Neuronal Activity in Somatosensory Cortex of Monkeys Using a Precision Grip. I. Receptive Fields and Discharge Patterns

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Salimi, Iran, Thomas Brochier, and Allan M. Smith. Neuronal activity in somatosensory cortex of monkeys using a precision grip. I. Receptive fields and discharge patterns. J. Neurophysiol. 81: 825–834, 1999. Three adolescent Macaca fascicularis monkeys weighing between 3.5 and 4 kg were trained to use a precision grip to grasp a metal tab mounted on a low friction vertical track and to lift and hold it in a 12- to 25-mm position window for 1 s. The surface texture of the metal tab in contact with the fingers and the weight of the object could be varied. The activity of 386 single cells with cutaneous receptive fields contacting the metal tab were recorded in Brodmann’s areas 3b, 1, 2, 5, and 7 of the somatosensory cortex. In this first of a series of papers, we describe three types of discharge pattern, the receptive-field properties, and the anatomic distribution of the neurons. The majority of the receptive fields were cutaneous and covered less than one digit, and a χ2 test did not reveal any significant differences in the Brodmann’s areas representing the thumb and index finger. Two broad categories of discharge pattern cells were identified. The first category, dynamic cells, showed a brief increase in activity beginning near grip onset, which quickly subsided despite continued pressure applied to the receptive field. Some of the dynamic neurons responded to both skin indentation and release. The second category, static cells, had higher activity during the stationary holding phase of the task. These static neurons demonstrated varying degrees of sensitivity to rates of pressure change on the skin. The percentage of dynamic versus static cells was about equal for areas 3b, 2, 5, and 7. Only area 1 had a higher proportion of dynamic cells (76%). A third category was identified that contained cells with significant pregrasp activity and included cortical cells with both dynamic or static discharge patterns. Cells in this category showed activity increases before movement in the absence of receptive-field stimulation, suggesting that, in addition to peripheral cutaneous input, these cells also receive strong excitation from movement-related regions of the brain.

INTRODUCTION

The glabrous skin of the hand and particularly the finger tips of both monkeys (Darian-Smith and Kenins 1980) and humans (Johansson and Vallbo 1979) is densely innervated by specialized mechanoreceptors. Mountcastle et al. (1969) were among the first to reveal the basic differences in tuning characteristics between different classes of mechanoreceptors innervating the glabrous skin in the monkey and to compare these properties with psychophysical data obtained from human subjects. Later, with the development of techniques to record single axons of cutaneous nerves innervating the hand in humans (Vallbo and Hagbarth 1968), it became possible to compare the transducing properties of single receptors with the subjective psychophysical responses in the same subject (Johansson and Vallbo 1983). Knibestol and Vallbo (1970) described four types of mechanoreceptors innervating the human hand based on the distinctness of the receptive fields and the responses to dynamic and sustained pressure. Subsequent studies have extended the description of these four receptor types and their transducing properties (Johansson 1976; Vallbo and Johansson 1976).

These four mechanoreceptor afferents seem to have complementary roles in controlling the precision grip. In behavioral tasks that require precision handling, the contribution of each type of cutaneous mechanoreceptor has been examined at different stages of lifting, holding, and releasing objects, as well as during abrupt changes in tangential forces (Cole and Johansson 1993; Johansson and Westling 1987, 1991; Macefield et al. 1996). Johansson and Westling (1991) showed that fast adapting type I units (FAI) respond best to small force changes related to initial contact, slip, and release of the object, whereas fast adapting type II units (FAII) discharge only one or two spikes during the initial acceleration and deceleration of the object. In contrast, slowly adapting type I units (SAI) appeared to be more sensitive to changes in grip force, and slowly adapting type II units (SAII) appeared to be more receptive to changes in the tangential load force.

The output from these low-threshold mechanoreceptor afferents is transmitted to the cerebral cortex where they contribute to the discrete sensory-event-driven control of prehensile force (Johansson and Cole 1992). Indeed, the somatosensory cortex is known to send direct projections to the motor cortex (Jones and Powell 1973; Pavlides et al. 1993), and Allison et al. (1991) showed that after somatosensory cortical lesions, stimulating the median nerve no longer evoked potentials in motor cortex. Also, reversible inactivation of the somatosensory cortex by injections of muscimol selectively disrupted fine manipulative finger movements, but did not disturb reaching and hand shaping, which required visual guidance (Hikosaka et al. 1985). Moreover, the participation of motor cortical neurons with cutaneous receptive fields in adapting grasping and lifting forces to different surface textures and weights has been demonstrated by Picard and Smith (1992a,b). Together these studies raise important questions about how cutaneous information is transformed in the somatosensory cortex to provide useful feedback for the control of grasping.

Using a grasp, lift, and hold task similar to that used by Johansson and Westling (1984), we wanted to determine whether in the monkey, somatosensory cortical neurons demonstrate the same four response patterns as found in peripheral afferents during the precision grip task (Johansson and Westling 1987, 1991; Macefield et al. 1996; Westling and Johansson 1987). In addition, we examined the evidence for
integration and transformation of afferent signals at the cortical level. The present paper offers a classification of neurons based on their response to sustained pressure on the receptive field and changes in activity in the absence of receptive-field stimulation.

METHODS

The apparatus and training procedures have been described in detail in previous publications (Espinoza and Smith 1990; Picard and Smith 1999a). Briefly, three adolescent Macaca fascicularis monkeys weighing between 3.5 and 4 kg were trained to use the thumb and index finger to grasp a metal tab mounted on a low friction vertical track and to lift it into a 12- to 25-mm-wide position window. Correctly lifting and maintaining the object within the window was signaled by a 1-kHz tone, and the task was performed without visual feedback. The apparatus provided a continuous measure of the grip and lifting load forces and vertical displacement, which were digitized by a laboratory computer at 100 Hz. The monkeys were required to maintain this position for 1.0 s to obtain a fruit juice reward. Between trials the monkeys were obliged to release the object and leave it untouched for 1.5 s. In general, grasping an object involves applying a grip force normal to the skin surface, whereas lifting the object entails the progressive transfer of the object mass (M) to the finger skin as a tangential, shear, or load force. Once the entire object mass has been transferred to the skin, the tangential force (F) will increase in proportion to the acceleration (A) applied to the object (F = MA). The grip or normal forces as well as the tangential, or shear or load forces were recorded on every trial.

Whenever possible in the course of these experiments, a block of 35 trials was recorded for each cell with 3 different surface textures and 3 different weights. The textures consisted of smooth metal, fine grain sandpaper (grit size: 200), and coarse grain sandpaper (grit size: 60). In addition, the responses of some cells to changes in the friction were tested by coating the smooth metallic surface with either petroleum jelly or talc to make the object more slippery. Inversely, the surface friction against the fingers could be increased by adding an adhesive such as rosin to the smooth metal. The apparatus was also equipped to deliver a brief (100 ms) downward force pulse that could perturb the hand-held object and, if unopposed, would cause the object to slip from between the fingers. A detailed description of the specific effects of varying textures, weights, and coatings as well as the impact of the perturbations will be presented in two companion papers.

Receptive fields

Receptive fields were tested using a fine camel-hair brush and a small blunt probe in addition to passive manipulation of the wrist and fingers. When located, the limits of the receptive field were sketched on a standard drawing of the hand. The modality was identified as being cutaneous if the neurons responded to light punctate pressure with a blunt probe that slightly deformed the skin or responded to stroking the receptive field with a soft camel-hair brush. Care was taken to prevent joint movement in the stimulated area when testing for cutaneous responses. The responses were identified as proprioceptive when the stimulus involved joint rotation as well as tapping or stretching the muscles. The responses were further classified as dynamic if the neural activity showed a brisk increase limited to the grasping and lifting phase and which decreased abruptly to spontaneous levels thereafter. The responses were called static, if the neural discharge continued for the duration of the holding phase. χ² tests were used to compare the receptive-field sizes and the proportional representation of each cell class within the various cytoarchitectural areas.

Surgical preparation and recording procedures

An 18-mm circular recording chamber was stereotaxically implanted over the somatosensory cortex at 18 mm lateral to the midline and 7 mm anterior of the stereotaxic interaural zero. After a postoperative recovery period, recording sessions were conducted daily. A hydraulic microdrive attached to an X-Y micropositioner was used to advance glass-insulated tungsten microelectrodes through the dura mater into the cortex. Single-unit activity was recorded in the thumb-index finger representation area of the somatosensory cortex.

Histological preparation and map reconstruction

By passing cathodal DC through the recording microelectrode (50 µA, 10 s), small electrolytic lesions were made on some penetrations to mark the location of particular cells or to indicate the depth and orientation of electrode penetrations. At the termination of recordings, the animals were killed with an overdose of pentobarbital sodium and perfused through the left ventricle with saline followed by a 10% solution of phosphate-buffered Formalin. The brain was removed and stored in the same solution. One in three 40-µm frozen parasagittal sections from the somatosensory cortex were mounted and stained with cresyl violet. The location of electrode penetrations and the recording sites were estimated with reference to the electrolytic lesions and were drawn from a camera lucida projection and plotted on sections 240 µm apart. The cortical cytoarchitectural areas were identified according to previously published criteria (Powell and Mountcastle 1959a,b; Jones et al. 1978). However, the border between areas 2 and 5 is difficult to distinguish resulting in different locations of this border (Hyvarinen and Poranen 1978a,b; Pons and Kaas 1986). Our separation was based on the increase in the columnar appearance of area 5 and the emergence of larger pyramidal cells in layer 5 in the index finger representation area. This put the location of the area 2–5 border for the index finger at ~6 mm from the crown of the central sulcus, which is also in agreement with Iwamura et al. (1993) and Pons and Kaas (1986) (Fig. 2, D–F).

RESULTS

From a total number of 386 cells active during the task, the locations of 331 were estimated in histological sections of the parietal lobe. Of these 331 cells, 8 were recorded in area 3a, 17 cells in area 3b, 89 cells in area 1, 131 cells in area 2, 67 cells in area 5, and 19 cells in area 7.

Modality, receptive fields, and cortical location of the recorded neurons

From the total sample of 386 task-related cells, the input modality was identified for 205. Of these 205 neurons, 151 (71%) responded to cutaneous stimulation. Joint displacement and muscle tapping activated 39 neurons (19%), which were thought to be mainly responses to activation of muscle and tendon receptors. Only six cells (3%) responded both to cutaneous stimulation and joint displacement or muscle tapping. The cutaneous receptive fields reported here were all confined to the glabrous skin of the thumb (digit 1) and the index (digit 2) and the thenar eminence.

In general, the cutaneous receptive fields were rather small throughout the entire rostrocaudal extent of the somatosensory cortex encompassing the thumb and index finger area of the somatosensory cortex from area 3a to area 7. Table 1 shows the sizes of receptive fields in each cytoarchitectural area of the 151 cells identified with cutaneous receptive fields. Small receptive fields covering less than one digit comprised the
The border of the face area in the more lateral sections.

and 5, whereas the thumb is predominantly represented along medial sections bordering the region representing digits 3, 4, and 5, whereas the thumb is predominantly represented along the border of the face area in the more lateral sections.

Sulci are shown in three selected sections from each monkey. The relative orientations of the central and intraparietal index finger region of the somatosensory cortex in two monkeys were called “pregrip activity cells.” Table 2 shows the proportion of each cell class across different cortical cytoarchitectural areas.

### TABLE 1. Distribution of receptive-field sizes across different cortical areas

<table>
<thead>
<tr>
<th>Cutaneous RF Size</th>
<th>Area 3B</th>
<th>Area 1</th>
<th>Area 2</th>
<th>Area 5</th>
<th>Area 7</th>
<th>All Cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤1 phalange</td>
<td>80</td>
<td>26</td>
<td>32</td>
<td>28</td>
<td>28.5</td>
<td>31</td>
</tr>
<tr>
<td>≤1 digit</td>
<td>0</td>
<td>20</td>
<td>40</td>
<td>26</td>
<td>28.5</td>
<td>31</td>
</tr>
<tr>
<td>≤2 digits or 1 digit + part of thenar</td>
<td>20</td>
<td>48</td>
<td>25</td>
<td>43</td>
<td>43</td>
<td>35</td>
</tr>
<tr>
<td>&gt;2 digit</td>
<td>0</td>
<td>6</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Number of cells</td>
<td>5</td>
<td>35</td>
<td>69</td>
<td>35</td>
<td>7</td>
<td>151</td>
</tr>
</tbody>
</table>

Values are percentages except in Number of cells. In spite of larger fields found in area 1, a χ² test did not find this difference significant (P < 0.05). RF, receptive field.

The majority of cells located, respectively, in areas 3b (80%), area 2 (72%), and area 5 (54%). The receptive fields of 47/151 cells (31%) were limited to a small spot on one phalangeal segment of either digit 1 or 2. No discontinuous receptive fields were found in this region, and when the receptive fields included two digits, the skin in between was invariably included.

Although the total number of cells in areas 3b with mapped receptive fields was very small (n = 5), the fields of 4/5 covered an area of less than one phalange. The receptive field of the other neuron covered part of the thumb and index fingers. Table 1 shows the receptive fields of area 3b neurons to be smaller than those of area 2, but this difference was not statistically significant. The receptive fields in 50/69 or 72% of neurons recorded in area 2 were also small, covering an area of less than one digit. Only 25% of the receptive fields of the area 2 cells covered an area larger than one digit but equal to or less than two complete digits, and only 3% included an area more than two digits. In area 5, 19/35 (54%) neurons had small receptive fields encompassing less than one digit. In area 1, 19/35 neurons (54%) had receptive fields that covered an area extending to more than one digit. Although area 1 neurons seemed to have relatively larger receptive fields compared with areas 3b and 2, a χ² test did not find this difference to be statistically significant.

### Location of the recorded neurons in the somatosensory cortex

Verification of the lesion sites in sections stained with cresyl violet indicated that our recordings covered the area extending from the central sulcus up to and including the posterior wall of the intraparietal sulcus (see Fig. 1). For each monkey, the cortical representation of the first and the second digits were distinct and had little overlap with one another. Our penetrations covered ~6 mm of the somatosensory cortex in the anteroposterior direction, and 2.25 mm mediolaterally. The majority of cells were recorded within 3.0 mm of the cortical surface, although some penetrations extended further into the depths of either the central or intraparietal sulcus.

Figure 1 shows some of the cells recorded in the thumb and index finger region of the somatosensory cortex in two monkeys. The relative orientations of the central and intraparietal sulci are shown in three selected sections from each monkey. The index finger is more strongly represented in the more medial sections bordering the region representing digits 3, 4, and 5, whereas the thumb is predominantly represented along the border of the face area in the more lateral sections.

### Classification of neurons according to the activation pattern in the task

Three hundred eighty-six cells, selected for activity modulation in the task, were examined for particular discharge patterns and receptive-field properties. One hundred fourteen cells were lost before their activity could be recorded in all conditions, and these cells were excluded from the present analysis. Of the remaining 272 cells, 24 cells had decreased discharge beginning at the onset of grip force and lasting until the release of the object. The discharge patterns of 248 neurons with increased activity during object lifting and holding were examined for common features and grouped together into three different categories.

Two main classes of cells were differentiated according to their discharge pattern during grasping, lifting, and stationary holding. “Dynamic cells” showed a brief rapid increase in discharge beginning at or near the onset of grasping and lifting forces, which quickly returned to the spontaneous activity level even though pressure was continuously applied to the receptive field. The discharge of these cells was either lower or equal to the spontaneous activity during stationary holding. During the release of the object, some of these cells exhibited another rapid increase in their discharge. Cells that showed levels of activity consistently higher than the spontaneous activity during the static holding phase of the task were called “static cells.” Some cells within the dynamic and static categories had early activity changes associated with movements of the hand but in the absence of receptive-field stimulation, and these were called “pregrip activity cells.” Table 2 shows the proportion of each cell class across different cortical cytoarchitectural areas.

### Response properties of dynamic cells

The activity of dynamic cells was limited primarily to the onset of the grip or load forces, the perturbation onset, and the object release. The majority of the cells in this category exhibited a burst of activity beginning at or near the initial grip of the object and decreasing to the spontaneous level, during static holding. Some dynamic cells had relatively low levels of spontaneous activity during the intertrial interval when the hand was not moving, whereas in others the spontaneous activity was quite high. As illustrated by the examples shown in Fig. 2, these cells did not exhibit any increase in the activity before contacting the manipulandum. In some, but not all dynamic cells, releasing the object was accompanied by another activity peak that was sometimes nearly as great as the peak at onset (top 2 traces of Fig. 2).
Response properties of static cells

For static cells, the initial grasping of the object generated a rapid increase in activity, which was generally sustained, although usually at lower rates, throughout the period of stationary holding. Releasing the object was accompanied by a conspicuous peak in the activity in some static cells. Examples of static cells are shown in Fig. 3. These cells had some spontaneous activity during the intertrial period, although no significant increase in pregrip activity was detected.

Some static cells had high discharge rates during the dynamic phase of the task in addition to their sustained discharge during static holding (Fig. 3, top 2 traces). The difference in firing frequency between the mean peak activity during the dynamic phase and the mean discharge during the final 500 ms of the static phase was defined as a dynamic index. For the dynamically sensitive static cells the average dynamic index was 104 spikes/s, whereas other cells within the static group had little or no dynamic sensitivity (bottom 2 traces of Fig. 3).

For these dynamically insensitive cells the mean dynamic index was 30 spikes/s. Figure 4 presents a histogram of the dynamic index. The dynamically sensitive cells displayed much greater activity during grasping and lifting. The mean ratio of peak discharge to sustained rates was 5.1 for these cells compared with 2.6 for the dynamically insensitive cells. This difference was statistically significant ($t = 2.66$, df = 48, $P < 0.001$).

Response properties of cells with pregrip activity

A substantial number (94/248 or 30%) of cells in somatosensory cortex demonstrated significant increases in activity

<table>
<thead>
<tr>
<th>TABLE 2. Discharge pattern in each cortical area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area 3b</td>
</tr>
<tr>
<td>Dynamic</td>
</tr>
<tr>
<td>Static</td>
</tr>
<tr>
<td>Pregrip</td>
</tr>
<tr>
<td>Number of cells</td>
</tr>
</tbody>
</table>

Values are percentages except in Number of cells. The percentage of cells with pregrip activity was significantly higher in area 7 compared with the other areas, but the percentage of dynamic and static cells were relatively evenly distributed across the areas.
before the hand contacted the manipulandum. The discharge rate showed a gradual increase (500–1,000 ms) before the grip onset. For some neurons the change occurred even before the onset of movement of the hand toward the manipulandum. Examples of these cells are shown in Fig. 5, which indicates that cells with pregrip activity have both the dynamic (top 2 traces) and static discharge patterns (bottom left).

Distribution of discharge patterns within the cytoarchitectural areas

In spite of the fact that ~52% of the cells recorded in area 1 were dynamic in contrast to the other areas that had about equal numbers of dynamic and static cells, this difference was not found to be statistically significant with a $\chi^2$ test (Table 2). In contrast, in area 7 a significantly higher proportion of cells showed pregrip activity (Table 2) marked by increases in activity well before the onset of grasping and in the absence of movement.

**DISCUSSION**

This paper has described a variety of discharge patterns encountered in the region representing the thumb and index finger in the somatosensory cortex during lifting and holding. Although the peak activity of many of the neurons was influenced by the physical features of the manipulated object, the discharge patterns had salient features that were consistent in all conditions and were thought to reflect the characteristics of identifiable classes of neurons.

Receptive-field characteristics and the cytoarchitectural areas

The cortical cytoarchitectural areas were identified using previously published criteria (Jones et al. 1978; Powell and Mountcastle 1959a,b). In this study the majority of cells recorded throughout the rostrocaudal extent of the thumb and forefinger representation had small receptive fields. We did not encounter any neurons with discontinuous or multiple-locus receptive fields in any of the cortical cytoarchitectural areas. Although we also failed to find any inhibitory fields such as recently described by DiCarlo et al. (1998), our methods of receptive-field testing with a single probe would probably not have been sufficiently sensitive to reveal these responses. Despite the apparently larger receptive fields of cells located in area 1, this difference was not statistically significant. Similarly, a $\chi^2$ test indicated that the greater number of dynamic cells in area 1 compared with areas 2, 5, and 7 was not statistically significant ($P > 0.05$).

In contrast to area 1 cells, the receptive fields of the majority of neurons in area 3b, area 2, and area 5 covered less than one digit. The observation of discrete receptive fields, particularly in areas 2 and 5 is somewhat discrepant with previous reports showing a majority of multiple digit receptive fields in these caudal regions of S1 (Ageranioti-Bléanger and Chapman 1992;...
Darian-Smith et al. 1984, 1985; Hyvarinen and Poranen 1978a,b; Iwamura et al. 1983a,b, 1985, 1993; Pons et al. 1985a,b; Wannier et al. 1991). A likely explanation of this discrepancy is that the cortical region explored in our study, unlike other investigations was limited to a small area representing the first and second digits and adjacent cortex, which may be functionally different from the rest of the hand representation area. Another possibility would be that repeated stimulation of the same small area of skin of the digits 1 and 2 during the daily training might have produced some use-dependent changes in the receptive fields of the digits at the cortical level (Jenkins and Merzenich 1987; Jenkins et al. 1990; Lee and Whitset 1992; Reconzone et al. 1992a–d). However, Merzenich and collaborators did not investigate changes in receptive-field size in areas 2 and 5, and the use-dependent changes in these regions is unknown. Moreover, Wannier et al. (1991) found larger receptive fields in posterior parietal regions in monkeys subjected to similar repeated stimulation during performance of a precision grip. In other studies of the cortical representation of the glabrous skin of the hand in the posterior subdivision of SI (Ageranioti-Belanger and Chapman 1992; Darian-Smith et al. 1984, 1985), the monkeys were trained to make scanning movements of various textures that may have stimulated larger areas of skin, resulting in larger receptive fields compared with the present study in which only a small area was stimulated over a long period. In still other studies (Hyvarinen and Poranen 1978b; Iwamura et al. 1983a,b, 1985, 1993; Pons et al. 1985a,b) the cortical mapping was conducted on untrained monkeys, and consequently no organizational changes would have been expected. Ultimately, however, cortical plasticity may not be necessary to explain our results, and, as already mentioned, the observation of small receptive fields within the thumb and index finger representation of area 2 and 5 might be related to the functional organization of the primary somatosensory cortex.

**Modality of neurons in rostrocaudal progression**

The majority of cells located in areas 3b, 1, and 2 (77%) responded to cutaneous stimulation. In area 2, 88% of the cells responded to skin stimulation, and in area 5, 66% of neurons responded at low thresholds to skin stimulation. This observation is also somewhat at variance with some other reports that have emphasized the prevalence of input from muscle, tendon and joint receptors to areas 2 and 5 (Krishnamurti et al. 1976; Merzenich et al. 1978; Mountcastle and Powell 1959; Pons et al. 1985a,b; Powell and Mountcastle 1959a,b). However, these studies have mainly investigated the representation of hairy skin, and several investigators have noted that cutaneous afferents predominate in the part of area 2 devoted to the glabrous skin of the hand (Hyvarinen and Poranen 1978a; Iwamura et al. 1985). Although the present study confirms these observations, it does not exclude the existence of proprioceptive afferents to areas 2 and 5, but only suggests instead that within the hand area, cutaneous afferents from the glabrous skin surpass the number of proprioceptive afferents.
Comparing cortical neurons to cutaneous afferents during grasping and lifting

The discharge patterns of the neurons in somatosensory cortex showed some striking similarities when compared with the four classes of tactile receptors recorded in human subjects during performance of a precision grip by Johansson and Westling (1987), Macefield et al. (1996), and Westling and Johansson (1987).

The responses of some dynamic and static cells both at grip onset and at object release might represent a reaction to applying and releasing pressure normal to the skin surface. Alternatively, the high-frequency bursts at object release might denote responses to tangential slip on the skin similar to the FAI receptors recorded by Macefield et al. (1996), which were more responsive to skin slip than to grip forces applied normal to the skin surface. A sensitivity to shear forces and slips occurring between the skin and the object may account for the activity observed on object release in some cortical cells.

According to Johansson and Westling (1987; Westling and Johansson 1987) and Macefield et al. (1996), FAII afferents had high-frequency responses to initial contact with the object but did not show any excitation to the unloading phase of the task. Some of the cortical dynamic cells in the present study also had high-frequency bursts of >100 Hz at grip onset, which adapted very rapidly as well. In addition, these cells also did not show any increase in activity at object release.

Again according to Johansson and Westling (1987), Macefield et al. (1996), and Westling and Johansson (1987), SAI receptors respond with a high-frequency burst of activity on initial contact and show a sustained but lower tonic activity during the static holding phase. The dynamically sensitive cortical static cells recorded in the present study disclosed a similar pattern of activity during precision grip. In contrast to SAI receptors, slowly adapting type II afferents have less dynamic sensitivity and respond with a constant discharge throughout the lifting and holding movement. Our dynamically insensitive cortical static cells also show this constant-activity pattern with little or no increase in the rate of discharge with object release. In addition to lower dynamic sensitivity, these neurons never exceeded a peak frequency of 100 Hz. Another property of SAI afferents is their sensitivity to the direction of the tangential load force applied on the skin. Indeed, these afferences can be activated differentially according to the direction of the applied load (Edin 1992; Vallbo et al. 1995). In our study, the object mass generated a load force consistently oriented in the downward direction during static holding, and the effect of directional sensitivity could not be assessed directly in the same single cell. Nevertheless, it is worth noting that 24 cells of our sample showed a tonic decrease in their discharge rate during static holding. It can be hypothesized that this discharge pattern was related to the directional sensitivity of some peripheral afferents. However, it is also possible that this decreased activity during static holding was due to intracortical inhibitory mechanisms (Di Carlo et al. 1998).

Some cortical static cells responded both to the onset of stimulation and to the release of the object, which has not been
reported for any of the slowly adapting peripheral afferents. This pattern may reflect a cortical convergence of fast and slowly adapting afferents because the activity pattern reflects some elements of both. Such cells could provide an emergent sensation related to long-lasting strain forces on the skin.

Premovement activity in somatosensory cortical neurons

In spite of the apparent similarity between the discharge patterns of the somatosensory cortical neurons and the four discharge patterns of the peripheral afferents, cells with pregrip activity appeared markedly different because the change in activity occasionally even preceded movement of the fingers. This premovement activity before grip force onset might arouse the suspicion that the monkey was either touching the apparatus before the grip onset. However, the training procedures required a stationary position of the hand away from the manipulandum between trials. Premovement activity in the somatosensory cortical neurons has been reported in other studies, and it is suggested that the afferents from motor areas can modulate the excitability of neurons in the somatosensory cortex (Jiang et al. 1991; Nelson 1987; Nelson et al. 1991; Williams et al. 1998). Premovement activity has also been reported in shoulder-related visuomotor responses of neurons of parietal area 5 (Kalaska 1996; Sakata et al. 1995), whereas the present study found a greater number of cells in area 7 demonstrating pregrip activity as compared with areas 3b, 1, 2, and 5. Both dynamic and static cortical cells in area 7b had pregrip activity, although a significant number of static cells with pregrip activity were found in area 2 as well. Somewhat surprisingly, no statistically significant difference was found between anterior and posterior somatosensory cortex in the proportion of dynamic cells with pregrip activity, although area 7 had a greater proportion of pregrip activity than area 2. The grasping and holding task was not designed to require visually guided reaching, and in fact the task was performed without visual feedback. Auditory cues might have played a role, but no specific auditory stimulus could be directly related to the pregrip activity of the cells. Iriki et al. (1996) have described activity increases in somatosensory cortex related to attention to the object’s physical attributes or preparation of a motor program for grasping, which may have affected the pregrip activity. However, these variables were not examined in the present study.

Proportion of different classes of cells across the recorded area

The classification of neurons in the somatosensory cortex was based on certain seemingly invariant characteristics observed during grasping, lifting, and holding. This classification was thought to represent distinctly different classes of neurons, rather than points on a continuum. At this time we cannot prove that input from the previously described four types of glabrous skin mechanoreceptors accounts for the similar features found among somatosensory cortical neurons, although it is tempting to believe that this might be the case. Some somatosensory cortical neurons appeared to show varying sen-
sensitivities to forces applied either normal or tangential to the skin surface.

Although in agreement with previously published studies (Paul et al. 1972; Powell and Mountcastle 1959a), we found that the number of dynamic cells was higher in area 1; this proportion was not statistically significant. Overall, the number of cells with dynamic and static discharge properties was not significantly different among any of the cytoarchitectural areas of the somatosensory cortex (shown in Table 2), which argues against a strict organization of the cortex based on peripheral receptor types. Finally, the higher proportion of the static cells in area 7 with increases in activity well in advance of the reaching and grasping movement (i.e., pregrip activity) supports a putative role for this area in the planning and preparation for movement.

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