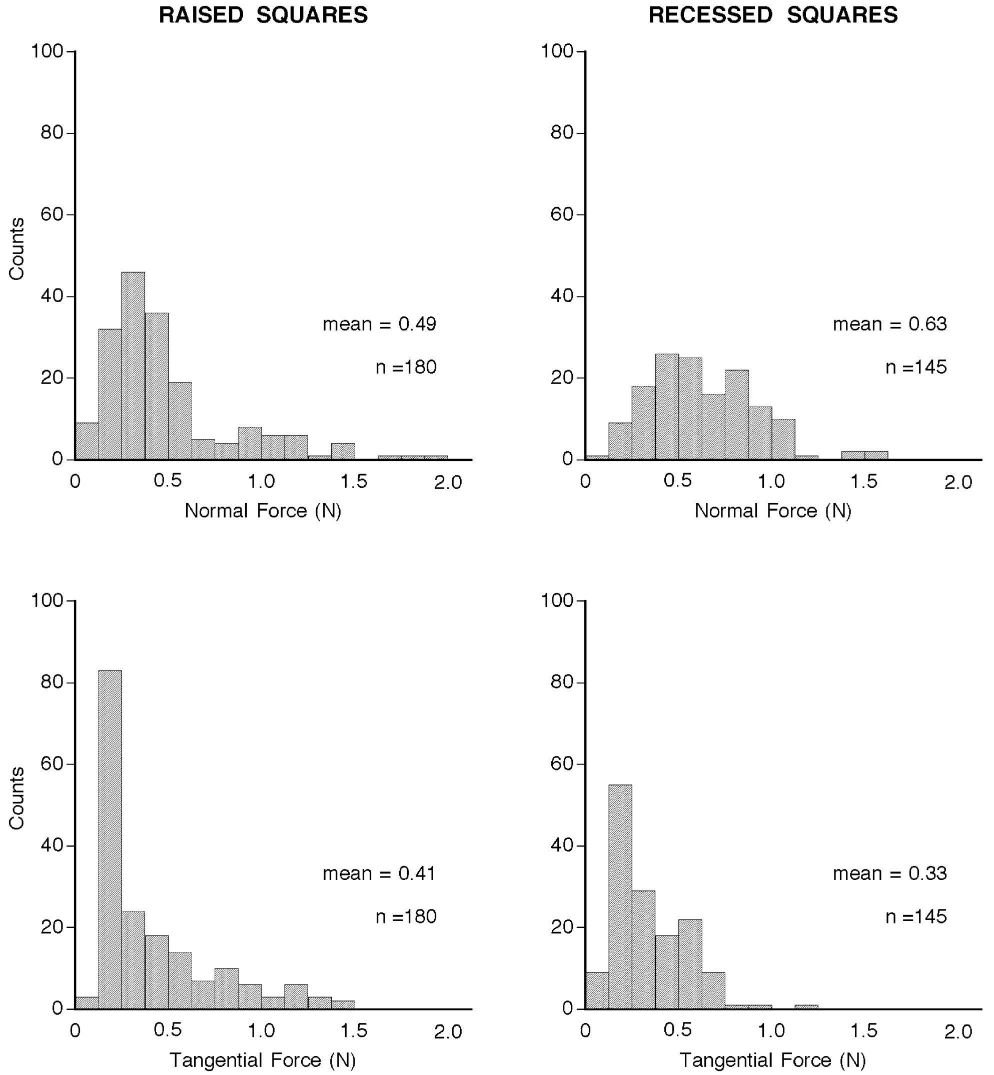

Fig. 4 The *upper part* shows the histograms comparing the mean normal forces for six subjects searching for raised (*left*) or recessed (*right*) squares. The *lower part* shows two histograms comparing the mean resultant tangential forces for the six subjects searching for raised (*left*) or recessed (*right*) squares

statistically significant. It seems that when the target stimulus is a recessed feature, a significantly higher normal force is employed.

Effect of target size

For both the raised and recessed squares, the location of each of the variously sized targets was different but these locations were constant from subject to subject. Since the targets were unseen and randomly presented, the subjects could not anticipate any target location. In general, the larger target sizes were found more quickly than the smaller targets. The mean exploratory time required to find the small raised squares was significantly greater (F=28.042, 4 df, P<0.001) but there was no significant difference among the times required to find the different sizes of recessed square. By dividing the detection time by the mean distance between the start position of the finger and the target square, it was possible to estimate the mean finger speeds for both the raised and recessed squares. The mean exploration speeds for all subjects to find each of the raised and recessed targets is shown in Table 2. The mean exploration speed was obviously influenced by the number of scans required between the upper rim of the disk and the physical location of the target. The larger raised targets were found more quickly than the smaller targets partly because the smaller targets were occasionally missed on the first pass over the surface and therefore required a second scan. The one exception was the 1.0-mm-side target, which was located very close to where the finger was initially positioned by the experimenter. Surprisingly, there was no significant effect of target size in the time taken to find the recessed squares. This may have been because of the generally less noticeable nature of the stimuli and the more restricted range of target sizes (2–8 mm).

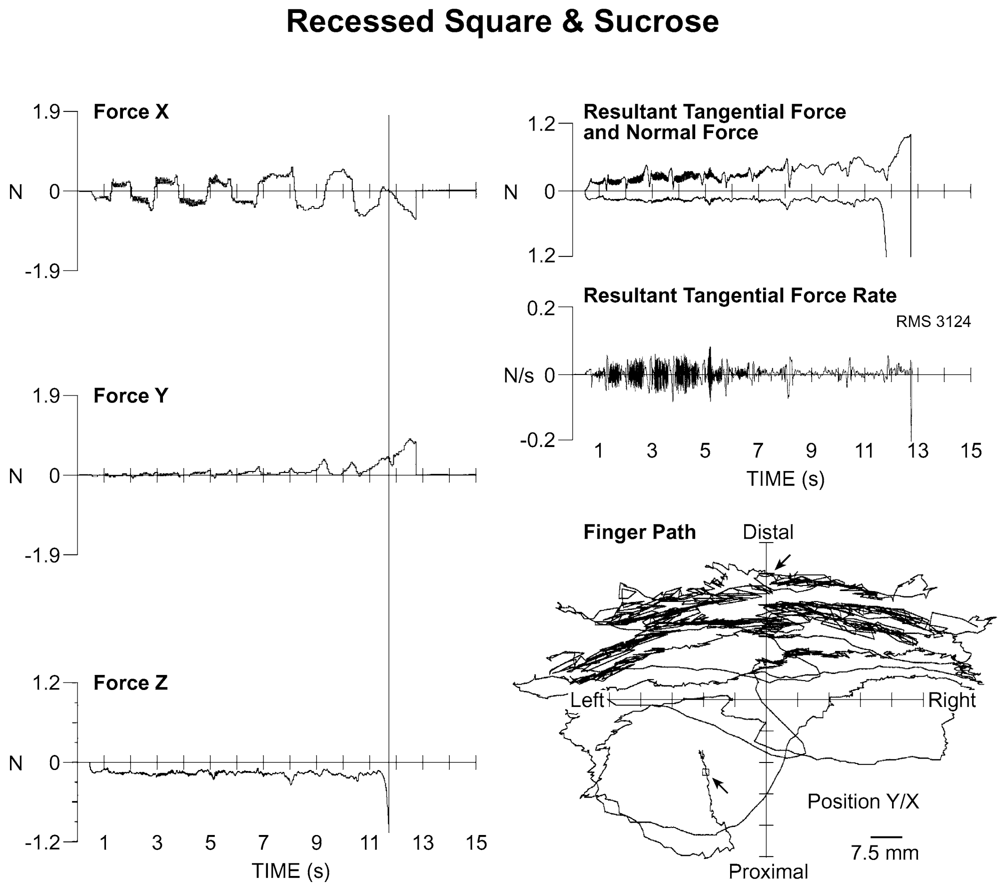

Fig. 5 Data obtained from a single trial from the same subject as in Figs. 2 and 3 searching for the smallest (0.2 mm) recessed square with a sucrose-coated fingertip. *Left* The three linear forces: *Force X, Force Y, Force Z*. *Upper right* The resultant tangential force is shown *above* and the normal force is shown *below* a common time base. The increase in normal force is the subject's indication that the target had been found. The rate of force change in the resultant tangential force is shown on the same time scale *below* (*RMS* root mean square of tangential force variation). *Lower right* The exploratory finger path (*upper arrow* start of the exploration path for the raised square, *lower arrow* end of the exploration path for the raised square)

Table 2 Mean speed (cm/s) recorded for subjects seeking the various squares with respect to size of side

	Mean speed (cm/s)					
Target character	0.2 mm	1.0 mm	2.0 mm	3.0 mm	4.0 mm	8.0 mm
Raised size	9.84±3.11	8.61±2.68	9.87±3.37	–	7.41±2.06	7.43±3.88
Sucrose raised squares	12.50±3.88	11.55±2.11	11.93±3.02	–	11.41±1.67	10.77±3.97
Recessed squares	–	–	8.38±6.26	6.65±1.44	8.07±297	7.60±2.39

Experiment 2: effect of sucrose coating

Effect of sucrose coating on mean kinetic friction

The sucrose coating caused the finger to adhere frequently to the supporting surface during the tactile exploration. This stick-slip phenomenon is illustrated in Fig. 5, which shows the saccadic finger path on a single trial for the same subject as that shown in Fig. 2. The associated three-dimensional forces, the computed resultant tangential force and its rate of change are also displayed in Fig. 5. The adhesiveness of the sucrose coating increased the mean kinetic friction from 0.84 for the trial shown in Fig. 2 to 1.63 for the example shown in Fig. 5. In general, the sucrose coating caused a statistically significant (P<0.001) increase in the mean coefficient of friction for all six subjects (Table 1). For the uncoated surface surrounding the raised squares, the mean coefficient of kinetic friction for all subjects was 0.90 (±0.3) compared with a mean coefficient of 1.60 (±0.4) for the same surface coated with sucrose. By comparasion, the surface surrounding the recessed squares was only 0.50. The greater mean kinetic friction increased the total time needed to find the tactile targets from an average of 3.2 s with the uncoated finger to 4.5 s, which was statistically significant (P<0.001).

Effect of sucrose coating on mean finger speed

For the six subjects, the mean finger speed was 8.6 cm/s for searching the uncoated surface and 11.6 cm/s for searching under the sucrose-coating condition. This difference was statistically significant (P<0.001; Table 1). However, as mentioned previously the sucrose caused frequent adhesion of the finger to the substrate producing a saccadic stick-slip movement of the finger that was subject to frequent fluctuations in acceleration. Ultimately, the sucrose-coated finger traveled further before encountering the targets, because, although it traveled

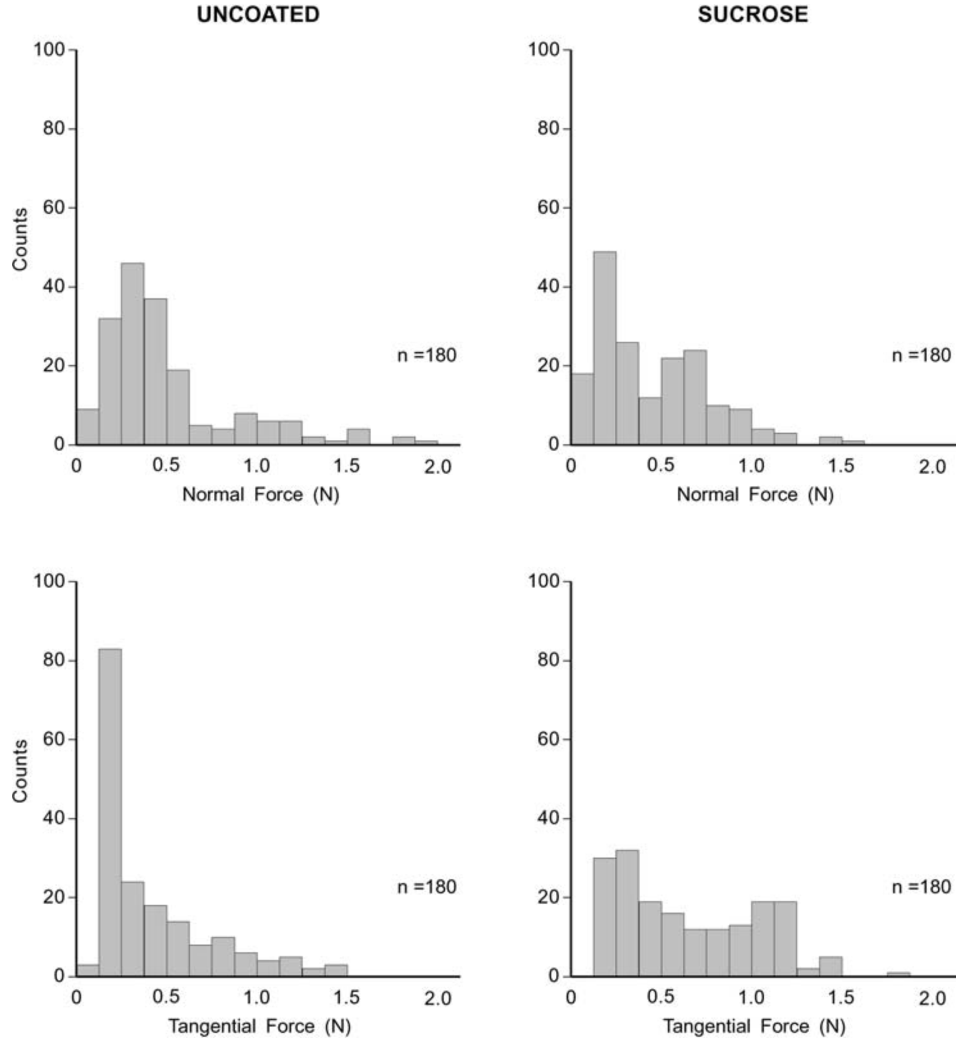

Fig. 6 *Top* Two histograms comparing the mean normal forces in each of 30 trials for six subjects (180 total) with the uncoated plastic surface and the same number of trials with the sucrose-coated surface. *Bottom* Two histograms comparing the mean resultant tangential forces in each of 30 trials for six subjects (180 total) with the uncoated plastic surface and the same number of trials with the sucrose-coated surface

faster on average, the total time to find the tactile targets was 1.3 s longer on average.

Normal contact forces

As can be seen from the single trials shown in Figs. 2 and 5, the contact force normal to skin surface (Fz) remained relatively constant throughout. The upper half of Fig. 6 shows two histograms comparing the mean normal force exerted on 180 trials with the uncoated surface with the mean normal force on 180 sucrose-coated trials. It can be seen that the normal forces in both distributions are very positively skewed. The mean contact force for the uncoated finger was 0.49 N (median=0.40 N), and with the sucrose-coated finger, the mean contact force was 0.45 N (median=0.36 N); this difference was not statistically significant (Wilcoxan matched pairs signed ranks test: $P>0.05$). At least for these two conditions, it appears that the subjects did not significantly modify the contact force when exploring surfaces with different adhesive properties.

Resultant tangential forces

Like the distribution of the normal forces, the distribution of tangential forces was also non-Gaussian and was positively skewed for the uncoated surface. The lower half of Fig. 6 shows the two histograms comparing the mean resultant tangential force exerted in 180 uncoated trials with the mean resultant tangential force in 180 sucrose-coated trials. However, the sucrose coating caused a significant increase in the mean resultant tangential force (F_{rtan}) during the tactile exploration from an average of 0.42 N (median: 0.27 N) for the uncoated surface to an average 0.65 N (median: 0.56 N) for the sucrose coating. A Wilcoxan matched pairs signed rank test revealed a significant increase ($P<0.001$) in the tangential force for the sucrose condition. The mean tangential force clearly increased and the distribution of forces for the sucrose-coated condition was a flatted, broadly irregular distribution without a conspicuous mode and not resembling a normal or Gaussian distribution. The sucrose coating produced the characteristics stick-slip feature of adhesive surfaces and significantly increased the mean surface friction (t=6.337, 179 df, P<0.001).

Exploratory finger speed in experiments 1 and 2

Finally, we compared the exploratory finger speeds for all subjects in all conditions in both experiment 1 and 2. Table 1 shows the mean speed for subjects exploring the three surfaces; recessed squares, uncoated raised squares and the sucrose-coated surface with a higher coefficient of friction. An analysis of variance followed by a *post hoc* comparisons test indicated that all three surfaces elicited significantly (P<0.05) different exploratory speeds. For the two surfaces containing the raised squares, this follows directly from the finding that the normal force was unchanged by the sucrose coating, whereas the resultant tangential force increased significantly. This three-surface comparison suggests that lower exploratory speeds are associated with the exploration of lower friction surfaces and that this includes slippery surfaces and surfaces with enough adhesion to produce a saccadic stick-slip movement. It may be that the exploratory speed is simply an inverse function of friction. It further suggests that exploratory speed may have been deliberately reduced to allow the skin of the fingertip to penetrate the recesses of the target squares and to maximize the extraction of this feature.

Discussion

Exploration strategy

The relatively unconstrained tactile exploration used by the six subjects in this study showed some surprisingly invariant characteristics: all subjects used similar left-right movements of the index finger to scan the field and, for the raised squares, they used a relatively constant normal contact force of about 0.5 N. This behaviour is very reminiscent of the exploratory procedures studied by Lederman and Klatzky (1987). However, the tactile exploratory task used in the present study differed from the Lederman and Klatzky (1987) task in two important ways. First, the subjects here were requested to find a tactile target rather than make a roughness judgement about the surface texture, and second, our subjects performed the task without any visual feedback to guide the finger movements. This latter difference explains why most subjects began by establishing a tactile reference point by first touching the rim of the target disk before initiating a systematic tactile search. The reason that the subjects preferred using lateral side-to-side finger movements to explore the surface might only be because these movements require less effort than proximal-distal movements with the forearm unrestrained. Moreover, side-to-side movements more closely resemble writing movements than alternating flexion-extensions of the finger and rotating the finger at the metacarpal phalangeal joint may have made it easier to maintain constant normal force.

Birznieks et al. (2002) recently made an extensive study of the directional sensitivity of rapidly and slowly adapting receptors in the fingertip and established that the receptors had preferred directions to tangential forces that were not uniformly distributed. They suggested that the majority of receptors were more sensitive along the long axis of the digit in the proximal-distal direction compared with the orthogonal radial direction. However, in our tactile exploration task, there was a consistent preference for movements orthogonal to the long axis of the finger, which may have additionally stimulated distal receptors located about the nail bed and some muscle receptors in the dorsal and palmer interossei.

The present study confirmed an observation made in two earlier studies of tactile exploration (Smith et al. 2002; Smith and Scott 1996) that as the coefficient of skin to surface friction is increased, the subjects increase the tangential force to displace the finger over the exploratory surface while maintaining a constant normal force. Since, according to Birznieks et al. (2002), the same receptors are sensitive to both normal and tangential forces, the maintenance of the normal force constant would preferentially sensitize mechanoreceptors to transient changes in shear forces on the skin signalling contact with the target.

The sucrose coating increased the skin surface friction and, as a result, the time taken to find the tactile target increased, although the sucrose coating did not otherwise interfere with the tactile recognition of the 0.2 mm×0.2 mm×280 μm asperity, which was still easily detectable.

Constant normal force

All subjects maintained a constant normal force when searching for raised stimuli but increased this normal force when the task required the detection of recessed squares. The detection of the recessed squares was acknowledged by all subjects to be more difficult than sensing the raised stimuli. Although this might have been a response to the lower friction of the surface supporting the recessed squares, it seems more likely that this was a deliberate attempt to increase the amount of skin penetrating the smaller depressions. Blake et al. (1997) have pointed out that, once the contact force normal to the surface is sufficient to cause the skin to deform around a raised asperity, any further increase in normal force does not further deform the skin, but only increases the pressure on that skin. In contrast, when skin contacts recessed structures, the normal force pushes the skin into the depressed areas, which probably explains why subjects used greater contact force when searching for the recessed squares in the present study.

Resultant tangential force

In contrast to the force exerted normal to the skin surface, the resultant tangential force varied with the friction of the supporting surface. It seems that when using the fingertip for making either tactile exploratory movements or subjective estimates of surface roughness or stickiness, the nervous system appears to move the fingertip in such a way so as to maximize its exposure to variations in tangential forces. The positive skew seen in both the normal and tangential force distributions probably reflects an attempt by the subject to achieve a minimum ratio between the two forces. When faced with exploring a sticky surface, the subjects were no longer able to maintain a constant tangential force. Instead, the stickiness introduced by the sucrose caused erratic variations in the tangential force resulting in the broad and irregular distribution of the mean tangential forces. These wide variations in the tangential force were responsible for the erratic and jerky exploratory movements.

Finally, Blake et al. (1997) have suggested that the small square protrusions used in the present study are a more effective stimulus for SAI afferents, whereas recessed features are a more effective stimulus for RAI afferents. This is somewhat paradoxical in view of the finding that RAI afferents are more sensitive to raised elements than are SAI afferents (LaMotte and Whitehouse 1986). Nevertheless, Blake et al. (1997) have shown that 0.8 mm×0.8 mm recessed squares activate RAI afferents but not SAI afferents. The present study suggests that the tactile exploration for surface protrusions is best served by a lighter contact force and higher tangential speeds, which would also increase the variations in the resultant tangential force. These conditions might preferentially stimulate activity in SAI afferents, although the 280-μm raised squares should have stimulated both afferent types

By contrast, the tactile search for recessed surface indentations is conducted with slightly higher normal forces but with lower accompanying tangential speeds and lower tangential resultant forces. These parameters might selectively stimulate RAI afferents. If RAI afferents correspond to Meissner cells and SAI afferents are equivalent to Merkel cell complexes, then the relative ease at detecting raised asperities compared with the recessed stimuli may reflect the greater density of Merkel cells, which, in the monkey fingertip, outnumber Meissner cells by about four to one according to a recent study by Paré et al 2002). However, the branching pattern of the afferent endings and the degree of multiple innervation of these receptors is an equally important consideration. Johansson and Vallbo (1979) have estimated that RAI afferents are the most numerous in the fingertip skin in man.

Acknowledgements The technical assistance of L. Lessard, J. Jodoin, C. Gauthier and C. Valiquette is gratefully acknowledged. We wish to thank Kenneth O. Johnson for his help in obtaining the raised and recessed squares and Michel Paré and Joël Monzée for their help with the data analysis. C. Elaine Chapman offered helpful criticism of the manuscript. This research was supported by grant RO1 NS38724 from the National Institute of Neurological Disorders and Stroke and the Comité d'Organisation du Programme des Stagiaires d'Été (COPSE) of the Université de Montréal.

References

Binkofski F, Kunesch E, Classen J, Seitz RJ, Freund HJ (2001) Tactile apraxia – unimodal apractic disorder of tactile object exploration associated with parietal lobe lesions. Brain 124:132–144

Birznieks I, Jenmalm P, Goodwin AW, Johansson RS (2002) Encoding of fingertip forces by human tactile afferents. J Neurosci 21:8222–8237

Blake DT, Johnson KO, Hsiao SS (1997) Monkey cutaneous SAI and RA responses to raised and depressed scanned patterns: effects of width, height, orientation, and a raised surround. J Neurophysiol 78:2503–2517

Bodegård A, Ledberg A, Geyer S, Naito E, Zilles K, Roland PE (2000) Object shape differences reflected by somatosensory cortical activation in human. J Neurosci 20:RC51(1–5)

Cadoret G, Smith AM (1996) Friction, not texture, dictates grip forces during object manipulation. J Neurophysiol 75:1963–1969

Flanagan JR, Wing AM (1993) Modulation of grip force with load force during point-to-point arm movements. Exp Brain Res 95:131–143

Hikosaka O, Tanaka M, Sakamoto M, Iwamura Y (1985) Deficits in manipulative behaviors induced by local injections of muscimol in the first somatosensory cortex of the conscious monkey. Brain Res 325:375–380

Johansson RS, Vallbo AB (1979) Tactile sensitivity in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. J Physiol (Lond) 286:283–300

Johansson RS, Westling G (1984) Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. Exp Brain Res 56:550–564

Johnson KO, Hsiao SS (1992) Tactile form and texture perception. Ann Rev Neurosci 15:227–250

Kunesch E, Binkofski F, Freund H-J (1989) Invariant temporal characteristics of manipulative hand movements. Exp Brain Res 78:539–546

LaMotte RH, Srinivasan MA (1996) Neural coding of shape: responses of cutaneous mechanoreceptors to a wavy surface stroked across the monkey fingerpad. J Neurophysiol 76:3787–3797

LaMotte RH, Whitehouse JM (1986) Tactile detection of a dot on a smooth surface: peripheral neural events. J Neurophysiol 56:1109–1128

Lederman SJ, Klatzky RL (1987) Hand movements: a window into haptic object recognition. Cognitive Psychol 19:342–368

Meftah EM, Belingard L, Chapman CE (2000) Relative effects of the spatial and temporal characteristics of scanned surfaces on human perception of tactile roughness using passive touch. Exp Brain Res 132:351–361

Morley JW, Goodwin AW, Darian-Smith I (1983) Tactile discrimination of gratings. Exp Brain Res 49:291–299

Paré M, Smith AM, Rice FL (2002) Distribution and terminal arborizations of cutaneous mechanoreceptors in the glabrous finger pad of the monkey. J Comp Neurol 445:347–359

Smith AM, Scott SH (1996) The subjective scaling of smooth surface friction. J Neurophysiol 75:1957–1962

Smith AM, Chapman CE, Deslandes M, Langlais J-S, Thibodeau M-P (2002) Role of friction and tangential force variation in the subjective scaling of tactile roughness. Exp Brain Res 144:211–223

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

Westling G, Johansson RS (1984) Factors influencing the force control during precision grip. Exp Brain Res 53:277–284