Neuronal Activity in Somatosensory Cortex of Monkeys Using a Precision Grip. III. Responses to Altered Friction Perturbations

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Salimi, Iran, Thomas Brochier, and Allan M. Smith. Neuronal activity in somatosensory cortex of monkeys using a precision grip. III. Responses to altered friction perturbations. J. Neurophysiol. 81: 845–857, 1999. The purpose of this investigation was to examine the activity changes in single units of the somatosensory cortex in response to lubricating and adhesive coatings applied to a hand-held object. Three monkeys were trained to grasp an object between the thumb and index fingers and to lift and hold it stationary within a narrow position window for 1 s before release. Grip forces normal to the skin surface, load forces tangential to the skin surface, and the displacement of the object were measured on each trial. Adhesive (rosin) and lubricant (petroleum jelly) coatings were applied to the smooth metal surface of the object to alter the friction against the skin. In addition, neuronal activity evoked by force pulse-perturbations generating shear forces and slip on the skin were compared with the patterns of activity elicited by grasping and lifting the coated surfaces. Following changes in surface coatings, both monkeys modulated the rate at which grip forces normal to the skin surface and load forces tangential to the skin surface were applied during the lifting phase of the task. As a result, the ratio of the rates of change of the two forces was proportionately scaled to the surface coating properties with the more slippery surfaces, having higher ratios. This precise control of normal and tangential forces enabled the monkeys to generate adequate grip forces and prevent slip of the object. From a total of 386 single neurons recorded in the hand area of the somatosensory cortex, 92 were tested with at least 1 coating. Cell discharge changed significantly with changes in surface coating in 62 (67%) of these cells. Of these coating-related cells, 51 were tested with both an adhesive and lubricating coating, and 45 showed significant differences in activity between the untreated metal surface and either the lubricant or the adhesive coating. These cells were divided into three main groups on the basis of their response patterns. In the first group (group A), the peak discharge increased significantly when the grasped surface was covered with lubricant. These cells appeared to be selectively sensitive to slip of the object on the skin. The second group (group B) was less activated by the adhesive surface compared with either the untreated metal or the lubricated surface, and they responded mainly to variations in the force normal to the skin surface. These cells provide useful feedback for the control of grip force. The third group (group C) responded to both slips and to changes in forces tangential to the skin. Most of these cells responded with a biphasic pattern reflecting the bidirectional changes in load force as the object was first accelerated and then decelerated. One hundred sixty-eight of the 386 isolated neurons were tested with brief perturbations during the task. Of these, 147 (88%) responded to the perturbation with a significant change in activity. In most of the cells, the response to the perturbation was shorter than 100 ms with a mean latency of 44.1 ± 16.3 (SD) ms. For each of the cell groups, the activity patterns triggered by the perturbations were consistent with the activity patterns generated during the grasping and lifting of the coated object.

INTRODUCTION

Friction is an objective measure of the physical interaction between two contacting surfaces and can be distinguished from texture that generally refers to the structural irregularities of a surface topography. For noncompliant surfaces, friction is generally defined as the ratio of the minimal tangential force needed to initiate motion (F) to the perpendicular load force (W): \( \mu = F/W \), where \( \mu \) is the coefficient of friction (Bowden and Tabor 1982). From the perceptual point of view, Ekman et al. (1965) suggested that the subjective sensation of roughness might be a power function of the coefficient of friction. However, this was later questioned by Taylor and Lederman (1975), who found that randomly adding liquid detergent to six grooved test surfaces had no effect on the ability of subjects to scale the surface roughness.

The reciprocal of the coefficient of friction has been called the slip ratio by Johansson and Westling (1984a), who were the first to point out the importance of friction as a parameter in the control of grip force. Although texture and friction covaried in most of their studies, Johansson and Westling (1984b) observed that washing and drying the hands reduced the friction of the fingers on a suede-covered object and caused a temporary increase in grip force. Longer term pharmacological inhibition of sweat by scopolamine has also been shown to cause similar increases in grip force (Smith et al. 1997). By applying lubricating and adhesive coatings to various surface textures, Cadoret and Smith (1996) were able to dissociate the effects of friction from texture and found consistently higher grip forces associated with lower coefficients of friction. In fact, Cadoret and Smith (1996) showed that when two different surface textures were equated for friction by the application of lubricants or adhesives, the applied grip forces were identical, supporting the conclusion that friction, not texture, determines the grip forces applied during object manipulation.

Physiological studies of single afferent fibers in the median nerve innervating the thumb and index fingers have shown that fast adapting type I (FAI), fast adapting type II (FAII), and slowly adapting type I (SAI) receptors of the glabrous skin of the hand are highly sensitive to slips across the skin (Johansson and Westling 1987; Macefield et al. 1996; Westling and Johansson 1987), whereas slowly adapting type II (SAII) receptors are said to respond more specifically to tangential shear forces (Edin et al. 1992; Macefield et al. 1996; Westling and Johansson 1987). The combined activities of these four mechanoreceptors provide the somatosensory cortex with an estimate of the friction at the skin-object interface, which could be
used to control grip and load forces efficiently during prehension.

The somatosensory cortex is known to send direct projections to neurons in motor cortex (Ghosh et al. 1987; Jones et al. 1978; Kim and Strick 1978; Vogt and Pandya 1978). In addition, the reversible inactivation of somatosensory cortex using muscimol disrupts the ability of monkeys to pick up small pieces of food using a precision grip (Hikosaka et al. 1985). From single-unit recordings in awake monkeys, Picard and Smith (1992a) showed that some neurons within motor cortex respond to changes in object surface texture during precision grasping. They also observed that the discharge of some motor cortical cells increased when a lubricant coating was used to decrease the friction of a smooth metal surface (Picard and Smith 1992a). Together these data suggest that the primary somatosensory cortex contributes, at least in part, to the modulation of motor cortical activity accompanying the handling of objects with different coefficients of friction.

Units in somatosensory cortex respond to stimulation of their cutaneous receptive fields with different textured surfaces (Darian-Smith et al. 1984; Phillips et al. 1988; Sinclair and Burton 1991; Sinclair et al. 1996; Tremblay et al. 1996). However, the effect of surface coatings was not examined in any of these studies. The present study sought to examine the responses of neurons of the somatosensory cortex to grasping lubricated or adhesive surfaces. To achieve this objective, we recorded the activity of single units within the postcentral cortical representation of the thumb and index finger region in monkeys trained to perform the same lift and hold task described in the companion papers (Salimi et al. 1999a,b). Adhesive or lubricant coatings were added to the object surface to alter the slipperiness against the fingers and to examine the effects of adhesion and slip on the skin. For some neurons the effects of the coatings were additionally tested with brief pulses of tangential shear force to the skin of the thumb and index finger.

METHODS

In general, the apparatus and task were identical to those described in the two previous papers (Salimi et al. 1999a,b). Briefly, three adolescent monkeys (Macaca fascicularis) were trained to grasp and lift a metal tab between thumb and index finger and to hold it stationary within a position window (12–25 mm) for 1 s. At the end of the holding phase, the monkeys received a fruit juice reward and were required to release the object to initiate a subsequent trial. An intertrial interval of 2 s was imposed before a new trial could be initiated. Load cells provided analogue signals carrying the grip force, the lifting or load force, and an optical encoder provided the vertical displacement. These signals were digitized at 250 Hz by a laboratory computer. Single-unit activity was recorded within the thumb and index finger representation over an area extending from the deep part of the central sulcus (areas 3a and 3b) to the posterior wall of the intraparietal sulcus (area 7b). Only cells with cutaneous receptive fields on the thumb and index finger or on the webbing between them making contact with the metal tab were retained in this study.

As described in the preceding papers, the weight of the manipulandum could be varied, and the gripped surfaces could be covered with different textures. The nature of the cortical discharge patterns associated with various object weights and textures are reported in a companion paper (Salimi et al. 1999b). In this paper, we describe the changes in single-cell activity produced by coating the gripping surface with lubricating and adhesive films and the responses produced by downward force-pulse perturbations. The simulated object weight was kept constant at 65 g for the first two monkeys and 30 g for the third monkey.

Lubricating and adhesive coatings

Three coatings were applied to the grasping tabs of the apparatus to modify the slipperiness or stickiness of the metal surface. Petroleum jelly (Vaseline) and occasionally talc were used to decrease friction. Behaviorally, these coatings increased the frequency of large scale slips between object and skin, which increased the number of performance errors. Conversely, an adhesive coating (rosin dissolved in lacquer thinner) reduced the probability of slips for the same surface by causing it to adhere to the skin of the fingers. Coatings were applied as frequently as necessary to maintain constant conditions. After each coating was tested, the monkey’s hand and fingers were cleaned and dried before another condition was initiated.

Force-pulse perturbations

The manipulandum could generate brief (100 ms) downward pulses of 1.5 N during the static holding. The perturbations were delivered 750 ms after the manipulandum had entered the position window. The force pulses reliably produced a shear force on the skin, which resulted in a downward displacement of several millimeters. If unopposed, the perturbations were strong enough to displace the manipulandum from the position window, resulting in loss of reward for the monkey. The monkeys were therefore motivated to compensate for the perturbation by stiffening the wrist and fingers to maintain the manipulandum within the position window. Once introduced, the perturbations were delivered at precisely the same time for ~30 consecutive trials. For most of the cells, the effects of the perturbation were tested with fine sandpaper (grit size 60) as the contact surface, but in some cases, smooth metal or coarse sandpaper were also used. Usually, two unperturbed control conditions with the same texture were recorded before and after the perturbation condition. These controls were necessary both for the statistical analysis of reflex and anticipatory responses and to extinguish the behavioral expectancy of the perturbation in subsequent conditions (Dugas and Smith 1992).

Statistical analysis

The statistical techniques were similar to those used to analyze the effects of texture and weight (Salimi et al. 1999b). The peak discharge frequency (which always occurred during the dynamic lifting phase) was a more sensitive measure of neuronal excitability than the average dynamic discharge rate and was noted on each trial, both within and between coatings conditions. The peak grip (normal) and load (tangential) forces were similarly identified (Salimi et al. 1999b). In addition, the peak first derivative of the grip force (i.e., the peak grip force rate) and the peak first derivative of the load force (i.e., the peak load force rate) were calculated and included in the analysis (Fig. 1). The average peak grip and load forces, the average peak rates of force change, and the average peak grip force/peak load force ratio were calculated for each condition for each cell and compared using t-tests to assess the effects of the coatings. To facilitate comparisons between cells and between surface conditions, the peak discharge and the peak of grip and load forces were normalized using the same method as in Salimi et al. (1999b).

Significant activity changes related to the perturbation were analyzed in two different ways. The occurrence of a reflexlike response was determined by comparing the mean firing frequency during the 200 ms before and after the perturbation onset with a t-test. Eighty-eight percent of the cells (147/168) demonstrated a significant (P < 0.05) modulation of activity after the perturbation onset, which was considered as perturbation evoked. We tested for an anticipatory response to the perturbation by comparing the mean discharge fre-
Behavioral effects of coatings on the grip and load forces

Several observations suggest that the addition of rosin and petroleum jelly had strong effects on the surface friction. With the adhesive coating, the surface was sufficiently sticky to require the monkey to deliberately unstick the fingers to release the object. It seems likely therefore that little if any slip on the skin actually occurred in the adhesive condition. On the other hand, it is obvious that object slip was more frequent with the lubricant coating than with the uncoated metal surface. During the initial lifting phase, the object often escaped from the fingers before any displacement actually occurred. Large slips of the object over the skin were also visible during the static holding phase. Although the monkey tried to compensate for these slips, the number of failed trials increased, and larger rewards had to be given to maintain the monkey’s motivation under these difficult conditions. Finally, the monkeys were unable to prevent slips when the perturbations were applied to the lubricated surface, and the object was invariably dropped before the required holding period had elapsed. These changes in surface friction were associated with systematic adjustments in the grip and load forces used to lift the object, and are summarized in Fig. 2 for the two monkeys for which the effect of friction was most frequently tested.

In both monkeys the peak grip force was greatest when handling the lubricated surface and least with the adhesive surface (Fig. 2A). The coatings, unexpectedly but significantly ($P < 0.05$), reduced the grip force rate (GFR) for both the adhesive and lubricant coating conditions compared with the dry smooth metal (Fig. 2B). Because the rosin coating increased the adhesion of the skin to the metal, whereas the petroleum jelly decreased the adhesion, it follows that the mean grip force rate could not be linearly related to the surface slipperiness.

In contrast to the grip force rate, the mean peak tangential force rate (LFR) decreased significantly for the lubricated condition only (Fig. 2C). This reduction of the tangential force rate was a reliable strategy to compensate for the increased slipperiness of the lubricated surface. In fact, the monkey had difficulty holding the object between the thumb and index finger, and, unlike the other two surface conditions, there were frequently large and visible slips of the object between the fingers. No significant modulation of the tangential force rate was noted with the adhesive condition.

The ratio between the peak normal force rate and the peak tangential force rate, shown in Fig. 2D, appeared to most accurately reflect the adaptation of the two forces to the surface coatings because it was lowest for adhesive coating and highest for the lubricated coating. For the adhesive coating the low ratio was due to a significant decrease in the mean normal force rate rather than to any increase in the mean tangential force rate. In contrast, the higher ratio under the lubricated condition was mainly caused by a systematic decrease in the tangential force rate. In general, the normal and tangential force rates were controlled independently, although a close coordination of the rates of application of these forces allowed the monkey to produce grip forces suitably adapted to the coating properties of the object surface as seen in Fig. 2A.

Modulation of neuronal activity with friction

From a total of 386 single neurons in the 3 monkeys, 92 were tested with either the adhesive or lubricant as well as with the untreated metal surface. The discharge of 62 cells (67%) showed a significant change in activity with the coatings. Of these, 51 were tested with both lubricant and adhesive coatings. Six of these 51 cells demonstrated significant differences between the 2 coating conditions but not between the coatings and the metal. These were excluded from further statistical analysis. For the remaining 45 cells, we used $t$-test comparisons to determine whether the peak discharge frequency was significantly altered by the coatings. Depending on whether the lubricant and adhesive coatings increased or decreased the peak discharge, the cells were assigned to one of eight possible categories and are plotted on the Venn diagram shown in Fig. 3.

Of the 45 cells analyzed, 22 displayed significant changes with only 1 of the 2 coatings, whereas the other 23 responded to both the lubricant and adhesive coatings. It can be seen from Fig. 3 that the cells were not equally distributed among the eight categories. The activity of 36 of 45 cells (80%) significantly changed with the lubricant coating. The peak frequency was significantly higher with the lubricant compared with the untreated surface for the majority of neurons (29/36; 81%). Of
these neurons, 11 responded to the lubricant alone, and for another 4 cells the peak activity was both significantly increased with the lubricant and significantly decreased with the adhesive. Together these 15 cells seem to form a homogeneous category of cells excited by slip of the object over the receptive field (Fig. 3, group A).

**FIG. 2.** Histograms of mean \((n = 45)\) peak grip force and mean peak normal and load force rates for 3 coating conditions for 2 of the 3 monkeys. \(A\): peak grip force. \(B\): peak grip force rate. \(C\): peak load force rate. \(D\): grip force rate/load force rate ratio. Asterisks indicate significant differences between smooth metal and coating conditions (paired Student’s \(t\)-test; ns, not significant; \(*P < 0.05; **P < 0.01; ***P < 0.001\)).

**FIG. 3.** Venn diagram showing activity increases or decreases with either lubricant or adhesive coating. Cells with response patterns corresponding to groups A, B, and C described in the text are shown in the shaded areas.
The adhesive coating modulated activity in 32/45 (71%) cells. In 17 cells, the activity was significantly greater when compared with the activity associated with the smooth metal condition. For 14 of these 17 cells, the activity was also increased with the lubricant (Fig. 3, group C). For the remaining 15/32 cells affected by the adhesive, the peak activity declined significantly when compared with the untreated metal. The activity of 7 of these 15 cells changed significantly with the adhesive only (Fig. 3, group B). Five other cell groups were represented on the Venn diagram shown in Fig. 3, but because only a small number of cells are contained in each of these groups, we felt it was premature to attempt a detailed analysis of their properties.

Interestingly, the relative proportion of static and dynamic cells did not differ significantly across group A, B, and C. Furthermore, we did not observe any systematic relationship between the recording site of the cells and their response to surface coating.

**Group A cells**

Fifteen cells showed an increase in activity with the lubricant condition but not with the adhesive coating and were classified in the A group. The discharge pattern of one of these cells is illustrated in Fig. 4. In both the control and adhesive conditions, the cell increased discharge at or about the onset of grasping and lifting. Following a transient peak during the loading phase, the activity decreased rapidly to a low-frequency level that remained fairly constant up to the release of the object. The pattern of the cell discharge was clearly changed when the smooth metal was lubricated with petroleum jelly. The firing rate increased more gradually throughout the grasping and lifting phase of the task, and the peak activity had a more extended duration. The transition between the dynamic and the static phase of discharge was also more gradual, and a lower but consistent tonic activity was maintained during stationary holding of the object.

The peak firing frequency of the cells in the A group covered a wide range. The average peak discharge frequency was high in some cells and comparatively lower in others. To facilitate comparisons between neurons with different levels of responsiveness, we normalized both the peak discharge frequency and the peak grip and load force rates using the procedures described in METHODS.

**Relation of cell group A to grip and load force rates**

The mean peak activity for each cell in each coating condition was plotted against the mean peak normal and tangential force rates as well as the peak normal force and the GFR/LFR ratio. For the 15 cells in group A, this included at least 3 coating conditions and occasionally either an additional repeated measure of the untreated metal condition or a 2nd coating condition. A significant negative correlation was seen between the peak discharge frequency measured under the 3 conditions of friction for the 15 cells of the A group and the peak load force rate applied by the monkey during the task (Fig. 5A). Although the cell discharge was unrelated to the grip force rate as shown in Fig. 5B, the normalized peak discharge was strongly correlated with both the mean peak grip force and the ratio of grip force rate to load force rate (GFR/LFR) as shown in Fig. 5A, C and D. This latter correlation was significant mainly because the lubricant condition was associated with both a considerably higher grip force rate than the other two conditions, and a significantly higher peak discharge as well. Despite the fact that the peak discharge rates did not differ significantly between the untreated metal and the adhesive coating condition as shown by a t-test, both the discharge frequency and the GFR/LFR ratio tended to be higher for the lubricant condition as shown in Fig. 5C. This correlation indicates the close relationship between the afferent-triggered modulation of activity of cells in group A, and the coordinated control of grip and load forces during prehension.

**Group B cells**

Seven cells decreased activity in the adhesive condition, but their activity was not significantly increased when the lubricant was added to the smooth metal. We have called this group B, and, like the cell illustrated in Fig. 6, four cells of this group responded strongly during the dynamic phase when tested with the untreated metal. The pattern of activity differed in the...
adhesive condition where the peak discharge during grasping and lifting was lower. In the lubricated condition, the activity increased more gradually than with the uncoated metal during the dynamic phase up to the peak and then gradually decreased during the holding phase. These more gradual changes in discharge appear to be correlated with the more gradual increases and decreases in the grip force with the lubricated object. The three other cells in the B group had static properties and responded to the coatings mainly during the holding phase. For these cells, adding adhesive led to a marked decrease in the static discharge frequency.

Relation of group B cells to grip and load force rates

In contrast to the group A cells, the discharge frequency in group B cells proved to be poorly correlated with the rate of load force increase as seen in Fig. 7A but were more strongly related to the rate of grip force increase shown in Fig. 7B. The slope of the regression line in Fig. 7B indicated that the discharge frequency increased with increasing grip force rate. As might be expected, the peak grip force was also correlated with the peak discharge of the B group cells. The peak activity of B group cells was reduced with adhesive or unchanged with...
petroleum jelly, although these coatings had opposite effects on surface slipperiness. It appears that group B cells were not strongly excited by either surface slipperiness or stickiness. Although the relationship between the activity of cells in group B and the grip force to load force ratio was statistically significant (Fig. 7C), the correlation coefficient was lower than either the correlation with grip force rate alone or the peak grip force shown in Fig. 7, B and D.

**Group C cells**

Fourteen cells increased peak discharge with both coating conditions, and we have classified these as belonging to group C. The pattern of neuronal discharge in the task was remarkably consistent among these cells. An example of this discharge pattern is illustrated in Fig. 8. With the uncoated smooth metal, this neuron showed two distinct activity peaks during the dynamic lifting phase. The first peak had a sharp onset and was synchronous with the first peak in the load force rate. The rate of discharge increased very rapidly during this initial grasping and lifting phase, and the peak was generally reached within 20–40 ms of grip onset. The change in direction of the load force rate from positive, during acceleration, to negative associated with the deceleration coincided with a significant decrease in the discharge frequency. A second peak was syn-

**FIG. 7.** Correlation of normalized peak activity with the normalized peak load force rate (A), peak grip force rate (B), the ratio of peak grip force rate to peak load force rate (C), and peak grip force (D) for the 7 cells classified in the B group (conventions are the same as in Fig. 5).

**FIG. 8.** Response of a cell classified in the C group to changes in surface coatings. The peak discharges were greater in the 2 coating conditions than with uncoated smooth metal. The histogram binwidth is 20 ms.
chronized with the negative peak of the load force rate during deceleration. During the static holding phase the activity returned to a low tonic discharge frequency. A similar pattern was observed in the adhesive condition but with higher discharge peaks than with the untreated metal surface. However, the discharge pattern of this cell was quite different with the lubricated surface. Although the peak discharge was greater than in the control condition, the activity tended to increase more gradually during the dynamic phase. The two peaks seemed to fuse together to form a single broader peak either because the load force rates were very slow or because slip occurred continuously throughout lifting. During the static holding phase, the activity was also greater than in the other two conditions.

Five other cells of the C group showed similar biphasic patterns of activity during the dynamic phase. The remaining cells were characterized by a single sharp peak that could be synchronized either with the positive (5 cells) or the negative peaks (4 cells) in the load force rate. These cells with a single peak appear to be directionally sensitive to changes in tangential forces, whereas cells with two peaks appear to be more broadly tuned to changes in tangential forces in opposite directions.

Relation of group C cells to grip and load force rates

The activity peak in group C cells proved to be correlated with both the load force rate and the grip force rate, and these relationships are illustrated in Fig. 9. As one might expect, the load force rate was generally lower with the lubricant than in the control condition, but it was nevertheless associated with a higher peak discharge as seen in Fig. 9A. Figure 9B also shows that the C group cells have a tendency to demonstrate a greater activity in association with the lowest grip force rates. This effect did not appear to be directly related to friction because the average grip force rates were quite similar for the lubricated and adhesive coating conditions. Although a linear correlation between peak discharge and the grip force rate to load force rate ratio achieved marginal statistical significance, a quadratic equation provided a better description of the data. As seen from Fig. 9C the GFR/LFR ratio has a curvilinear relationship with peak activity. Moreover a similar relationship is also found between the peak discharge of C group cells and the peak grip force shown in Fig. 9D.

Force changes due to the perturbation

The perturbations produced a sudden increase in the tangential force, which displaced the object and elicited a reflexlike increase in grip force. In contrast to grasping and lifting, where change in grip force precedes the change in tangential load force, this order is reversed with the perturbation, and the change in load force precedes the changes in grip force. The load force rate traces provided an indication about the vertical forces generated by the manipulandum (Fig. 10, load force rate traces). Immediately after the per-
turbation onset, the load force increased sharply up to a peak 1.5 N. The rate of the load force changes was \( \sim 25 \) N/s during this initial phase. Then the load force returned to its initial level (negative peak of load force rate) and remained constant up to the release of the object. In some cases, this tangential force change was followed by a second positive peak in the load force rate (see example of group C in Fig. 10) due probably to the reflexlike response to the perturbation as the monkey adjusted the grip force to compensate for the abrupt change in load force. However, because the perturbations were predictable from one trial to another, the animal gradually increased the grip force before the perturbation onset to attenuate the slips on the skin. These anticipatory adjustments could start from the beginning of the holding phase, but they were more pronounced in the 300 ms that just preceded the perturbation (see examples of groups A and C in Fig. 10). However, the anticipatory adjustments were voluntary responses, and sometimes they failed to appear altogether (see example of group B in Fig. 10). In contrast the reflexlike adjustment of the grip force was always present following the perturbation. This reflex response started within 55–70 ms after the force pulse and in most of the cases ended before the release of the object (all 3 examples in Fig. 10). It was characterized by a rapid increase of grip force followed by a more gradual decrease once the load force had stabilized. Cadoret and Smith (1997) noted another strategy used occasionally by the monkeys, which was simply to lift the manipulandum higher in the position window on perturbed trials than on the control trials (see example of group C in Fig. 10). This strategy allowed the object to be maintained within the position window even when the object was pulled downward by the force pulse. Within 85–100 ms after the perturbation, the monkey compensated for the downward displacement by an opposite upward movement generated at the wrist. This reflex adjustment restored the object to its preperturbation position.

Neuronal responses to the perturbations

From a total of 386 task-modulated cells with cutaneous receptive fields, 168 were tested in the perturbed condition. Only 6 of 168 cells (4%) showed a significant change in discharge frequency before the perturbation onset. In four of these cells, this anticipatory response was excitatory, whereas it was characterized by an inhibition of the discharge in the two other cells.

In contrast, 147 of 168 cells responded with a reflexlike response to the perturbation. The response latency to the perturbation was measured from a poststimulus time histogram synchronized on the force pulse onset with a binwidth of 5 ms (Fig. 11). In the majority of the cells, the onset of the reflex

FIG. 10. Mean (30 trials) responses to the perturbation for the 3 cells illustrated in Figs. 3 (group A), 5 (group B), and 7 (group C). The force traces and the cell discharge were synchronized on the perturbation onset. Thin lines, unperturbed trials; thick lines, perturbed trials. Histogram binwidth is 20 ms.

FIG. 11. Latency distribution of the reflex response to the force-pulse perturbation in 131 cells of the primary somatosensory cortex, with response latencies <100 ms.
response was sharp and could be accurately detected on the histogram. The reflex activity onset latency was defined as the time at which the discharge frequency increased or decreased from the mean preperturbation activity by ±2 SD.

The neuronal response latency to the perturbation proved to be <100 ms in most of the responding cells (131/147; 89%) with a mean value of 44.1 ± 16.3 (SD) ms (Fig. 11). The distribution of the latencies proved to be skewed with a majority of the cells responding within 30–50 ms after the perturbation with a few cells having latencies >60 ms. Both the mean and distribution of the latencies were very similar to that previously reported in the primary motor cortex by Picard and Smith (1992b). Sixteen of the 147 perturbation-related cells (11%) had a response latency of >100 ms and ranged up to 160 ms. The long latencies suggest that the activity of these cells might be a consequence of the grip force increase rather than a more direct response to the slips and shear forces generated by the load force increase. It is more likely that these cells were responding to either the grip force adjustments or the vertical displacements that were initiated between 60 and 100 ms after the perturbation onset.

**Perturbation-evoked response patterns**

A variety of reflex response patterns were distinguished among the 147 perturbation-related cells. As previously mentioned, the response latencies varied from one cell to another. Furthermore, some cells responded with one sharp single peak of activity following the perturbation onset, whereas others presented a more gradual increase in activity, and still others showed two peaks of discharge. These various response patterns were thought to represent events such as slip, or shear on the skin, and the response pattern to the tangential force pulse would therefore be predictable from the modulation of neuronal activity with the different coatings. For example, a cell that discharged strongly with the lubricant would be most likely to be sensitive to the slips induced by the perturbation. We therefore compared the perturbation-evoked response patterns for the three groups of cells with distinct responses to the coatings (groups A, B, and C). This comparison was made initially for the three cells already shown in Figs. 4, 6, and 8, and their responses to the perturbation are illustrated in Fig. 10. The response to the perturbation was then averaged across all the recorded units of each group. The poststimulus discharge frequency was normalized from the average and standard deviation of the cell discharge for the 250 ms following the perturbation. These normalized poststimulus histograms were then averaged across all the cells in each group and are shown in Fig. 12.

The response to the perturbation of the same group A cell shown in Fig. 4 is illustrated in Fig. 10. After a 35-ms postperturbation delay, the discharge increased steeply and reached a peak during the initial loading phase. A high rate of discharge was maintained for >50 ms, and the activity returned to its preperturbation level before the occurrence of the negative peak in the load force rate. This cell appeared to be specifically sensitive to the load force changes because the grip force had not changed at the time of peak discharge. Figure 12, top, shows that the average discharge of group A cells increased gradually throughout the load force increase and reached a peak 70 ms after the perturbation onset. The activity then decreased progressively and returned to its preperturbation level within 200 ms.

Figure 10 shows the perturbation response of the group B cell shown in Fig. 6. The response latency was longer for this unit than for the A group cells. The first increase of discharge frequency was steep, but the peak discharge was reached only after >100 ms, which is after the grip force increase had already begun. The activity was then reduced before the release of the object. The average postperturbation discharge frequency of the B group cells shown in Fig. 12 did not show any obvious changes during the first 100 ms after the perturbation, and the peak activity only occurred 130 ms after the perturbation.

The response to the perturbation of the group C cell shown in Fig. 9 is illustrated in Fig. 10C. In this unit, the discharge latency was very short when compared with the A and B cell groups. The rate of discharge increased rapidly and reached a first peak in synchrony with the first peak in the load force rate. The reversal of the load force rate from positive to negative coincided with a pause in discharge, and a second peak of discharge occurred during the negative peak in load force rate. It can be seen from Fig. 10C that the amplitude of the negative peak of the load force rate is greater than that of the positive peak and is associated with a greater second peak in the neuronal activity. This relationship between the cell activity and the variations in the load force rate was similar to that previously reported during the lifting phase. The biphasic pattern of discharge was clearly apparent in the group response of the C group cells (Fig. 12). The first change in the rate of discharge appeared after a 30-ms latency, and the frequency increased steeply. Following the first peak of activity, the rate of discharge decreased and then returned to a high-frequency level after 150 ms.

**DISCUSSION**

Although the actual friction could not be measured in our experiment, the monkey’s behavior strongly suggested that the lubricant or adhesive coatings significantly altered the surface properties of the smooth metal. The object frequently and unexpectedly escaped from the fingers when a lubricant was added to the smooth metal surface. In the rosin condition, the monkeys had to voluntarily unstick the finger to release the object. Similar effects of coatings on precision grip have been observed in human subjects (Cadoret and Smith 1996), and significant differences were found between the coefficients of friction measured for petroleum jelly, smooth metal, and rosin. The mean coefficient of friction averaged over two control subjects were 0.22, 0.53, and 2.64 for petroleum jelly, smooth metal, and rosin respectively (unpublished observations). Also, Cadoret and Smith (1996) reported radical changes of surface friction when petroleum jelly or rosin were added on a smooth polyamide plastic surface.

**Variations of grip and load force rates with coatings**

In agreement with Johansson and Westling (1984b), our data demonstrate that the ratio between the normal force rate and the tangential force rate is adjusted to the friction of the grasped object such that the more slippery the object, the higher the ratio. Johansson and Westling (1984b) also sug-
gested that these changes in the force coordination with friction were principally influenced by changes in the grip force rate without modulation in the load force rate. This means that the more slippery the object, the higher the grip force rate. The performance of the monkeys in our study indicated that this was not invariably the case and that the load force rate and the grip force rate could be controlled independently in response to surface coatings. In fact, with the lubricant we observed that the grip force rate decreased and that the high value of the GFR/LFR ratio was due to a sharp decrease in the load force rate. The abrupt changes in the load force rate in the lubricant condition was similar to that described in human subjects who have to lift an object with an unexpectedly slippery surface (see Fig. 7, C and D, in Johansson and Westling 1984b). Following a first adjustment to the new surface during the preload phase, the subject often produced secondary adjustments in response to object slips. These secondary adjustments were characterized by a sudden drop in the load force rate only rarely accompanied by changes in the grip force rate.

These changes in the load force rate may be viewed in two different ways that are not mutually exclusive. Large slips on the skin will cause a reduction in the tangential load directly and produce an immediate decrease in the measured load force rate. However, in the present case this is unlikely because the changes in the coordination of the two forces are not precisely coincident with the slip events but instead appear after a 60- to 80-ms delay (Johansson and Westling 1984b). Alternatively, the decrease in LFR, like the increase in grip force, could be viewed as an adjustment of the load force in response to the object slip. This is a common daily experience, and reducing the load force rate is used when a hand-held object slips and more proximal muscles at the wrist, elbow, and shoulder are activated to decrease the object acceleration and allow grip forces to catch up to reestablish a secure grasp.

It is noteworthy that the increases in grip force needed to compensate for increased slipperiness can occur without increasing the grip force rate (Fig. 2). This divergence between increasing the peak grip force while reducing the grip force rate implies a particular and probably learned strategy to keep a constant relationship between grip and load forces. That is, if the monkey had increased the grip force rate and decreased the load force rate in the lubricated condition, the grip force would have become rapidly excessive for the corresponding level of load force.

FIG. 12. Histogram of the normalized responses to the perturbation averaged across all cells in groups A, B, and C. The time scale starts at the perturbation onset. Histogram binwidth is 1.0 ms.
Modulation of neural activity related to object slips

The data from the present study strongly suggest that the A group cells are sensitive to slips on the skin. All slips occur when the load forces exceed the required grip force given the frictional properties of the surface. The peak discharge measured for these cells during the dynamic phase appears greater in the lubricated condition than with the untreated metal or adhesive coating. Furthermore, as illustrated in Fig. 4, the major changes in cell activity coincided with the positive peak of the load force rate, i.e., during the vertical acceleration where the occurrence of slips was likely to be most frequent. The responses to the force-pulse perturbations further supported the idea of a specific sensitivity of the A group cells to object slip. Although the activity changes due to the perturbation occurred at relatively short latencies (35–40 ms), the A group cells were not recruited immediately, which is consistent with a response to slip rather than a response to the shear force that produced the slip. Group A cells attained a maximum discharge frequency as late as 70–80 ms after the perturbation, which is consistent with slip-sensitive responses seen in skin mechanoreceptors (Johansson and Westling 1988; Macefield et al. 1996). The regression lines on Fig. 5 give an indication about the contribution of the A group cells to the control of the precision grip. For this group of units, a negative correlation exists between the peak activity and the peak load force rate. This relationship is difficult to interpret because one cannot say with certainty which is the causal element in the correlation. However, because no peripheral afferents have been shown to be more active for the lower values of load force rate (Macefield et al. 1996), it is unlikely that somatosensory cortical cells present such a characteristic. We suggest instead that the slip response encoded by the A group units could directly influence the discharge pattern of motor cortical cells to decrease the load force rate, that is, to slow the rate of lifting. In other respects, the activity of the A group cell was also correlated with the peak grip force measured at the end of the loading phase. However, these units do not discharge in response to the grip force increases that follow the perturbation.

Modulation of neural activity related to grip force changes

In addition to the specificity of their discharge pattern during the task (Fig. 6), the cells classified in the B group disclosed a differential responsiveness to the changes in the tangential and normal forces with coatings. Unlike A group cells, the peak discharge of the B group units was not correlated with the load force rate during grasping and lifting (Fig. 7A). This suggests that these units are insensitive to load-dependent events such as shear forces and slips on the skin. On the other hand, the peak activity of the B group units showed a significant positive correlation with both the peak grip force and the peak grip force rate. This grip force effect seems independent of the surface slipperiness because the amplitude of the peak discharge was not altered with the lubricated surface compared with the untreated metal, although the two surfaces presumably had different (although unmeasured) coefficients of friction. This observation adds further weight to the hypothesis that slip on the skin had no major effect on the activity of the B group cells.

The response of the B group cells to the perturbation was consistent with the results obtained in the various coating conditions. These cells responded with a somewhat longer latency to the transient increase in load force and only when the subsequent increase in grip force has been initiated (i.e., around 100 ms after the perturbation). Such a delayed response implies that the increased discharge was triggered by the increased grip force generated by the reflexlike reaction and was not a direct response to the increase in tangential force on the skin. Although Macefield et al. (1996) reported that only the slowly adapting afferent respond to both normal and tangential forces on the skin, Wannier et al. (1991) observed phasic and phasic- tonic responses to changes in normal pressure on the skin during grasping by cutaneous cells in somatosensory cortex. In agreement with this observation, the present study suggests that both dynamic and static neurons of the somatosensory cortex respond to both normal and tangential forces on the skin.

Modulation of neural activity related to shear forces

Because both shear and slip on the skin occur in relation to changes in load force, it is not easy to determine which of these events caused the activity changes in cortical cells during grasping and lifting. However, the coatings provide a potential method for distinguishing the effects of shear from the effects of slip. As already mentioned, slips would certainly be more frequent in the lubricated condition, whereas the surface made adhesive with rosin would increase the tangential stretch of the skin without actual slip. The dynamic discharge of the 14 cells classified in the C group increased in the adhesive condition, and these cells discharged with a biphasic pattern during the loading phase that clearly followed the positive and negative peaks in the load force rate. These biphasic activity changes were even more apparent following the force-pulse perturbation where the peaks of discharge were scaled to the positive and negative peaks of load force rate (Fig. 10C). Together, these observations indicate a particular sensitivity of C group cells to shear on the skin. The strong activation of C group cells in the lubricated condition where the change in tangential force rate were weak and gradual might appear initially contradictory. However, we suggest that this increased activity with the lubricant reflects an additional sensitivity to slips on the skin. In fact, the biphasic discharge pattern was never associated with lubricated surface, and the discharge formed a single broad peak lasting throughout the tangential loading of the skin.

In our sample, the large majority of the cells that increased activity with the adhesive also increased their discharge with the lubricated surface as well (14/17) and were classified in the C group. This activity pattern suggests that the C group cells received direct afferents from the skin coding for both slip and shear forces. This hypothesis would be supported by the fact that a category of slowly adapting cutaneous afferents has been shown to respond to both stretch and relative motion on the skin (Srinivasan et al. 1990). Alternatively, it is possible that C group cells receive convergent afferents from multiple receptors such as the rapidly adapting type I afferents sensitive to slip and slowly adapting type II afferents that are mainly activated by skin stretch.

In summary, the neurons of the somatosensory cortex show at least three different response patterns to surface coatings that
change the slipperiness against the skin. The utility of cells responding to slip (i.e., group A) is obvious both for the perception of movement on the skin and force control in grasping. Group B cells responding to pressure normal to the skin surface would be useful for both localizing pressure on the skin and providing appropriate feedback for grip force regulation. The utility of cells in group C, which are activated by both slip and tangential shear force, is puzzling, but the fact that cells with similar properties were found in the motor cortex (Picard and Smith 1992a,b) suggests that perhaps they play a role in directing exploratory movements of the hand.

The technical assistance of L. Lessard, J. Jodoin, C. Gauthier, and G. Messier is gratefully acknowledged. We also thank Drs. C. E. Chapman and R. W. Dykes for critical reading of the manuscript.

This research was supported by a grant to Groupe de Recherche en Sciences Neurologiques from the Medical Research Council of Canada and fellowships from the Fonds pour la Formation des Chercheurs et l'Aide à la Recherche. Address for reprint requests: A. M. Smith, Centre de Recherche en Sciences Neurologiques, Dépt. Psychiatrie, Université de Montréal, Montreal, Quebec H3C 3J7, Canada.

Received 20 November 1997; accepted in final form 23 October 1998.

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