

Tactile Detection of Slip: Surface Microgeometry and Peripheral Neural Codes

M. A. SRINIVASAN, J. M. WHITEHOUSE, AND R. H. LAMOTTE

Department of Anesthesiology, Yale University School of Medicine, New Haven, Connecticut 06510

SUMMARY AND CONCLUSIONS

1. The role of the microgeometry of planar surfaces in the detection of sliding of the surfaces on human and monkey fingerpads was investigated. By the use of a servo-controlled tactile stimulator to press and stroke glass plates on passive fingerpads of human subjects, the ability of humans to discriminate the direction of skin stretch caused by friction and to detect the sliding motion (slip) of the plates with or without micrometer-sized surface features was determined. To identify the associated peripheral neural codes, evoked responses to the same stimuli were recorded from single, low-threshold mechanoreceptive afferent fibers innervating the fingerpads of anesthetized macaque monkeys.

2. Humans could not detect the slip of a smooth glass plate on the fingerpad. However, the direction of skin stretch was perceived based on the information conveyed by the slowly adapting afferents that respond differentially to the stretch directions. Whereas the direction of skin stretch signaled the direction of impending slip, the perception of relative motion between the plate and the finger required the existence of detectable surface features.

3. Barely detectable micrometer-sized protrusions on smooth surfaces led to the detection of slip of these surfaces, because of the exclusive activation of rapidly adapting fibers of either the Meissner (RA) or the Pacinian (PC) type to specific geometries of the microfeatures. The motion of a smooth plate with a very small single raised dot (4 μm high, 550 μm diam) caused the sequential activation of neighboring RAs along the dot path, thus providing a reliable spatiotemporal code. The stroking of the plate with a fine homogeneous texture composed of a matrix of dots (1 μm high, 50 μm diam, and spaced at 100 μm center-to-center) induced vibrations in the fingerpad that activated only the PCs and resulted in an intensive code.

4. The results show that surprisingly small features on smooth surfaces are detected by humans and lead to the detection of slip of these surfaces, with the geometry of the microfeatures governing the associated neural codes. When the surface features are of sizes greater than the response thresholds of all the receptors, redundant spatiotemporal and intensive information is available for the detection of slip.

INTRODUCTION

Tactile exploration of barely detectable features such as scratches on flat surfaces requires active stroking. To grasp and lift a fragile object, for instance a wineglass, it is important to be able to detect any slip between the skin and the object surfaces so that the minimum normal force to prevent slip can be applied. These two seemingly different tactile tasks have in common the stretching of skin because of frictional forces, with or without slip between the skin and the object surfaces. It is essential to detect the absence,

incipience, or occurrence of slip, and its attributes such as its direction and relative velocity, to correctly interpret the spatiotemporal tactile information obtained in exploring or manipulating objects.

Consider the general case of an object in contact with a region of skin, either or both of which may be in motion. At the corresponding contacting points on the object and the skin surfaces, the velocity components normal to the contact surface must always be equal for the object not to penetrate or lose contact with the skin. However, the velocity components tangential to the contact surface may differ at those points to cause slip between the object and the skin surfaces. When an object is actively stroked with the skin surface, the proprioceptive sense (Darian-Smith 1984; Loomis and Lederman 1986) can signal the presence of limb movement, but only the cutaneous mechanoreceptors innervating the area of contact can code the occurrence of relative motion between the skin and the object surfaces. This conclusion is supported by the observation that when subjects with anesthetized fingertips were asked to lift objects with the use of a two-finger grasp without looking, the fingers slid over the object, which remained motionless on the table (Johansson and Westling 1984). Alternatively, when an object is stroked on a stationary, passive skin surface, the proprioceptive information is absent, and only the mechanoreceptors in the skin respond.

Thus, under both active and passive touch, it is the cutaneous mechanoreceptors innervating the contact area that enable the detection of slip. They code the existence and attributes of relative motion, as well as micrometer-to-centimeter-sized features of the object surfaces. This explains why the performance of subjects was about the same under active versus passive touch when detecting a very small raised dot on a smooth surface (Johansson and LaMotte 1983; LaMotte and Whitehouse 1986), when reading braille (R. H. Day and R. G. Dickinson, unpublished observations), when detecting differences in the spacing of dot arrays (Lamb 1983), or when discriminating the roughness of gratings (Lederman 1981). In such tasks, when the contact force and velocity of strokes are held approximately constant, the proprioceptive information plays a negligible role. Consequently, there is no loss of generality in investigating the neural coding of slip only under passive conditions.

The peripheral neural coding of a mechanical stimulus applied to the skin surface is in general based on the types of cutaneous mechanoreceptors activated and the spatiotemporal pattern of response of each type. Whenever an object in contact with the skin surface moves relative to it

or vice versa, depending on the type of relative motion, either the region of contact moves on the skin surface or remains stationary. The stroking of skin by a small probe or by a flat surface that simultaneously changes its orientation so as to be tangential to a curved skin surface are examples where the region of contact moves on the skin surface. In such cases the presence of relative motion is conveyed by the successive activation of neighboring groups of mechanoreceptors, and the subjects (deprived of visual or other extraneous cues), having the ability to locate the region of skin where the mechanoreceptors are active, can detect the motion.

However, the fingerpads are commonly employed for tangential scanning motions, possibly because of the dexterity and the fine motion control that can be exercised, as well as the high spatial density of mechanoreceptors and the associated fine spatial resolution (Darian-Smith and Kenins 1980; Johansson and Valbo 1979). During such tactile detection of surfaces, contact forces as well as the relative orientation of the finger with respect to the object surface are maintained roughly constant. This causes the contact region to move on the object surface, but the changes in the area or the location of the region of contact on the skin surface are very small. The detection of slip must then be based on the spatiotemporal events occurring on the skin within the region of contact.

When the sizes of object surface features are of the same order as the typical area of contact on the fingerpad, because of the high innervation densities of Meissner corpuscles and Merkel cells (Darian-Smith and Kenins 1980; Johansson and Valbo 1979) and their proximity to the skin surface, the motion of a feature activates considerable numbers of these receptors in the vicinity of the feature. Examples of such features are the braille-sized dots (Darian-Smith et al. 1980; Johnson 1983; Johnson and Lamb 1981; Morley et al. 1983; Phillips and Johnson 1985) and smoothly contoured surfaces of varying curvature (LaMotte and Srinivasan 1987a,b; Srinivasan and LaMotte 1987). They cause moving patterns of responses among the corresponding populations of rapidly and slowly adapting fibers (RAs and SAs, respectively) innervating the contact area, which provide reliable spatiotemporal neural codes for relative motion. Although Pacinian corpuscles also respond to the motion of the macrofeatures on the skin, it is likely that their low-innervation density, large size, and deep location within the fingerpad limit them to transmit only temporal or intensive codes via the associated afferent fibers (PCs). Relative motion of macrofeatures on the skin can therefore be detected from redundant cues provided by multiple receptor populations.

However, when the features on a surface are so small that they selectively activate only one class of receptors, we may be able to isolate the roles played by the different receptor-types in signaling the slip of that surface. With the use of photolithography, LaMotte et al. (1982) have demonstrated the construction of microfeatures on plane glass surfaces, such as a small raised dot or a homogeneous texture consisting of an array of raised dots. Further, LaMotte and Whitehouse (1986) have shown that human observers can detect 1- to 3- μm -high single raised dot of 550 μm diam on a smooth glass plate and that only RAs in monkey

fingerpads respond to the motion of a single dot of such small size.

Of particular relevance is the fact that these small dots cannot be detected by stationary contact but give a vivid impression of their presence when the plates are stroked. Just as slip between the fingerpad and the glass surface is essential for the detection of microfeatures, it is possible that these features are essential for the detection of slip. To investigate this issue, we chose a smooth glass plate without any detectable features, a smooth plate with a single microdot, and a texture composed of arrays of microdots as the stimulus surfaces. They represent three extreme idealizations of microfeatures on surfaces normally encountered—lack of any feature, a single microfeature on a smooth ground, and uniformly distributed asperity on a smooth surface—with the feature sizes chosen to be close to human detection thresholds. We are interested in the following specific questions: 1) is the tactile detection of slip between the fingerpad and each of these surfaces possible, and 2) which primary mechanoreceptive afferent fibers are responsible for the detection and what is the code for the presence and direction of relative motion? In investigating these questions, we simplified the problem by stroking the plates under precisely controlled conditions on stationary, passive fingerpads. It should be noted that the general conclusions reached here are valid for active stroking also, because it is the relative motion between the fingerpad and the stimulus surfaces that is important in the issues raised above, rather than whether active or passive touch was employed.

METHODS

Surfaces used for stimulation

Glass plates with three different types of surfaces were used for the stimulation of both human and monkey fingerpads: 1) a smooth plate that we shall refer to as the 'blank plate'; 2) a smooth plate with a centrally located 4- μm -high single raised dot of 550 μm diam, and 3) a plate with a homogeneous texture consisting of a matrix of 1- μm -high raised dots of 50 μm diam and spaced at 100 μm center-to-center. The glass plates were the ones used for microscope slides and initially had no detectable features on their surfaces. The single dot and dot texture had precisely controlled geometries achieved with isotropic etching of the glass plates by the use of contact photolithography (LaMotte et al. 1982; LaMotte and Whitehouse 1986). These two geometries represent two extreme idealizations of the microgeometry of commonly encountered surfaces. The dimensions of the dots in both cases were such that observers with normal cutaneous sensibility could not detect the presence of dots with stationary contact but were able to detect them when they stroked the plates. Each plate was transparent so that the contact area with the skin and the occurrence of slip could be viewed through it, either during manual or machine-controlled stroking.

Machine-controlled stimulation

In both the psychophysical and the neurophysiological experiments described below, a servo-controlled mechanical stimulator driven by a hydraulic system (LaMotte et al. 1983) was used to apply the glass plates to the human and monkey fingerpads. The stimulator was capable of moving the plates in a vertical or horizontal direction at preprogrammed velocities, as well as maintaining the plates in a desired position. A resolution of ~ 2 μm in the vertical direction and ~ 6 μm in the horizontal direction was

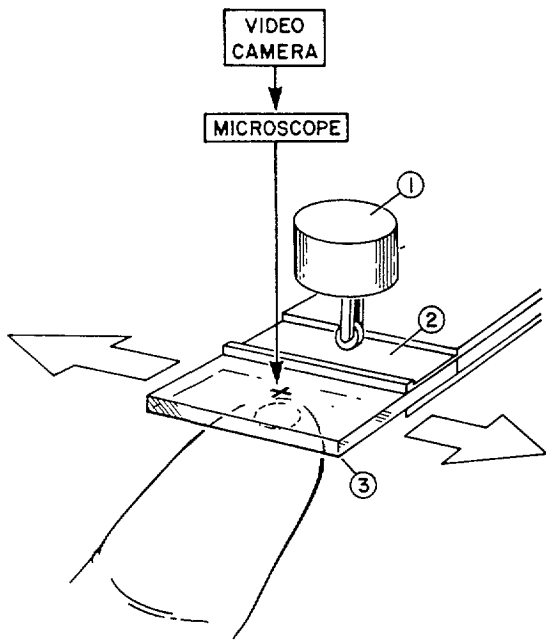


FIG. 1. Schematic of the experimental set up. Each of the three transparent plates (3) were clamped to a spring-loaded lever (2) that exerted an upward force against a force transducer (1). Contact area with the skin, the initial skin stretch, and the occurrence of slip could be viewed through a dissection microscope and a videocamera. Horizontal arrows: directions of stroking with constant horizontal velocity (10 mm/s) and vertical force (20 g).

achieved by means of linear variable displacement transducers (LVDTs) for position measurement along each axis of movement, and analog feedback circuits connected to a mini-computer (NorthStar Horizon) for servo-control. In addition, the total compressive force exerted by a glass plate on a fingerpad could be measured with a force transducer (Sensotek, resolution ~ 1 g). The force was transmitted to the transducer through contact with a spring-loaded lever, which was clamped to the glass plate at one end and connected to the stimulator by means of a hinge at the other (Fig. 1). Local analog feedback circuits enabled a desired compressional force applied on the fingerpad to be maintained constant, either when the horizontal position of the plate was fixed or during stroking. The timing and sequence of the stimuli were controlled by the computer.

For the psychophysical or neurophysiological experiments, the human or monkey hand, respectively, was placed on a rigid platform with the palm facing upward. The finger to be stimulated was slightly elevated to allow the contact region between each plate and the fingerpad to be on the volar distal one-third of the distal phalanx. The backside of the finger was pressed against plasticine to prevent any lateral movement of the finger. The sides of the fingerpad were not restrained, thereby allowing the fingertip to deform as it might when actively stroking a stationary surface.

For each stroke, the mechanical stimulator brought down the plate with a vertical velocity of 1 mm/s onto the stationary, passive fingerpad until an indentation force of 20 g was reached. Maintaining the force constant, the plate was first held in that horizontal position for 1 s. By accelerating rapidly (within ~ 10 ms) to a horizontal velocity of 10 mm/s in either direction perpendicular to the proximal-distal axis of the finger, the plate was then stroked across the fingerpad. The stroke continued until a desired stroke distance was reached, and the plate was lifted off the fingerpad. Only in the psychophysical experiments, the horizontal velocity was smoothly decelerated from 10 mm/s to 1

mm/s before lifting the plate off the fingerpad. The time interval between the end of one stroke and the beginning of the next was 5 s. It was chosen to be sufficient to allow the skin to come back to its resting state before the next stroke but not to be so long as to affect decisions by the subjects in the psychophysical discrimination experiments.

To observe whether slip between the fingerpad and the glass plates occurred during a stroke, a videocamera mounted on a dissection microscope was placed vertically above the fingerpad (Fig. 1). The distal phalanx as well as the contact region could be viewed on a videomonitor at a desired magnification, usually $\times 20$. Additional information displayed in each videoframe during machine-controlled stimulation included 1) the elapsed time and cumulative counts of videofields and nerve impulses reset at the start of each trial and 2) a numerical voltage analog of the contact force. The occurrence of each nerve impulse was displayed as a short horizontal line on the left border of each video-frame with its vertical location denoting the time of occurrence. The above information was recorded on a videocassette recorder for off-line analyses.

Psychophysical experiments

Psychophysical experiments were conducted on five subjects to determine the human capacity to discriminate the direction of lateral skin stretch with or without slip under the blank plate and to detect the presence or absence of relative motion under each of the three plates. A two-interval, two-alternative, forced choice paradigm was employed. In each experiment and on each trial, the plate was stroked twice across the distal pad of the middle finger. The second stroke was either identical to or different from the first, and the subject was required to state which was the case. Thus, in each trial, two possible stimulus pairs, Standard-Standard (S_1) or Standard-Comparison (S_2), were presented pseudorandomly with equal probability. The subject was asked to respond in either of two ways, (R_1) or (R_2), corresponding to his or her judgement of which of the stimulus pairs was presented. The percentage of trials for which the subjects responded correctly was taken to be a measure of their performance. The subjects were said to have discriminated between the standard and the comparison if they responded correctly to 75% of the trials, the midvalue between chance and perfect discrimination. In addition, a bias-free measure of discriminability d' (Johnson 1980) was calculated from the pairs of conditional probabilities, $P(R_1|S_1)$ and $P(R_1|S_2)$, which represented the proportion of trials in which the subject stated that S_1 occurred when in fact S_1 and S_2 , respectively, were delivered. In the absence of response bias, a d' of 1.35 corresponds to correct responses on 75% of the trials.

EXPERIMENT 1. The capacity of five subjects to discriminate the direction of lateral skin stretch caused by the blank plate was determined under two conditions. 1) *Absence of slip*: the standard and comparison stimuli consisted of short strokes in opposite directions on the lateral-medial axis (Table 1; LM refers to the

TABLE 1. Psychophysical experiments

	Discrimination of the Direction of Skin Stretch: Blank Plate		Detection of Slip: Blank, Single Dot, and Textured Plates
	(a) Stretch	(b) Stretch + movement	
Standard comparison	Short LM (ML) Short ML (LM)	Long LM (ML) Long ML (LM)	Short LM Long LM

LM, strokes in a lateral-to-medial direction; ML, strokes in a medial-to-lateral direction.

strokes from lateral to medial direction and ML, medial to lateral). The total stroke length was 5.5 mm, which essentially stretched the fingerpad skin in a given direction without any observable slip between the plate and the skin. The first 3 mm of the stroke was traversed at a velocity of 10 mm/s followed by the distances of 1 mm during the deceleration phase (6 equal decrements of velocity in 0.6 s), and 1.5 mm at a velocity of 1 mm/s. 2) *Presence of slip*: the standard and comparison stimuli consisted of long strokes in opposite directions. The total stroke length was 14 mm, which, in addition to producing the skin stretch, resulted in continued motion, or slip, of the plate on the skin surface (Table 1). The first 12 mm of the stroke was traversed at a velocity of 10 mm/s followed by a distance of 2 mm during the deceleration phase (6 equal decrements of velocity in 1.2 s). The absence of slip in the short stroke and its presence in the long stroke were verified by observations of the videoimage. For either of the conditions, each subject was presented with 32 trials. Stroking from medial to lateral as well as in the opposite direction were used as standards in equal number of trials.

EXPERIMENT II. The capacity of the subjects to detect the presence of relative motion was determined for each of the three plates (Table 1). In each case, the standard stimulus was a short stroke in a particular direction, and the comparison was a long stroke in the same direction. Two sets of 64 trials each were presented to the subjects. 1) *Set 1*: trials with the blank plate were alternated with trials with the single dot plate. 2) *Set 2*: trials with the blank plate were alternated with trials with the textured plate. Five subjects were tested with each set, with two of the subjects being common to both the sets. Thus, in the pooled results, eight subjects were tested with the blank plate and five each with the single dot and textured plates. The two subjects tested with both the sets received 64 trials with the blank plate and 32 trials with the single dot and textured plates, whereas all the others received 32 trials under each of the plates.

The parameters of the short and long strokes were chosen such that the total time a plate was on the fingerpad was the same in either case (duration = 3.4 s, including the stationary contact for 1 s before the beginning of each stroke) thus eliminating an extraneous cue for discrimination. In addition, the smooth deceleration was needed to prevent the sudden jerk at the end of either stroke that would have occurred earlier in the short stroke. The stroke distance of 1.5 mm at a velocity of 1 mm/s towards the end of the short stroke was necessary to prevent any cue arising out of the relaxation of the skin that would have occurred, had the plate been stationary during that time. In stroking with the plate with a single dot, care was taken to position the plate such that the dot was in the center of the contact area at midstroke.

Neurophysiological experiments

Our purpose was to identify the types of cutaneous peripheral nerve fibers contributing to the perception of the direction of skin stretch and the occurrence of relative motion of the three glass plates stroked across the fingerpad. Evoked neural responses to the stroking of the plates were recorded electrophysiologically from single low-threshold mechanoreceptive afferent fibers innervating the fingerpads of juvenile *Macacca fascicularis* monkeys anesthetized with sodium pentobarbital (Nembutal; initial dose of 33 mg/kg followed by doses of 4 mg/kg given intravenously whenever needed to maintain areflexia). The positioning of the monkey finger, the fiber identification procedures, mapping of receptive fields with Von Frey filaments, and the recording of fiber responses to controlled stimuli were as described by LaMotte and Whitehouse (1986).

The procedure for stroking the plates on the monkey fingerpad under constant force and horizontal velocity with the use of the

mechanical stimulator was as described before. The parameters of the short and long strokes were the same as in the psychophysical experiments, except that the gradual deceleration phase towards the end of each stroke was eliminated. Ten repetitions of each stroke (with the plate lifted off the fingerpad at the end of each stroke) were given to determine the consistency of the fiber responses. In addition, during the stimulation of some SAs with the blank plate, alternating short and long strokes in the same direction were given. This procedure mimicked the psychophysical experiments for the detection of slip under the blank plate and also served to minimize the effects of long-term adaptation of the fibers, which could possibly cause a difference in the responses to the short and long strokes when delivered as separate sets of 10 strokes each. To distinguish clearly the fiber responses to the blank and textured surfaces, a one-half blank and one-half textured surface was used. The stroke length for this plate was 28 mm, double the long stroke used in the psychophysical experiments without the smooth deceleration phase.

Some fibers were studied with the use of handheld plates by maintaining the force and the horizontal velocity approximately constant at about the same values as in machine-controlled stroking. Any variation in their values simulated perturbations that would normally occur in active touch.

RESULTS

Psychophysical experiments

The subjects were first required to discriminate the directions of skin stretch induced by the blank plate stroked in opposite directions, perpendicular to the proximal-distal axis of the finger. The subjects were tested under two experimental conditions, either when slip was absent (short strokes) or when there was continued relative motion between the blank plate and the fingerpad (long strokes). As is apparent from Fig. 2, the subjects could easily discriminate the directions of skin stretch in the absence of slip [mean

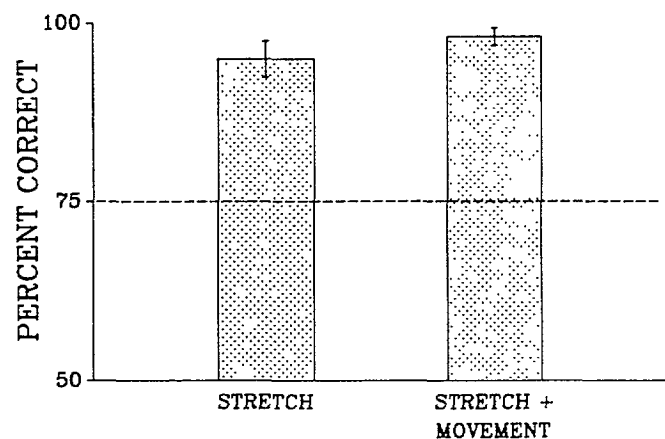


FIG. 2. Capacity of human subjects to discriminate directions of skin stretch caused by a blank plate stroked in opposite directions. Mean percentages of correct judgements by 5 subjects is displayed along with the standard errors of the means. Threshold of discrimination was defined as correct responses on 75% of trials, midvalue between chance and perfect discrimination. 'Stretch' indicates the result for short strokes of 5.5 mm, which essentially stretched the fingerpad skin in either direction without any observable slip. 'Stretch + Movement' refers to the results for long strokes of 14 mm, which, in addition to producing skin stretch, resulted in continued relative motion, or slip, of the plate on the skin. Subjects could discriminate the direction of skin stretch under both short and long strokes.

scores: percentage correct (pc) = 95 ± 2.5 SE; $d' = 4.5$] and in the presence of relative motion (pc = 98.1 ± 1.3 ; $d' = 5.3$). Two subjects scored 100% correct under both the experimental conditions, and the lowest score among the other three subjects was 87.5%. These three subjects scored better in the presence of slip than in its absence, but the differences were not significant (3–6%). The biases in the individual responses as to whether the second stroke was standard or comparison were either nonexistent or quite low. Although the task was one of discrimination, it was clear from the remarks made by the subjects that they could as easily identify the direction of skin stretch during each stroke.

The ability of the subjects to detect slip between each of the three plates and the fingerpad was determined from discriminations between the short and long strokes in the same direction. The existence of the continued motion of the blank plate against the skin could not be detected by any of the eight subjects (Fig. 3; pc = 65.6 ± 2.3 ; $d' = 0.9$), but the presence of even minimally detectable features on otherwise blank plates enabled the detection of relative motion; all the subjects detected the continued motion of both the single dot plate (pc = 88.8 ± 3.2 ; $d' = 3.5$) and the textured plate (pc = 86.9 ± 1.5 ; $d' = 2.6$). For the single dot plate, the subjects reported that they detected the successive positions of the dot on the skin as it travelled along a straight path. In contrast, for the textured plate, they felt only the vibrations of the skin induced by the texture of the plate while in motion and not the individual dots on the plate.

Neurophysiological experiments

Responses were recorded from 33 slowly adapting type I (SA), 20 rapidly adapting Meissner corpuscle (RA), and 15 rapidly adapting Pacinian corpuscle (PC) afferent fibers activated by either machine-controlled or handheld stimulation. The SAs and RAs had their receptive fields centrally located on the distal fingerpad. For PCs the most sensitive spots within the receptive fields were typically located on

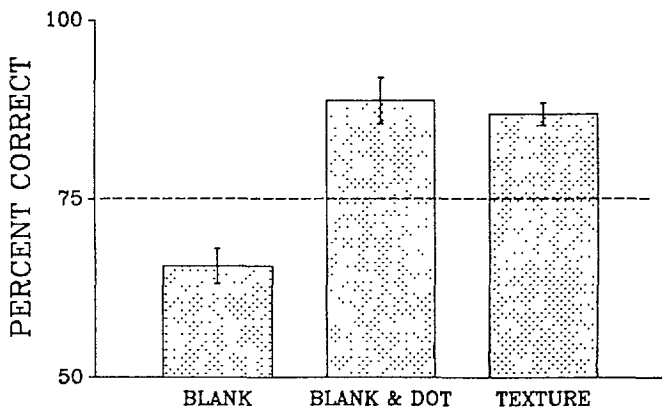


FIG. 3. Capacity of human subjects to detect the slip of the blank plate, the plate with a single raised dot, and the plate with a homogeneous texture composed of a matrix of raised dots (same format as Fig. 2). Task was to discriminate between short and long strokes in the same direction. Subjects could not detect the slip of the blank plate but could perceive the relative motion of the plates with the single dot and the homogeneous texture.

the distal fingerpad. Not all the stimuli were given to all the fibers. However, the responses of each of the fibers to the repetitions of a given stimulus were very consistent and repeatable. The variations in the quantitative measures of the responses to machine-controlled stimulations are given below and were due to differences in the responses among different fibers within each class to identical stimuli. The results of the handheld stimulation experiments were in complete agreement with the machine-controlled experiments with respect to the conclusions described below.

When the monkey fingerpads were stimulated by repeated long strokes with the blank plate, all the RAs and PCs responded only during the skin-stretching phase at the beginning of each stroke with very few impulses (typically 1–3) and were inactive during the constant velocity relative motion of the plate (Fig. 4). The number of impulses either did not differ for the two stroke directions or differed by no more than one or two. Only the SAs responded continuously during both short and long strokes (discharge rates of 16 SAs averaged over both directions = 16.7 ± 2.3 imp/s SE), usually with a marked difference in the responses to the two stroke directions. The discharge rates of directionally selective SAs differed by a factor of up to 10 times for the two directions, even though the degree of lateral stretch was about the same. Among the SAs stimulated by machine-controlled stroking, seven responded more to stroking in a medial to lateral direction (mean discharge rates for the two directions were 21.7 ± 3.6 and 9.2 ± 3.5 imp/s); four were sensitive to the opposite direction (mean discharge rates were 13.6 ± 5.4 and 28.1 ± 9.1 imp/s), and five gave approximately symmetric responses (mean discharge rates were 15.1 ± 6.7 and 15.0 ± 6.7 imp/s). Because only the SAs responded with a distinct directional bias, we conclude that the direction of skin stretch is coded solely by the SAs (see DISCUSSION).

When alternating short and long strokes in the same direction were given with the blank plate under machine control, no difference in SA responses could be discerned (discharge rates of 6 SAs averaged over both directions were 19.3 ± 4.4 imp/s for the short strokes and 19.0 ± 4.4 imp/s for the long strokes). As described above, RAs and PCs respond only during the skin-stretching phase at the beginning of each stroke and are inactive during the relative motion of the plate. Therefore their response would be identical to the short and long strokes in the same direction. Thus humans have no access to any information regarding the existence of relative motion of a blank plate by tactile sense alone, and hence their inability to detect it.

The responses of SAs, RAs, and PCs innervating the fingerpad to smooth plates with single dots of different heights (550 μm diam) stroked at various velocities has been recorded by LaMotte and Whitehouse (1986). In this study, the dot height thresholds were 8 μm or greater for SAs and 21 μm or greater for PCs. Only the RA dot height thresholds were found to be low enough to account for the human detection thresholds of ~ 1 –3 μm . The responses of the RAs to the stroking of the single-dot plate used in the present study confirmed the earlier results (Fig. 5). This shows unequivocally that the RAs are solely responsible for the detection of the motion of the 4- μm -high single dot on the plane surface being stroked on the fingerpad.

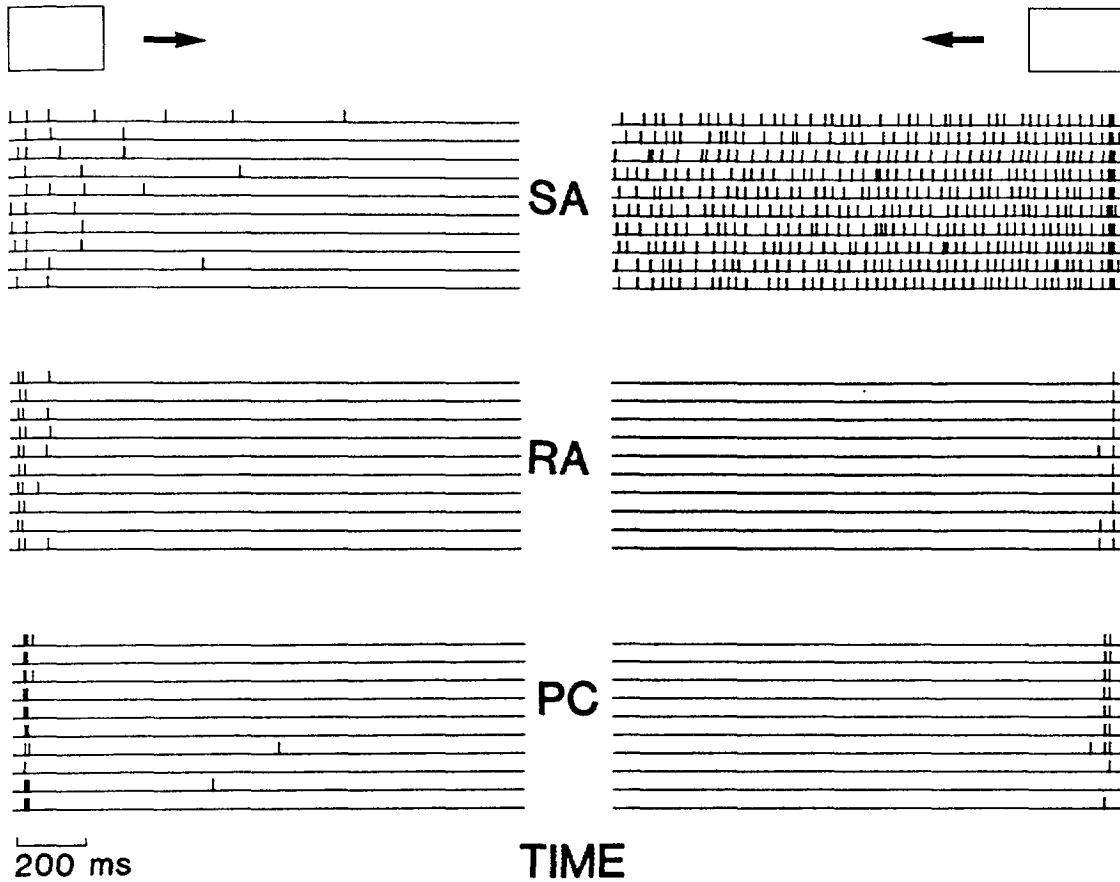


FIG. 4. Responses of typical slowly adapting (SA7), rapidly adapting (RA10), and Pacinian (PC11) mechanoreceptive afferent fibers to the blank plate stroked across the stationary, passive monkey fingerpad in opposite directions. Stroke distance of 14 mm was traversed with a velocity of 10 mm/s under a constant force of 20 g. Directions of strokes (and increasing time) for *left* and *right* panels are indicated by arrows. Each vertical tick represents the time of occurrence of an action potential, and each horizontal line demarcates responses to a single stroke. Whereas the RA and PC responded only during the initial skin-stretching phase without much bias for the two directions, the SA continued to respond during the steady movement phase with a distinct directional bias.

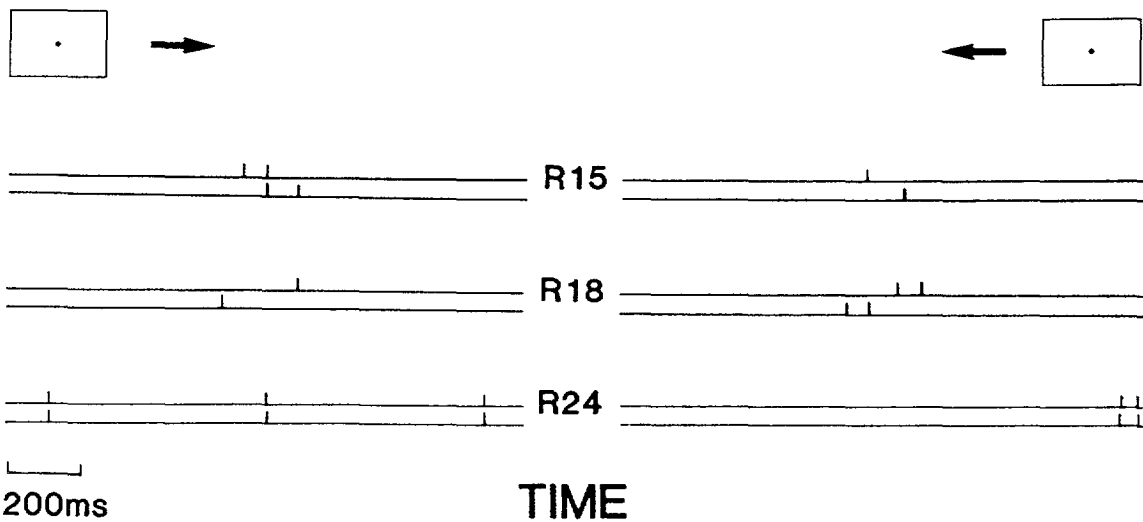


FIG. 5. Responses of 3 RAs to the stroking of the plate with a single dot (same stroke parameters and format as Fig. 4). Vertical ticks near the middle of strokes are responses to the dot. Only RA24 responded to the initial skin stretch in each direction.

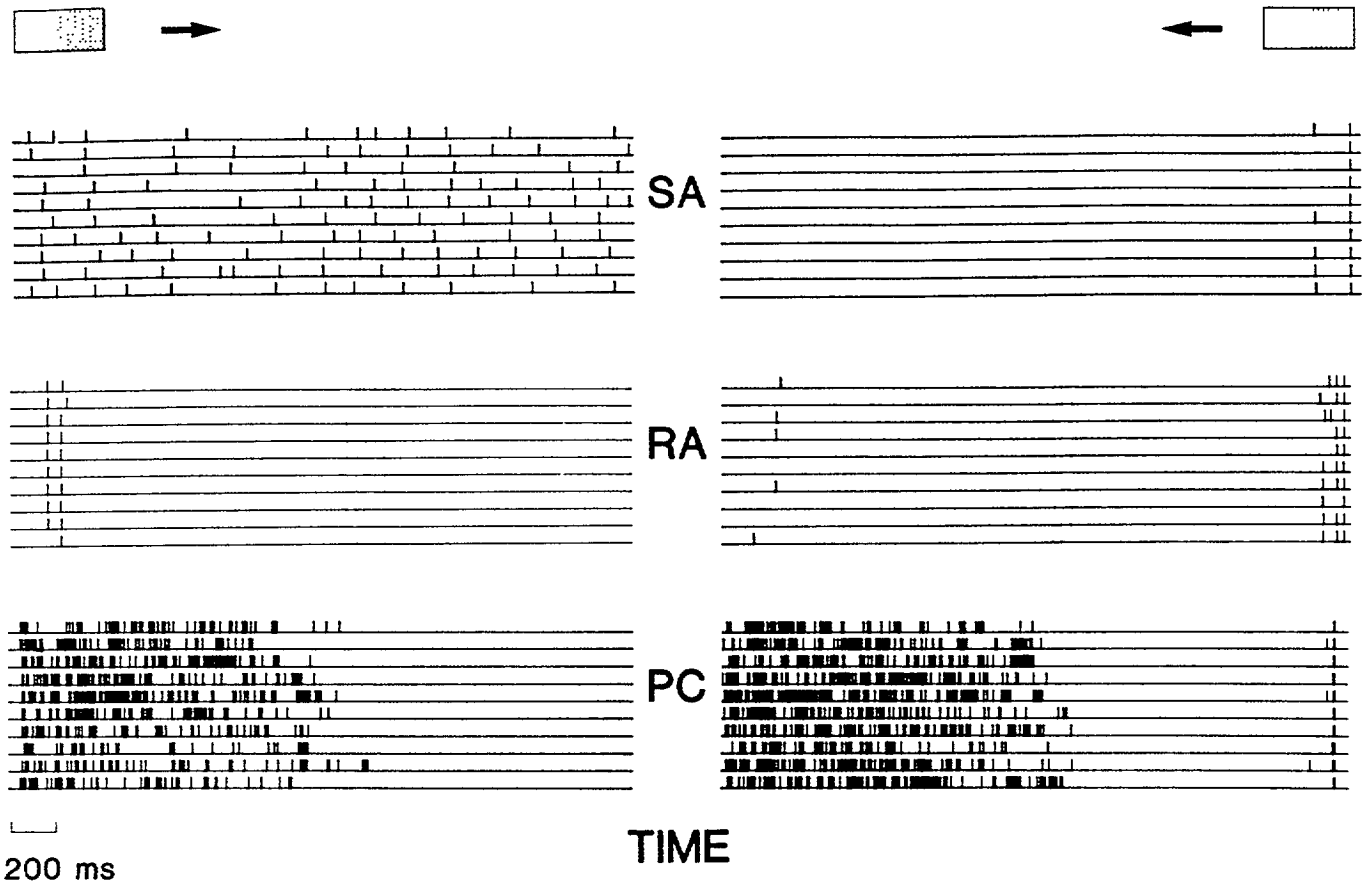


FIG. 6. Responses of typical SA (S8), RA (R24), and PC (P12) to a glass plate that was one-half textured and one-half blank (same format as Fig. 4). Contact area at the beginning of a stroke was on the textured side for left-to-right strokes and on the blank side for right-to-left strokes. Stroke distance of 28 mm traversed at 10 mm/s under a force of 20 g was used, such that the blank-texture border was on the most sensitive spot on the receptive field of the fiber at midstroke. SA responses showed no discernable differences to the two halves of the plate, and the RA responded to the initial skin stretching phase, each responding as they would for a blank plate. In contrast, the PC responded continuously only to the textured half.

To clearly demonstrate the differences in the SA, RA, and PC responses to microtextures, the monkey fingerpad was stroked with a one-half blank and one-half textured plate. The SAs displayed their response bias to the stroke direction (Fig. 6) and showed no difference in response to the two halves of the plate in either direction, except for one fiber. This fiber responded only to one of the stroke directions and responded more to the blank side. It was observed that the friction was higher on the blank side, which resulted in higher skin stretch and consequently the higher SA response. All the other SAs were not as sensitive to differences in skin stretch between the blank and textured surfaces. The RAs responded only to the initial skin stretch in either direction with 1–3 imp, with no discernable differences in their response to stretching by the blank and textured halves. However, the majority of the PCs (10 out of 15—the remaining 5 had higher dot height thresholds for texture) responded continuously to only the textured half of the plate for strokes in both directions. Thus PCs, and not SAs or RAs, coded the motion of the barely detectable textured surface on the fingerpad.

DISCUSSION

We begin the discussion by summarizing the arguments made in the introductory part of this paper. In the active

exploration or manipulation of the environment, or when objects in contact with passive skin move relative to it, the tactile information obtained is, in general, spatiotemporal. A correct interpretation of this information is based on the detection of the absence or the occurrence of slip. By definition, slip is said to occur when the tangential velocity components of the points on the object surface in contact with the skin are nonzero relative to the corresponding contacting points on the skin surface. Because slip is a relative motion with respect to the skin surface, it can be signaled reliably only by the cutaneous mechanoreceptors innervating the contact area. When the region of contact itself moves over the skin, slip can be detected through the successive activation of neighboring groups of mechanoreceptors. But when slip occurs such that the region of contact is stationary on the skin, spatiotemporal events within the region of contact—such as a macroscopic feature on the object surface moving across the contact area—enable the detection of slip through the spatiotemporal activation of SA, RA, and PC populations. However, when the object has no detectable features or barely detectable micron-sized features, it is by no means obvious under what situations slip is detectable, and if so, what the neural code is. We may then be able to isolate the different roles played by the different types of receptors in conveying information

about the slip of surfaces such as the glass plates used in this study.

The mechanical events on the skin in the present experiments are as follows. The tactile stimulator pressed a glass plate vertically down on to the fingerpads until a force of 20 g was reached, resulting in an elliptical area of contact (~ 8 mm diam on human fingerpads and ~ 6 mm diam on monkey fingerpads). After holding the plate steady for 1 s, the stimulator accelerated the plate horizontally to 10 mm/s within a short period of ~ 10 ms. During this time interval, the friction between the plate and the skin caused the region of skin in contact to move with the plate, without appreciable slip or change in the contact area. This resulted in the stretching of the skin behind the trailing edge of the contact region. For the long strokes, the stimulator continued to move the plate at 10 mm/s, and the frictional force was soon overcome by the applied horizontal shear force. The plate then began to slide on the skin surface with no readily observable change in either the contact region on the skin or the stretching of the skin on the trailing side. For the short strokes, the only difference was the lack of sliding of the plate on the skin. In either case this distorted state of the fingerpad remained steady until the plate was lifted off the skin surface. Because of the viscoelastic nature of its constituent soft tissues, the fingerpad then began to assume its resting configuration over time, with most of the recovery occurring within a couple of seconds after the unloading.

Clearly, during active tactile scanning of rigid surfaces or manipulation of rigid objects in the environment, the events on the skin follow approximately the same sequence described above. However, an important distinction is to be made between the steady slip investigated here and the intermittent 'stick-slip' (for example, Bowden and Tabor 1973) type of phenomenon observed by Johansson and Westling (1987) in their investigation of human precision grip. When subjects lifted an object instrumented with an accelerometer with the use of the precision grip between the tips of the thumb and the forefinger, small distinct slips that resulted in vibrations of the object were observed (Johansson and Westling 1987). Each of these slips were strong enough to activate SAIs, RAs, and PCs and caused automatic increase in the grip force, thus preventing continued relative motion of the object with respect to the region of skin in contact with it. Weaker responses from SAIs and RAs were observed in the absence of detectable vibrations in the object as well, presumably because of localized slips limited to small fractions of the contact area. Short-duration slips involving either partial or complete contact regions were not observed in our experiments, possibly because the machine-controlled stroking was under constant force. Indeed, when Johansson and Westling (1984) anesthetized the fingertips of the subjects, no secondary adjustments in grip forces occurred, and the fingers slid over the object.

Discrimination of the direction of skin stretch

The psychophysical results clearly demonstrate that the subjects could easily discriminate the direction of skin stretch both in the absence of slip as well as when there was continued relative motion. Further, the remarks made by

the subjects showed that they could identify the direction of skin stretch caused by each stroke. The discriminability of the subjects is in complete agreement with the results reported by Gould et al. (1979): when a probe was glued to the forearm skin and 1-mm excursions parallel to the skin surface were given in the lateral-medial or proximal-distal directions, the subjects discriminated opposite directions of skin stretch with approximately the same percentage correct scores that we obtained.

The responses of the cutaneous afferents show that, whereas the initiation of skin stretch may be signaled by all three fiber types, RAs and PCs respond only during the initial stretching phase with very few impulses and exhibit no observable directional bias. In contrast, the majority of the SAs had a significant directional bias in their responses, and the ratio of the discharge rates for the two directions during steady stretch could be as high as 10, even though the degree of lateral stretch was about the same. Because the sensation of skin stretch and its direction persists beyond the initial stretching phase during a stroke, with only the SAs responding with a distinct directional bias we conclude that the direction of skin stretch is coded solely by the SAs.

To explain the ability of their human subjects to discriminate skin-stretch direction, Gould et al. (1979) speculated that SAIIs are the most likely candidates to signal skin-stretch direction. The exquisite directional sensitivity of SAIIs to skin stretch has been observed in humans with the use of the techniques of microneurography (Johansson 1978; Knibestol 1975; Knibestol and Vallbo 1970). Westling and Johansson (1987) have found that the majority of SAIIs exhibited directional preferences to shear forces imposed on the skin in opposite directions. Whereas SAIIs are presumably associated with Ruffini endings, no clear distinction between SAIs and SAIIs has been reported in the literature on single-fiber recordings in monkeys. In our present as well as other (for example, LaMotte and Srinivasan 1987a,b; Srinivasan and LaMotte 1987) neurophysiological experiments, the individual SAs, although variable in their responsiveness to skin stretch, could not be clearly distinguished as type I or type II. Because we have found fibers that were more responsive to either direction of lateral stretch [as is the case with SAIIs, see Westling and Johansson 1987 (p. 136)] the neuronal population is likely to be heterogeneous in its direction sensitivity. It is then not clear as to the mechanism by which the direction of skin stretch is perceived under passive conditions, as demonstrated by the human subjects. Two of the possibilities are 1) differences in the responses of fibers innervating specific skin locations, for example, the skin in front of the leading edge of the contact area is subjected to compression parallel to the skin surface, whereas the skin behind the trailing edge (including where it is anchored to the fingernail) is subjected to tension—these differences are likely to affect the responses of receptor populations at those locations and result in a reliable code for the direction of skin stretch, and 2) specific weighted vectorial average of the population response composed of cutaneous fibers that are only broadly tuned to skin stretch directions. An example of such an algorithm has been proposed by Georgopoulos et al. (1986) for cortical neurons broadly tuned to monkey arm-motion directions. However, the computation of

movement direction using this algorithm assumes that the central processor knows the preferred direction of each cell of the population.

Detection of slip

It is known that when kinetic friction is less than static friction, there will be a tendency for intermittent motion in the form of stick-slip (Bowden and Tabor 1973). Therefore, in proposing a priori hypotheses as to whether or not humans can detect the motion of a blank plate stroked on their fingerpads, the possibility of small but distinct short-duration slips that cover either the entire area of contact or only a small fraction of it must be considered. These events on the skin, similar to those observed by Johansson and Westling (1987), may then be signaled by any of the three afferent fiber types. However, no stick-slip phenomenon was observed in our experiments with any of the plates. In fact, none of the eight subjects could detect the relative motion of the blank plate (Fig. 3). In addition, the ability of the subjects to discriminate skin-stretch directions was almost the same whether or not relative motion was present (Fig. 2). Therefore no cues such as vibration caused by stick-slip were available to the subjects to detect the motion of the blank plate. The neurophysiological evidence shows that both RAs and PCs were silent after the initial skin-stretching phase, whether or not the blank plate moved relative to the skin surface. Also, whereas SA responses were dependent on the direction of skin stretch, the motion of the plate did not affect their response. This was demonstrated clearly by the lack of any differences in responses to alternating short and long strokes in the same direction. Thus the subjects had no cues to detect the sliding of the blank plate, and hence were unable to detect it. The perception of slip therefore required existence of detectable surface features.

The single dot on an otherwise blank plate represents an idealization of a local microfeature against ground. It is known that 1) humans can detect the dot only when there is relative motion between the single-dot plate and the fingerpad, irrespective of whether active or passive touch was employed (Johansson and LaMotte 1983; LaMotte and Whitehouse 1986), 2) the human detection threshold for dot height depends on dot diameter—the higher the diameter, the lower the threshold height (Johansson and LaMotte 1983), and 3) for 550- μm -diam dots, the human detection threshold for dot heights was 1–3 μm , and only the RAs responded to such small dot heights (LaMotte and Whitehouse 1986). The dot height thresholds were 8 μm or greater for SAs and 21 μm or greater for PCs. In addition, LaMotte and Whitehouse (1986) have observed that the mechanical event that triggers the RAs to respond is likely to be the passage of the leading edge of the dot across the peak of a papillary ridge. Thus the a priori hypothesis for the detectability of slip of the plate with a 4- μm -high, 550- μm -diam single dot would be that the subjects would be able to detect the slip and that it would be signaled by the RAs responding to the passage of the dot across their receptive fields. Our psychophysical experiments to test the hypothesis unequivocally showed that all the subjects could detect the motion of the single-dot plate. In addition, they could feel the consecutive positions of the dot along its

path of travel. We also verified with recordings from a few RAs, in addition to those reported by LaMotte and Whitehouse (1986), that they do respond to the 4- μm -high, 550- μm -diam dot. Therefore we conclude that the detection of slip in this case is solely based on the successive activation of neighboring RAs along the dot path, which is a reliable spatiotemporal code for the motion.

In contrast to the local microfeature that the single dot represents, the homogeneous texture composed of a matrix of dots represents an idealization of a distributed microfeature on a surface. The basic element of the texture was a 1- μm -high, 50- μm -diam dot that, by itself, would be below the human detection threshold (Johansson and LaMotte 1983). However, the a priori possibilities for the detection of the sliding of the plate with a matrix of such dots are 1) stick-slip that might lead to intermittent local stretching of the skin, 2) kinetic friction may be less than the static friction and hence stretch-sensitive SAs might be able to discern the difference, and 3) vibratory cues to SAs, RAs, and PCs caused by the unevenness of the textured surface that is being stroked on the skin. On both human and monkey fingerpads, no stick-slip was observed. The subjects could not feel the individual dots of the texture during stroking, in agreement with the fact that the size of each dot was below human detection threshold for single dots. But they could clearly discriminate the absence and occurrence of the motion of the textured plate relative to the skin surface in contact, based on the vibrations of the skin induced by the texture during the motion.

In neurophysiological experiments with one-half blank and one-half textured plates, the SAs and RAs did not respond differently to the textured surface when compared with their responses to the blank surface. We have already demonstrated that these afferents could not code the motion of the blank plate, and hence it follows that they are unable to detect the motion of the textured plates. It is possible in principle that SAs similar to the one that differentiated between the two halves of the plate might be able to detect slip based on differences in skin-stretch amounts, because of differences that might exist between static and kinetic frictions. However, such an intensive code would be unreliable, because varying amounts of lateral stretch could be imposed by applying varying amounts of shear force with a blank plate without causing any slip. The dramatic differences in the response of the majority of the PCs to the blank and textured halves, when combined with the introspective observations of the subjects that they felt the skin vibrate under the motion of the textured plate, demonstrate that PC responses are solely responsible for the detection of the slip of the textured plate. But the neural code is distinctly different from that of the RAs signaling the passage of the single dot. Whereas the spatial density of PCs is far less than those of SAs and RAs in the fingers (Darian-Smith and Kennins 1980; Johansson and Vallbo 1979), because of their exquisite sensitivity to the high-frequency vibrations (~ 200 Hz) (see Talbot et al. 1968) transmitted through wave propagation inside the finger, they have large receptive fields. We can thus detect the existence of the vibratory pattern but cannot spatially locate the individual dots.

The results have been summarized in Table 2. Existence of detectable surface features is necessary for the detection

TABLE 2. Summary of results

Experimental Task	Stimulus Surfaces	Sensory Discrimination	Fiber Responses		
			SA	RA	PC
Direction of skin stretch	Blank plate	Yes (5/5)*	Yes	No	No
Detection of slip	Blank plate	No (0/8)	No	No	No
	Single dot plate	Yes (5/5)	No	Yes	No
	Textured plate	Yes (5/5)	No	No	Yes

SA, slowly adapting afferents; RA, Meissner afferents; PC, Pacinian afferents. *The ratio of tested subjects supporting the conclusion.

of slip. However, surprisingly small features on smooth surfaces are detected by humans and lead to the detection of slip of these surfaces, with the geometry of the microfeatures governing the associated neural codes. The division of labor among the different types of fiber populations in signaling the different events on the skin is clear-cut: SAs signal the direction of skin stretch and hence the direction of impending slip; RAs and PCs signal the occurrence of slip with spatiotemporal or intensive codes, depending on whether the microfeature is a local one on a smooth background or is distributed on the surface, respectively. When the surface features are of sizes greater than the response thresholds of all the receptors, redundant spatiotemporal and intensive information from all three afferent fiber types is available for the detection of slip.

M. A. Srinivasan gratefully acknowledges Prof. Robert Mann for encouragement and support.

The work reported here was supported by Public Health Service Grant 15888.

Present address of M. A. Srinivasan and address for reprint requests: 36-763 Research Laboratory of Electronics, Massachusetts Institute of Technology, Cambridge, MA 02139.

Received 28 July 1989; accepted in final form 19 January 1990.

REFERENCES

- BOWDEN, F. P. AND TABOR, D. *Friction—An Introduction to Tribology*. Garden City, NY: Anchor, 1973.
- DARIAN-SMITH, I. The sense of touch: performance and peripheral neural processes. In: *Handbook of Physiology. The Nervous System. Sensory Processes*. Bethesda, MD: Am. Physiol. Soc., Bethesda, MD, 1984, vol. III, chapt. 17, p. 739–788.
- representation of two spatial dimensions of a textured surface moving across the monkey's finger pad. *J. Physiol. Lond.* 309: 135–146, 1980.
- DARIAN-SMITH, I. AND KENINS, P. Innervation density of mechanoreceptive fibers supplying glabrous skin of the monkey's index finger. *J. Physiol. Lond.* 309: 147–155, 1980.
- GEORGOPOULOS, A. P., SCHWARTZ, A. B., AND KETTNER, R. E. Neuronal population coding of movement direction. *Science. Wash. DC* 233: 1416–1419, 1986.
- GOULD, W. R., VIERCK, JR., C. J., AND LUCK, M. M. Cues supporting recognition of the orientation or direction of movement of tactile stimuli. In: *Sensory Functions of the Skin in Humans*, edited by D. R. Kenshalo. New York: Plenum, 1979, p. 63–78.
- JOHANSSON, R. S. Tactile sensibility in the human hand: receptive field characteristics of mechanoreceptive units in the glabrous skin area. *J. Physiol. Lond.* 281: 101–123, 1978.
- JOHANSSON, R. S. AND LAMOTTE, R. H. Tactile detection thresholds for a single asperity on an otherwise smooth surface. *Somatosens. Res.* 1: 21–31, 1983.
- JOHANSSON, R. S. AND VALLBO, A. B. Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. *J. Physiol. Lond.* 286: 283–300, 1979.
- JOHANSSON, R. S. AND WESTLING, G. 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, 1984.
- JOHANSSON, R. S. AND WESTLING, G. Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Exp. Brain Res.* 66: 141–154, 1987.
- JOHNSON, K. O. Sensory discrimination: decision process. *J. Neurophysiol.* 43: 1771–1792, 1980.
- JOHNSON, K. O. Neural mechanisms of tactual form and texture discrimination. *Federation Proc.* 42: 2542–2547, 1983.
- JOHNSON, K. O. AND LAMB, G. D. Neural mechanisms of spatial tactile discrimination: neural patterns evoked by Braille-like dot patterns in the monkey. *J. Physiol. Lond.* 310: 117–144, 1981.
- KNIBESTOL, M. Stimulus-response functions of slowly adapting mechanoreceptors in the human glabrous skin area. *J. Physiol. Lond.* 245: 63–80, 1975.
- KNIBESTOL, M. AND VALLBO, A. B. Single unit analysis of mechanoreceptor activity from the human glabrous skin. *Acta Physiol. Scand.* 80: 178–195, 1970.
- LAMB, G. D. Tactile discrimination of textured surfaces: Psychophysical performance measurements in humans. *J. Physiol. Lond.* 338: 551–565, 1983.
- LAMOTTE, R. H., JOHANSSON, R. S., AND PROBER, D. Construction of three-dimensional microstructures to be used in studies of the cutaneous perception of texture. *J. Electrophysiol. Tech.* 9: 165–181, 1982.
- LAMOTTE, R. H. AND SRINIVASAN, M. A. Tactile discrimination of shape: responses of slowly adapting mechanoreceptive afferents to a step stroked across the monkey fingerpad. *J. Neurosci.* 7: 1655–1671, 1987a.
- LAMOTTE, R. H. AND SRINIVASAN, M. A. Tactile discrimination of shape: responses of rapidly adapting mechanoreceptive afferents to a step stroked across the monkey fingerpad. *J. Neurosci.* 7: 1672–1681, 1987b.
- LAMOTTE, R. H. AND WHITEHOUSE, J. Tactile detection of a dot on a smooth surface: peripheral neural events. *J. Neurophysiol.* 56: 1109–1128, 1986.
- LAMOTTE, R. H., WHITEHOUSE, G. M., ROBINSON, C. J., AND DAVIS, F. A tactile stimulator for controlled movements of textured surfaces across the skin. *J. Electrophysiol. Tech.* 10: 1–17, 1983.
- LEDERMAN, S. J. The perception of surface roughness by active and passive touch. *Bull. Psychon. Soc.* 18: 253–255, 1981.
- LOOMIS, J. M. AND LEDERMAN, S. J. Tactual Perception. In: *Handbook of Perception and Human Performance*, edited by K. R. Boff, L. Kaufman, and J. P. Thomas. New York: Wiley, 1986, Vol. II, chapt. 31, p. 1–41.
- MORLEY, J. W., GOODWIN, A. W., AND DARIAN-SMITH, I. Tactile discrimination of gratings. *Exp. Brain Res.* 49: 291–299, 1983.
- PHILLIPS, J. R. AND JOHNSON, K. O. Neural mechanisms of scanned and stationary touch. *J. Acoust. Soc. Am.* 77: 220–224, 1985.
- SRINIVASAN, M. A. AND LAMOTTE, R. H. Tactile discrimination of shape: responses of slowly and rapidly adapting mechanoreceptive afferents to a step indented into the monkey fingerpad. *J. Neurosci.* 7: 1682–1697, 1987.
- TALBOT, W. H., DARIAN-SMITH, I., KORNHUBER, H. H., AND MOUNTCASTLE, V. R. The sense of flutter-vibration: comparison of the human capacity with response patterns of mechanoreceptive afferents from the monkey hand. *J. Neurophysiol.* 31: 301–334, 1968.
- WESTLING, G. AND JOHANSSON, R. S. Responses in glabrous skin mechanoreceptors during precision grip in humans. *Exp. Brain Res.* 66: 128–140, 1987.