Comparison of the Neuronal Activity in the SMA and the Ventral Cingulate Cortex During Prehension in the Monkey

GENEVIEVE CADORET AND ALLAN M. SMITH
Centre de Recherche en Sciences Neurologiques, Département de Physiologie, Université de Montréal, Montreal, Quebec H3C 3T8, Canada

Cadoret, Geneviève and Allan M. Smith. Comparison of the neuronal activity in the SMA and the ventral cingulate cortex during prehension in the monkey. J. Neurophysiol. 77: 153–166, 1997. Two monkeys were trained to use the thumb and forefinger to lift and hold an instrumented apparatus within a narrow position window for 1 s. The device was equipped to measure the position and the grip and lifting forces exerted by the animal. On blocks of trials the weight and surface texture could be varied or a force-pulse perturbation could be systematically delivered 750 ms after the object entered the window. If unopposed, the perturbation would displace the hand from the position window, and in preparation for this perturbation the monkeys either increased their grip force before the perturbation or raised the object higher within the position window. Two clearly separated clusters of cells in the medial wall of the frontal lobe were found to be active in relation to the task. One group of cells (n = 115) was located in the caudal and medial part of area 6, in the supplementary motor area (SMA), and the other (n = 92) was located in the ventral bank of the cingulate sulcus (CMAv), in area 23c. In each area, neurons were characterized by their sensorimotor features clearly related to the hand in addition to their modulated activity in the task. In the SMA, 71% (42 of 59) of the neurons tested for receptive fields responded to peripheral and mainly proprioceptive stimulation, and 71% of them (30 of 42) received inputs from the hand. In the CMAv, 77% (48 of 62) of the neurons responded to peripheral proprioceptive stimulation, and 77% (37 of 48) exhibited receptive fields originating from the hand. Intracortical microstimulation applied to 43 sites in the SMA evoked discrete hand movements at 12 loci, whereas in the CMAv hand movements were observed at 8 of 27 sites tested with an average threshold of >15 μA. A strong similarity was observed between the SMA and CMAv neurons in their sensorimotor features as well as the modulation of their activity in relation to the prehension task. In both areas the activity was poorly related to grip force and significant correlation with peak grip force was observed for only 9 and 7% of the CMAv and SMA neurons, respectively. In the SMA only five cells exhibited increased activity before the perturbation and in the CMAv no changes in activity were found despite the presence of clear preparatory increases in grip force in anticipation of the perturbation. The perturbation evoked reflexlike excitation of 38% (25 of 65) of the neurons in the CMAv and 28% (20 of 71) of the cells in the SMA; these cells were similar in magnitude and latency (~50 ms) in both areas. In both the SMA and CMAv, most of the neurons increased their firing rate <200 ms before the grip force onset and the overlap in the distribution of neuronal response times suggests a parallel activation of the SMA and CMAv neurons during the prehension task.

INTRODUCTION

Since the description of the supplementary motor area (SMA) by Penfield and Welch (1951) and Woolsey et al. (1952), the topography of the medial wall motor areas of the frontal lobe has changed considerably. From the more recent maps (Dum and Strick 1991a,b; He et al. 1995; Luppino et al. 1991, 1993), the medial motor areas include two regions in the medial part of area 6, the SMA and the pre-SMA (Luppino et al. 1993; Matzusaka et al. 1992), and two regions in the cingulate cortex. The cingulate cortex can be subdivided into a rostral cingulate area and a caudal cingulate area. The latter can be further subdivided into a ventral (CMAv) and a dorsal region (Dum and Strick 1991a,b; He et al. 1995). The association of these areas with motor functions is essentially supported by their anatomic projections to the spinal cord and their connections with the primary motor cortex (Dum and Strick 1991a,b, 1995; Luppino et al. 1993; Tokuno and Tanji 1993). In addition, the discrete movements evoked by intracortical microstimulation (ICMS) (Luppino et al. 1991; Matzusaka et al. 1992) and the changes in the neuronal activity accompanying learned movements (Cadoret and Smith 1995; Matzusaka et al. 1992; Shima et al. 1991) confirm that these areas participate in the neural control of voluntary movement. Despite several proposed functional differences (Matzusaka et al. 1992; Shima et al. 1991), the precise role played by these areas in motor control remains undefined. In the pre-SMA, activity changes were more frequently observed in response to visual cues and were more time locked to stimuli triggering movements than in the SMA, where neuronal activity was more movement related (Matzusaka et al. 1992; Tanji 1994). In the cingulate cortex, more neurons demonstrating early premovement discharge and preferential activity during internally guided movement were found in the rostral region than further caudally (Shima et al. 1991). The functional differences between the medial motor areas have been described mainly in the rostrocaudal direction for medial area 6 and for the cingulate cortex. In the present study we wanted to establish a comparison between the region of area 6 known as the SMA and the one of the cingulate motor areas. The neuronal activities in two caudal medial motor areas: the SMA and the CMAv were compared during a prehension task in awake monkeys. Both regions were thought to be potentially related to grasping because they project to the cervical segments of the spinal cord (Dum and Strick 1991a,b, 1995; Galea and Darian-Smith 1994; He et al. 1995; Hutchins et al. 1988) and the arm region of the primary motor cortex (Dum and Strick 1991a; Tokuno and Tanji 1993). Moreover, Dum and Strick (1995) have recently shown that, like the motor cortex, both the SMA and cingu-
late motor area appear to establish direct connections with the spinal motoneurons of the wrist and fingers. Also, a modulation of the neuronal activity during distal movements has been reported in each area (Brinkman and Porter 1979; Shima et al. 1991; Smith 1979; Tanji and Kurata 1979; Tanji et al. 1988).

An essential characteristic of controlled grasping is the use of somatosensory feedback for the appropriate scaling and coordination of the grasping and lifting forces used in object manipulation (Johansson 1991). These afferents provide information about the physical properties of grasped objects, such as weight, texture, and frictional characteristics, and arise mainly from the cutaneous mechanoreceptors in the glabrous skin of the fingers (Johansson and Westling 1984a,b, 1987). Previous studies have shown that primary motor cortex (Picard and Smith 1992a) and cerebellar neurons (Dugas and Smith 1992; Espinoza and Smith 1990) were also very responsive to feedback from the glabrous skin of the hand and consequently were thought to participate in the sensorimotor integration necessary for efficient grasping. In the motor cortex, 52% of the neurons with either cutaneous or proprioceptive receptive fields showed a modulation of their activity as a function of texture (Picard and Smith 1992a). To date, the evidence that the SMA and cingulate cortex receive peripheral inputs and participate in sensorimotor integration has been rather uncertain. Although these areas are interconnected with the somatosensory cortex (Dum and Strick 1993; Jones and Powell 1969; Jones et al. 1978; Morecraft et al. 1987), several studies failed to report any responses in these regions to peripheral stimulation (Brinkman and Porter 1979; Shima et al. 1991; Wise and Tanji 1981). In contrast, other studies have found SMA neurons that receive proprioceptive inputs (Hummelsheim et al. 1988; Matsuzaka et al. 1992; Smith 1979; Wiesen-danger et al. 1973). Moreover, in the present study, we found that a high proportion of neurons with activity related to grasping in the SMA and in the CMAv also received peripheral inputs from the hand.

Peripheral information about the physical properties of grasped objects facilitates the moment-to-moment adjustment of grip forces and can also be memorized for subsequent manipulatory actions. When a predictable perturbation was introduced during steady holding against gravity, monkeys (Dugas and Smith 1992), like humans (Johansson and Westling 1988; Lacquaniti and Maoli 1989), developed preparatory responses, adjusting the grip forces not only as a function of the physical properties of the object, such as texture and weight, but also in relation to the anticipated magnitude of force-pulse perturbations. Recent studies have shown that SMA neurons play an important role in controlling sequential movements on the basis of memorized information (Tanji 1994; Tanji and Shima 1994). In the present study we used the prehension task with a readily predictable perturbation to determine whether the SMA and CMAv neurons might also play a role in anticipatory strategies based on the memory of perturbations on previous trials.

METHODS

Two adolescent male *Macaca fascicularis* monkeys weighing 4.2 and 4 kg were used in this experiment. Some of the results for one of the monkeys have been presented previously (Cadoret and Smith 1995).

Apparatus

The apparatus used to measure the grasping and lifting forces was similar to that used by Espinoza and Smith (1990). The monkeys were required to grasp and lift a metal tab, the weight and surface texture of which could be varied. Strain gauges measured both the horizontal grip force and the vertical lifting or load force exerted by the animals. A position transducer measured the movement of the object in the vertical axis.

Task

As described previously (Espinoza and Smith 1990), monkeys were trained to grasp the object between the thumb and forefinger and to lift the object within a vertical position window between 12 and 25 mm that was signaled by a 1-kHz tone. The animal was then required to hold the object stationary for 1 s. Correct responses were rewarded with apple juice. Once the monkey had released the object at the end of a trial, an intertrial interval of 2 s was imposed before a subsequent trial could be initiated. On separate blocks of trials, a 50-ms downward force-pulse perturbation was applied to the object during the stationary holding phase to produce a sudden added shear force on the fingers. The force of the perturbation varied between 1.5 and 2.0 N. To evoke self-paced preparatory responses, this perturbation was invariably delivered 750 ms after the onset of the tone indicating that the object had entered the position window. For both monkeys the testing procedures began with a block of unperturbed control trials, preceding a block of perturbed extinction trials and then followed by a second block of unperturbed extinction trials.

For some cells, additional testing was conducted with different textures and weights. The three textures employed were polished metal (12 and 25 mm that was signaled by a 1-kHz tone). The animal was then required to hold the object stationary for 1 s. Correct responses were rewarded with apple juice. Once the monkey had released the object at the end of a trial, an intertrial interval of 2 s was imposed before a subsequent trial could be initiated. On separate blocks of trials, a 50-ms downward force-pulse perturbation was applied to the object during the stationary holding phase to produce a sudden added shear force on the fingers. The force of the perturbation varied between 1.5 and 2.0 N. To evoke self-paced preparatory responses, this perturbation was invariably delivered 750 ms after the onset of the tone indicating that the object had entered the position window. For both monkeys the testing procedures began with a block of unperturbed control trials, preceding a block of perturbed extinction trials and then followed by a second block of unperturbed extinction trials.

Surgical preparation

After the monkeys had achieved a consistent level of performance in the grasping task with and without the perturbation (≥85% success) they were prepared for chronic single-cell recordings. Following previously published procedures (Espinoza and Smith 1990; Evarts 1965), the monkeys were anesthetized with pentobarbital sodium (30 mg/kg) and a circular chamber of 18 mm ID was stereotaxically implanted. The localization of the hand region of the ventral cingulate cortex was confirmed by a preliminary mapping study in two anesthetized monkeys. The chamber was positioned over the midline, at either 15 or 18 mm anterior to the stereotaxic interaural zero, to afford simultaneous access to the medial wall of the frontal lobe and the full mediolateral extent of the frontal cingulate sulcus.

Recording procedures

Several days after the monkeys had fully recovered from surgery, recordings sessions were conducted on a daily basis. The two regions, the SMA and the cingulate sulcus, were explored alternatively. Glass-insulated tungsten microelectrodes (0.5–1.5 MΩ) were introduced during steady holding against gravity, monosynaptic response, adjusting the grip forces not only as a function of the physical properties of the object, such as texture and weight, but also in relation to the anticipated magnitude of force-pulse perturbations. Recent studies have shown that SMA neurons play an important role in controlling sequential movements on the basis of memorized information (Tanji 1994; Tanji and Shima 1994). In the present study we used the prehension task with a readily predictable perturbation to determine whether the SMA and CMAv neurons might also play a role in anticipatory strategies based on the memory of perturbations on previous trials.
Histological analysis and reconstruction of recording sites

Input-output properties of the cingulate neurons have been monitored during the execution of the task. Modulated neurons were those that showed changes in discharge during at least two consecutive bins (20 ms) deviated by more than 3 SD of the mean value, calculated during a control period of 500 ms preceding the task. These neurons were tested to determine whether the perturbation, weight, or texture had any significant influence on the neuronal response. The mean firing frequency was calculated on a trial-by-trial basis and compared across conditions with an analysis of variance followed by a Tukey’s honestly significant difference test for paired comparisons (P < 0.01). For each cell, the relation between the neuronal activity and the grip force exerted by the monkey was tested first on a block of unperturbed trials. For the phasic cells associated with the dynamic phase of the perturbation, the correlation coefficient was calculated between the mean firing frequency of the cell and the peak grip force developed during the dynamic phase. For the tonic cells, active during the static phase of the task, the relation was measured between the mean firing frequency and the mean grip force.

The neuronal response to the perturbation was analyzed in two ways. First, the responses following the perturbation were measured by averaging the cell activity for each trial over a 150-ms period before and after the perturbation. The average firing frequency was calculated on a trial-by-trial basis and compared across conditions with an analysis of variance followed by a Tukey’s honestly significant difference test for paired comparisons (P < 0.01). For each cell, the correlation coefficient was calculated between the mean firing frequency of the cell and the peak grip force developed during the dynamic phase. For the tonic cells, active during the static phase of the task, the relation was measured between the mean firing frequency and the mean grip force.

RESULTS

Identification of the cells

A total of 207 neurons was recorded in the medial wall of the frontal lobe and in the cingulate sulcus in two monkeys. Of these, 115 cells were located in the SMA (42 in monkey 1, 73 in monkey 2) and 92 cells were located in the CMAv (in monkey 2). The histological localization and the input-output properties of the cingulate neurons have been previously published (Cadoret and Smith 1995), and these data will only be described in comparison with the SMA neurons.
Identification of cingulate cells

Task-related cingulate neurons were recorded in the ventral bank of the cingulate cortex, at the rostral limit of the area 23c. Of these neurons, 62 neurons were tested for receptive fields and 37 cells received input from the hand. As described in Fig. 1, the majority of these cells (29 of 37) received proprioceptive input (14 cells were activated by thumb movements and 15 cells were related to displacement of the other fingers); only 8 cells demonstrated cutaneous receptive fields on the glabrous skin of the hand. Brief wrist or finger movements could be evoked by ICMS in 10 of 27 sites. For seven of these responses the threshold varied between 15 and 40 μA.

Identification of SMA cells

LOCALIZATION. The localization of the recording sites was estimated from the histological examination of the coagulation points and the evidence of tracks in the cortex. As indicated in Figs. 2A and 3A, in both monkeys the recorded cells were located in the medial wall of the frontal lobe just caudal to the genu of the arcuate sulcus. From these recording sites and the properties of the cells, which are presented later, we assumed that the recorded neurons were effectively in the SMA and not the pre-SMA described by Matsuzaka et al. (1992). Figures 2B and 3B represent the mediolateral extent of the penetrations in the cortex. In both monkeys, the deeper and more medial part of the medial wall was not explored.

INPUT-OUTPUT PROPERTIES. The sensorimotor features of the recorded neurons in the SMA were very similar to those of CMAv neurons. Half of the cells (59 of 115) in the SMA were tested for receptive fields and 71% of them could be identified as related to the upper limb. From the 42 arm-related cells, 30 received input from the hand whereas 12 others were instead related to the arm or wrist. These neurons are included in Figs. 2C and 3C, which represent the proximodistal arm representation in the SMA. The hand representation in the SMA is displayed in the unfolded maps in Figs. 2D and 3D. As indicated on these maps, hand-related neurons and task-related neurons were found throughout the entire depth of the medial wall. Most of the hand-related neurons in the SMA received proprioceptive inputs. Sixteen cells were selectively activated by passive movements of the thumb and 11 by manipulation of the fingers, but only 3 cells demonstrated cutaneous receptive fields on the glabrous skin of the hand.
ICMS was applied at 43 recording sites and evoked upper limb movements at 25 loci. At 12 sites, movements were limited to the fingers, whereas at 13 sites ICMS evoked movements of the wrist or arm. For 10 of the responses, the threshold varied between 20 and 40 μA, whereas for 11 responses the threshold was <20 μA. For six cells, a clear correspondence between the afferent inputs and the muscular response to the ICMS could be observed.

Firing patterns of discharge

Most task-related cingulate and SMA neurons fired phasically before the grip force onset (Fig. 4). The main difference observed between the two areas was a higher proportion of phasic-tonic neurons (18.3%) in the SMA than in the ventral cingulate cortex (7.6%). In both areas, additional patterns of discharge were also observed. For example, ramplike increases of discharge, or complex modulations involving increases and decreases in activity, were observed in a small proportion of cells.

In the SMA, 22% (25 of 115) of the neurons demonstrated a significant change in activity during the release phase, compared with 33% (32 of 92) of the neurons in the CMAv (Cadoret and Smith 1995). Most frequently this release activity began with the grip force decrease. Figure 5 illustrates two examples of cells from the SMA and cingulate cortex receiving proprioceptive inputs from the finger muscles, showing this modulation of activity during the release phase. No differences in the onset times of the neuronal responses were observed between the two areas. The distributions of onset times of both activated cells and cells related specifically to the hand overlapped considerably (Fig. 6). In other studies of SMA and cingulate neurons, the responses preceding movement onset by ~500 ms were used to distinguish between short- and long-lead neurons (Okano and Tanji 1987; Shima et al. 1991). According to this criterion, most of the cells recorded in this study were short-lead neurons (71% in the CMAv and 77% in the SMA).

Relation to the prehensile force

In a previous study, Smith (1979) found that the activity of SMA neurons was not as clearly related to grip force as the activity of cells in the motor cortex. Of 61 cells demonstrating reliable changes in firing frequency during the performance of the maintained precision grip, only 2 neurons increased their discharge with increased finger force and no modulation was observed to be related to the mean rate of force change. In the present experiment, although the grip task was slightly different, we again found only a low incidence of activity modulation in the SMA and the CMAv related to prehensile force. Of 64
Responses to the perturbation

The effects of perturbation were tested for 71% (65 of 92) of the cells in the CMAv and 62% (71 of 115) in the SMA.

Postperturbation effects

The force-pulse perturbation during the object holding evoked a reflexlike response in the finger muscles with a latency of 30–50 ms in the primate (Dugas and Smith 1992). This muscular activation resulted in an increase of the grip force that peaked 50–100 ms after the stimulus. In the present study, an increase of the grip force was observed for 97% of the blocks of trials tested during the recording of CMAv neurons and 96% of the blocks during the recording of SMA cells. The mean onset of the postperturbation with the 115-g weight and the rough surface was $44.36 \pm 11.73$ (SE) ms and the latency peak was at $116.73 \pm 15.48$ ms.

The force pulse evoked a significant change in the neuronal activity time locked to the perturbation onset in 25 of 65 cells (38%) in the CMAv and in 20 of 71 neurons (28%) in the SMA. Table 1 compares the responses to the perturbation in both areas as a function of the input properties of the neurons. In each area, most of the cells responded to the perturbation with an increase in activity. Only a small number of neurons that were tonically active during the static phase exhibited an inhibition of the activity after the perturbation. As suggested for the motor cortex (Picard and Smith 1992b), this decrease in activity in the SMA and in the CMAv might correspond to an unloading of muscle spindles. Although representing only a small proportion overall, the neurons receiving cutaneous inputs appeared to respond more readily to the perturbation than neurons receiving proprioceptive input.

MAGNITUDE OF NEURONAL RESPONSES. The magnitude of the neuronal response to the perturbation was defined as the absolute value of the difference between the peak of the grip force. Of 8 tonic neurons in the cingulate cortex and 11 tonic ones in the SMA, only 1 cell in each area exhibited a significant relation between the mean firing frequency and the peak grip force. Of 8 tonic neurons in the cingulate cortex and 11 tonic ones in the SMA, only 1 cell in each area exhibited a significant relation between the mean firing frequency of the cell and the mean grip force. In the SMA, six cells were further tested with different weights but only one cell, which received proprioceptive input from the thumb muscles, demonstrated a weight effect, and that was associated with an inverse or negative relation with the grip force.

In both areas some effect of the texture of the grasped surface was observed. Of 13 cells tested in the SMA, 6 demonstrated a change in activity with a change in texture, whereas in the cingulate cortex, 4 of 6 neurons demonstrated a texture effect. For most of the cells in both areas, these effects of texture were dissociated from the changes in grip force.

FIG. 4. Distribution of the discharge patterns in the supplementary motor area (SMA) ($n = 115$) and in the ventral cingulate cortex ($n = 92$).
firing frequency of the cell 150 ms after the perturbation and the slip of the object estimated from the velocity of the test object. For two of three cells, identified as receiving proprioceptive input, an increase in the tangential force of the perturbation induced an increase of the reflex response.

**RESPONSE LATENCY.** When the neuronal responses to the perturbation were sufficiently abrupt (in 15 units in the SMA and in 22 units in the CMAv), the response latencies were determined from the peristimulus histograms centered on the proprioceptive input, an increase in the tangential force of the perturbation induced an increase of the reflex response.

**FIG. 5.** Mean firing frequency of 2 neurons, 1 from the SMA and the other from the ventral cingulate cortex, showing an increase of activity at the beginning of the task and during the release phase. Top traces: mean grip force profiles. On the left the cellular discharge is aligned on the grip force onset; on the right the firing rate is aligned on the beginning of the grip force decrease. Both neurons receive proprioceptive inputs. The SMA cell was excited by stretching the finger extensor muscles, whereas the cingulate neuron was excited by stretching the finger flexors muscles. RF, receptive field.

**FIG. 6.** Distribution of neuronal response onset times with respect to the grip onset in the ventral cingulate cortex and the SMA. The histograms at left represent all the cells with activity changes in relation to the grip task, whereas in the histograms at right only the cells defined as hand related by their sensorimotor features are included.
TABLE 1.  Responses to the perturbation

<table>
<thead>
<tr>
<th></th>
<th>Postperturbation</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Increase</td>
<td>Decrease</td>
<td>Preperturbation</td>
<td></td>
</tr>
<tr>
<td>Cingulate</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proprioceptive</td>
<td>9/35 (26)</td>
<td>2/35 (6)</td>
<td>0/35 (0)</td>
<td></td>
</tr>
<tr>
<td>Cutaneous</td>
<td>6/6 (100)</td>
<td>0/6 (0)</td>
<td>0/6 (0)</td>
<td></td>
</tr>
<tr>
<td>Unidentified</td>
<td>6/24 (25)</td>
<td>2/24 (8)</td>
<td>0/24 (0)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>21/65 (32)</td>
<td>4/65 (6)</td>
<td>0/65 (0)</td>
<td></td>
</tr>
<tr>
<td>SMA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cutaneous</td>
<td>2/3 (66)</td>
<td>0/3 (0)</td>
<td>0/3 (0)</td>
<td></td>
</tr>
<tr>
<td>Unidentified</td>
<td>4/41 (10)</td>
<td>3/41 (7)</td>
<td>2/41 (5)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>14/71 (20)</td>
<td>6/71 (8)</td>
<td>5/71 (7)</td>
<td></td>
</tr>
</tbody>
</table>

Values in parentheses are percentages. SMA, supplementary motor area.

9, the distribution of the latencies was similar in both regions. In the CMAv 86% of the neurons responded to the perturbation with a delay of 50–55 ms, compared with 57% in the SMA.

Preperturbation effects

Of the neurons tested with the perturbation, 61 in the SMA and 48 in the CMAv were recorded while the monkeys exhibited a clear preparatory behavior in anticipation of the perturbation. To prevent excessive slip of the object, the monkeys typically developed two preparatory strategies. They either positioned the object higher in the window during the static phase or they increased their grip force before the perturbation or both. Figure 10A illustrates these two strategies in a single block of perturbed trials compared with unperturbed trials.

A change in position was considered as significant (P ≤ 0.01) if the mean position measured 50 ms before the perturbation on perturbed trials exceeded the mean position under control conditions. The mean increase of position for both monkeys was 2.44 ± 0.82 mm. The increase in grip force was considered as significant if the mean grip force on perturbed trials exceeded the mean grip force on control trials by >2 SD. The onset of the grip force increase was defined as the point at which the mean grip force on perturbed and unperturbed trials diverged by 2 SD. As shown in Fig. 10B, the onset of the anticipatory grip increase varied between 110 and 970 ms before the perturbation and the magnitude of the grip increase corresponded to 6–115% of the force used on unperturbed trials. In general, the increased grip force strategy was used more often than the position strategy. Table 2 summarizes the occurrence of these strategies associated with recording from the cingulate area and SMA in both monkeys.

FIG. 7. Mean discharge frequency of a cingulate cell with a cutaneous receptive field covering the glabrous skin of the hand, showing an increase of activity and a greater response to perturbation with the smooth surface texture. For each texture, mean grip force traces are superimposed and aligned on the perturbation onset (thin lines: unperturbed conditions; thick lines: perturbed condition).
These preparatory changes in position and grip were influenced by the weight of the object and the force of the perturbation, but not by changes in texture. In one monkey, anticipatory strategies were tested with two object weights (65 and 115 g). Whereas the position strategy was frequently used with the 115-g weight, with the lighter weight no difference in position was observed between the perturbed and the unperturbed trials. The anticipatory grip increase before the perturbation occurred later and the monkey generated less grip force with the 65-g weight compared with the 115-g weight. In the second monkey, two force-pulse perturbations were tested (1.5 and 2 N). The increase in the pulse magnitude increased the probability of a preparatory position change. Figure 10C illustrates two series of five conditions, including three control conditions and two perturbed conditions with two pulse magnitudes. With the stronger force-pulse perturbation, the mean position in the window was higher than with the weaker perturbation. Also, when the perturbation was more forceful, the anticipatory grip force increase occurred earlier and the monkey generated more force (Fig. 10D).

DISASSOCIATION BETWEEN THE PREPARATORY BEHAVIOR AND THE NEURONAL RESPONSES. Despite these anticipatory strategies, only five cells in the SMA demonstrated a change in neuronal activity before the actual perturbation. Figure 11 shows one of these cells, which increased its firing rate before the perturbation onset. This cell, whose activity was time locked to the grip force onset, appeared to receive input from the palmar interossei muscles. As for the other cells, the significance of this increase in neuronal activity before the perturbation is rather difficult to define. In the case of the neuron illustrated in Fig. 11, the change in the neuronal activity preceding the perturbation was not related to the grip force exerted by the monkey. A correlation calculated between the mean firing frequency and the mean grip force during the preparatory period did not reveal any significant relation. Furthermore, when the perturbation was tested with a heavier object weight, the preparatory grip force increased but not the neuronal activity. For three of the five anticipatory cells the increase of neuronal activity before the perturbation was associated with a short inhibition time locked to the onset of the perturbation. For one of the anticipatory cells, a relationship between the increase of the neuronal activity before the perturbation and the timing of the perturbation was observed. Three delays of perturbation were tested (400, 600, and 900 ms). The increased in the perturbation was associated with greater anticipatory activity in the cell (Fig. 12).

In the cingulate cortex, no evidence of preparatory change of activity was observed, although the animal displayed clear anticipatory behavior during recording of 48 of the 65 cells tested.

DISCUSSION

Hand representation in the SMA and in the CMAv

The present study provided a comparison of the neuronal activity in two medial motor areas, the SMA and the CMAv, during performance of a prehension task in monkeys. Neurons either with receptive fields on the hand or with activity modulation during grasping were found in both medial motor areas. One group was located in the medial interhemispheric cortex of area 6 and was identified as the hand region of the SMA (Luppino et al. 1991; Mitz and Wise 1987), whereas the other group occupying the lateral CMAv (Cadoret and Smith 1991a,b; He et al. 1995) or area 24d (Matelli et al. 1991). In the cingulate cortex, the
proprioceptive inputs than cutaneous afferents. The discharge patterns during grasping and lifting were relatively similar. From the distribution of the onset times of activity, it appeared that neurons in both regions were recruited at about the same time during performance of the task. Most cells could be considered as short-lead neurons because they changed their activity within much less than the 500 ms before movement onset reported by Okano and Tanji (1987) in the SMA. During a key press task, in a self-paced condition, Okano and Tanji reported that 73% of the SMA neurons exhibited a short-lead activity change. In contrast, in the CMAv, we found more short-lead neurons (71%) than the 47.6% observed by Shima et al. (1991). However, this difference in the proportions is probably due to different populations of neurons. Shima et al. (1991) included in the posterior cingulate cortex the neurons from the dorsal and the CMAv, whereas in the present study all neurons were recorded in the CMAv. This similar temporal relationship between SMA and CMAv neurons suggests a parallel activation of these areas in prehension.

The similarity between the SMA and the CMAv should not be construed to imply that these medial cortical motor areas are functionally homogeneous. For example, a difference between the two groups of neurons was found in the proportion of phasic-tonic neurons. In the SMA 20% of cells discharged in a phasic-tonic pattern, similar to the motor cortex neurons (from Picard and Smith 1992a), whereas in the CMAv this proportion comprised only 8%. Although this difference might be influenced by the cell sampling during data collection, it might also reflect a functional difference between the SMA and the CMAv. SMA neurons might therefore be more involved in tonic grasping and holding, whereas CMAv neurons may be more concerned with the phasic grasping and releasing.

**Sensorimotor integration**

Although SMA and CMAv neurons demonstrated clearly modulated activity in relation to the task, there appeared to be no clear correlation between discharge frequency and the force of the precision grip, although in humans a correlation was found between cerebral blood flow and finger forces in the posterior part of SMA and in the dorsal bank of the posterior cingulate sulcus (Dettmers et al. 1995). Picard and Smith (1992a) found that the activity of ∼40% of the motor cortical units with proprioceptive receptive fields was correlated with pinch force, whereas in the present study the neurons in both the SMA and CMAv were poorly related to the grip force magnitude, even though both regions demonstrated responses restricted to the distal intrinsic muscles of the hand by ICMS. However, the thresholds to evoke motor responses were most frequently >15 μA (Hummelsheim et al. 1986b; Luppino et al. 1991) and the train duration was >30–40 ms. This suggests that the corticospinal efferents from the SMA and CMAv neurons are either less numerous or less efficient than those from area 4 motor cortex neurons (Picard and Smith 1992a).

Fewer medial wall motor area neurons received cutaneous input compared with motor cortex cells, although some of these neurons showed activity changes in relation to the grasped surface texture or demonstrated vigorous responses...
to the slip of the object between the fingers. The small number of cutaneous neurons seems to indicate that SMA and CMAv are less implicated in the modulation of the grip forces based on the cutaneous feedback. SMA and CMAv neurons received essentially sensory inputs from the muscle and tendon afferents. Given the importance of proprioceptive input for both the perception of movement and position (Gandevia et al. 1990, 1992), the SMA and the CMAv neurons with somatosensory receptive fields may be more involved in relaying feedback signals from hand muscles during prehension than in initiating motor strategies based on expectancy. These latter functions may be performed by the more rostral motor areas of the medial wall.

**Table 2. Anticipatory strategies**

<table>
<thead>
<tr>
<th>Strategies</th>
<th>Blocks of Trials Associated With Cingulate Cells</th>
<th>Blocks of Trials Associated With SMA Cells</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Percent</td>
</tr>
<tr>
<td>Position + Grip</td>
<td>17</td>
<td>35</td>
</tr>
<tr>
<td>Grip</td>
<td>23</td>
<td>48</td>
</tr>
<tr>
<td>Position</td>
<td>8</td>
<td>17</td>
</tr>
<tr>
<td>Total Grip</td>
<td>40</td>
<td>56</td>
</tr>
<tr>
<td>Total Position</td>
<td>25</td>
<td>42</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Strategies</th>
<th>Monkey 1</th>
<th>Monkey 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Percent</td>
</tr>
<tr>
<td>Position + Grip</td>
<td>38</td>
<td>43</td>
</tr>
<tr>
<td>Grip</td>
<td>37</td>
<td>42</td>
</tr>
<tr>
<td>Position</td>
<td>13</td>
<td>15</td>
</tr>
<tr>
<td>Total Grip</td>
<td>75</td>
<td>21</td>
</tr>
<tr>
<td>Total Position</td>
<td>51</td>
<td>16</td>
</tr>
</tbody>
</table>

SMA, supplementary motor area.

**Reflex responses**

As reported by Wise and Tanji (1981) for units related to leg movements, grip-related SMA and cingulate neurons were less sensitive to perturbations than primary motor cortical neurons. The proportion of cells responsive to perturbations was lower in the SMA (28%) than either the CMAv (38%) or the motor cortex (61% from Picard and Smith 1992b). In both areas, the magnitude of the reflex responses was lower than the responses reported in the motor cortex (Picard and Smith 1992b), which may reflect the smaller proportion of cells receiving cutaneous input. It has been shown that cutaneous responses to perturbations of handheld objects provide a stronger excitation of motor cortical cells than the feedback originating from the proprioceptive receptors (Picard and Smith 1992b). That is, cells with cutaneous receptive fields were more sensitive to perturbations applying tangential forces to the skin than the neurons receiving proprioceptive afferents from intrinsic and extrinsic hand muscles.

The reflexlike grip force increases evoked by perturba-
FIG. 11. Mean discharge frequency of 1 SMA neuron whose activity increased in relation to the preparatory grip force increase. The mean object displacement, load force, and grip force traces are superimposed for the 1st control (thin lines), perturbed (medium lines), and 2nd control (thick lines) conditions.

Preparatory responses

The introduction of a predictable perturbation during the precision grip triggered anticipatory responses in both monkeys. These preparatory responses consisted of increasing the grip force and raising the object to a higher position before the perturbation onset. These two strategies were complementary and both reduced the probability of an error in which either the object would slip from the hand or the hand would be displaced from the window. Johansson and Westling (1988) reported that anticipatory grip force increases were modulated as a function of the weight and the texture of the grasped object in human subjects. In the present experiment a modulation of the anticipatory strategy was also observed with different object weights or perturbation forces but not with different textures. It is probable that in the static holding phase was not long enough to observe variations influenced by the changes in texture, or the changes in friction were not great enough to affect the anticipatory responses.

It seems reasonable to assume that the anticipatory responses were triggered from memory, because no specific stimuli in the task were used to alert the animal of an impending perturbation. The only available cues were derived from the experience obtained from the first trial. Subsequently each trial served as a memory trace for the suc-
FIG. 12. Differential effects of the perturbation delay on the anticipatory neuronal responses in 1 SMA neuron. The 3 delays of perturbation were 400, 600, and 900 ms after the entrance in the window. Mean object displacement, load force, and grip force traces are superimposed for these 3 perturbed conditions.

The authors gratefully acknowledge the technical assistance of the late R. Bouchoux, C. Gauthier, J. Jodoin, L. Lessard, and G. Messier in the execution of this study. This research was supported by a grant to the Groupe de Recherche en Sciences Neurologiques from the Medical Research Council of Canada and a fellowship from the Fonds pour la Formation de Chercheurs et l’Aide à la Recherche Groupe de Recherche sur le Système Nerveux Central.

Address for reprint requests: A. Smith, Centre de Recherche en Sciences Neurologiques, Département de Physiologie, Université de Montréal, Case Postale 6128, succ Centre Ville, Montreal, Quebec H3C 3T8, Canada.

Received 19 June 1996; accepted in final form 19 September 1996.

REFERENCES


