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RAPID PUBLICATION

Representation of Tactile Signals in Primate Supplementary Motor Area

RANULFO ROMO, SALVADOR RUIZ, PATRICIA CRESPO, ANTONIO ZAINOS, AND HUGO MERCHANT
Instituto de Fisiología Celular, Universidad Nacional Autónoma de México, 04510 Mexico D.F. Mexico

SUMMARY AND CONCLUSIONS

1. We have studied the neuronal activity in the supplementary motor area (SMA) of two monkeys who categorized the speed of moving tactile stimuli delivered to the glabrous skin of the hand ipsilateral to the site of cortical recording and contralateral to the responding arm.

2. A large number of SMA neurons responded to the stimuli of all speeds (176 of 522) but only when those stimuli controlled behavior.

3. A second class of SMA neurons responded differentially in the categorization task (35 during the stimuli and 51 during the reaction time period) and predicted its outcome.

4. To dissociate the interrupt target switches presses from the tactile categorization responses, sixteen neurons, which responded to the stimuli in all speeds, and 11 neurons, which discharged differentially, were tested in a visual control task. None of these two classes of neurons responded in this situation.

5. It is concluded that the SMA ipsilateral to sensory input and contralateral to the responding arm is involved in the sensory decision process in this somesthetic categorization task.

INTRODUCTION

The results of neurophysiological studies made in primate supplementary motor area (SMA) suggest that this region of the frontal cortex is involved in the preparation and execution of movements (Alexander and Crutcher 1990; Kurata and Tanji 1985; Roland et al. 1980; Romo and Schultz 1987, 1992; Tanji and Kurata 1985; Tanji et al. 1980). For example, it has been shown that neurons in the SMA respond tightly to visual, auditory, and somesthetic stimuli when the animal uses these signals to initiate a movement (Kurata and Tanji 1985; Romo and Schultz 1987; Tanji and Kurata 1982, 1985). Also, it has been shown that a large number of neurons of the SMA discharge in instruction-delay-trigger paradigms (Alexander and Crutcher 1990; Romo and Schultz 1987, 1992; Tanji and Kurata 1985; Tanji et al. 1980). Most of these responses occur during the delay period and reflect the preparatory activity for movement execution. According to these studies, the SMA is involved in the processing of sensory information at the sensory-motor transition, from which motor activity is transmitted to other brain structures and to the spinal cord (Dum and Strick 1991) for the performance of movements in a wide range of behavioral conditions. Despite this conclusion, most of the studies made in the SMA have addressed mainly its motor function. In a recent study, Mountcastle and colleagues have shown the presence in the motor cortex of neural signals, which reflect the sensory discrimination processing, in a sensory somesthetic discrimination task (Mountcastle et al. 1992). This paradigm had been used previously by these authors to investigate in combined psychophysical and neurophysiological experiments the neuronal operations in the postcentral gyrus during sensory discrimination (Mountcastle et al. 1990). We followed this strategy to address the question whether the SMA is involved in processing sensory information and its possible role in the sensory motor interface. We present below the results obtained from recording individual neurons of the SMA of two monkeys performing a tactile-categorization task. The results indicate that a large number of neurons in the SMA discharge during the somesthetic stimuli; and, that other neurons show differential discharges, which reflect the categorization of the somesthetic stimuli.

METHODS

General

Two monkeys Macaca mulatta (5.5 kg female and 6 kg male) were trained in a somesthetic task and, after they reached proficiency in the task, were implanted with a stainless steel chamber centered over the SMA, for single neuron recording and, with a head holder for head fixation. Also, stainless-steel teflon coated wires were chronically implanted in the muscles of the arm and forearm for EMG recordings; the wires were brought to a connector fixed in the scalp. The chamber, head holder, and connector were secured by screws and acrylic in the scalp. All these procedures were carried out under aseptic conditions and general anesthesia.

Somesthetic task

Animals were trained in a somesthetic task in which they were required to categorize the speed of a probe (2-mm round tip) moving across the glabrous skin of one of the fingers of the left, restrained hand, and indicate categorization by interrupting with their free hand one of two target switches placed at reaching distance and at eye level. The stimuli consisted of a set of 10 speeds from 12 to 30 mm/s, in a fixed traverse distance of 6 mm, direction and force (10 gf) in which half of them were considered as lower (12, 14, 16, 18, and 20 mm/s) and the rest as higher (22, 24, 26, 28, and 30 mm/s).

The left arm of the animal was secured in a half cast and palm up by a special design, which allowed glueing the back of the hand. The free hand operated an immovable key (elbow joint at ~90°) and two interrupt switches located at reaching distance (250 mm from the animal's shoulder) and eye level of the animal. The centers of the medial and lateral interrupt switches were located at 70 and 90 mm to the right of the midsagittal plane, respectively. Stimuli were presented by a tactile stimulator built in our laboratory for studying motion processing in the somatosensory system of primates (Romo et al. 1993).

Animals were introduced to the categorization task by teaching them to indicate detection of the moving tactile stimulus. In this initial training mode stimuli of two clearly distinct speeds (12 and 30 mm/s) were delivered across the glabrous skin, in different traverse distances (6–10 mm) and directions (distal to proximal and opposite, medial to lateral and opposite) and of constant force

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(10 gf). Once the animal could indicate detection (>95%) of these two speeds, he was taught to indicate whether the speed was 12 or 30 mm/s, by projecting his free hand to one of the two target interrupt switches (medial for 12 and lateral for 30 mm/s). The animal did so very quickly, and the more difficult task of categorization was then begun by presenting randomly the set of the ten speeds.

The trained monkey began a trial when he detected a step indentation of the skin by placing his free hand into an immovable key in a period of time, which did not exceed 1 s (see Fig. 1*A*). He maintained this interruption through a variable delay period (1-4 s) until the 2-mm probe moved at any of the ten speeds. He indicated the detection of the end of the motion by removing his hand from the key (in a period of time of 600 ms), and whether the speed was higher or lower by projecting his free hand to one of the two target switches (medial switch was used to indicate lower and the lateral one for higher speeds) within 1 s. The animal was rewarded for correct categorization of the speed by a drop of water. The tactile stimuli were neither visible nor audible in any part of the task. The numbers of correct and wrong categorizations in a run [which consisted of 10 trials per class (speeds) presented randomly] were used to construct psychometric functions. These psychometric functions were plotted as the percentage of judgments of the speed being higher than 20 mm/s (Fig. 1*B*), or lower than 22 mm/s (Fig. 3*C*).

Neurophysiological recordings

The activity of single neurons was recorded extracellularly with glass-coated platinum-iridium electrodes (2-3.5 MΩ), which were passed transdurally into the SMA. Neural signals from the microelectrode were conventionally amplified, filtered, and monitored with oscilloscopes and heard with earphones. Neuronal discharges were converted into standard digital pulses by means of an adjustable Schmitt trigger. EMGs were collected through chronically implanted wires in flexor and extensor muscles of the moving arm in all recording session. EMG activity was filtered, rectified, displayed on conventional oscilloscopes, and converted into digital pulses by an adjustable Schmitt trigger. Stimulus, behavioral control and data collection were carried out through a personal computer using standard computer interfaces. The time intervals between neural EMGs and between behavioral events were measured with a resolution of 100 μs collected and stored. On-line raster displays were generated on a conventional monitor. Completed data files were copied for off-line analysis.

Analysis

We determined whether a neuron was active in the task by examining the raster plots in reference to each behavioral events: initial probe indentation of the skin, detection of the indentation by closure of the key, beginning and ending of the moving tactile stimuli, key release (reaction time), end of movement time (interruption of the target switches). A second estimate of a neuron's response was made by convolving the spike trains for each trial with a Gaussian kernel (Silverman 1986). The resulting spike density function provides an estimate of the probability spike occurrence over time. Quantitative analysis was then performed on the mean and standard deviation of the spike density functions referred to each epoch of the task. The neuronal responses were then classified according to the correlation between the increases and decreases of the absolute mean values in the spike density of the different epochs of the task. The statistical significant differences in spike density in two time epochs (control period and the suspected change) were assessed with a sliding window procedure on the basis of the nonparametric one tailed Wilcoxon matched-pairs signed rank test ($P < 0.001$). Also, the nonparametric test of Kruskal-Wallis was used to determine significant differences ($P < 0.05$) between the responses occurring during the stimuli, together with a test of multiple comparisons (Siegel and Castellan 1988).

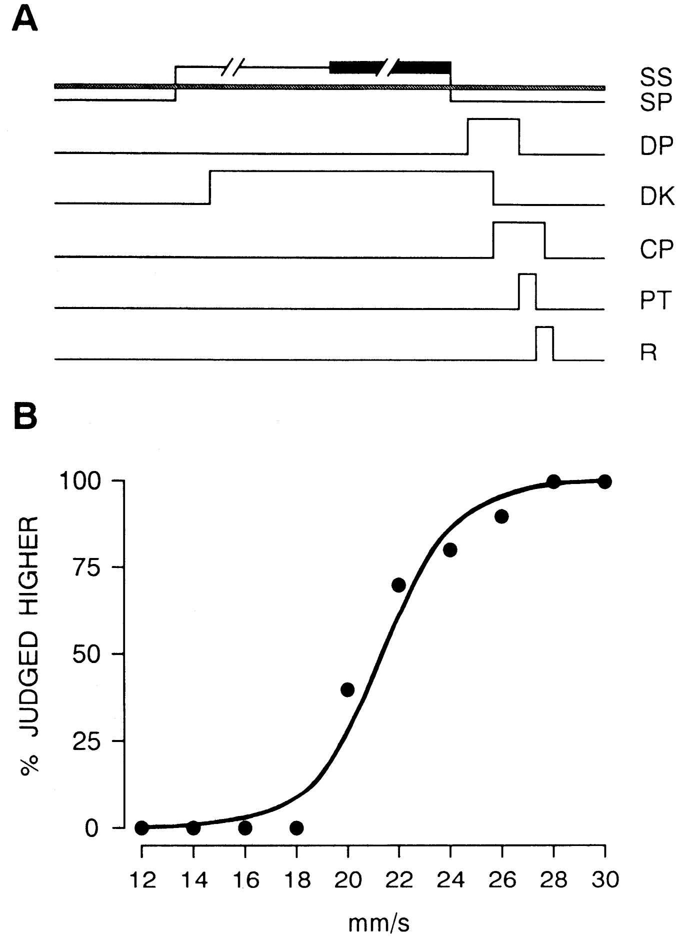

FIG. 1. *A*: schematic outline of the tactile categorization task. Bold broken line indicates variable speed across the glabrous skin. SS, skin surface; SP, stimulus probe; DP, detect period; DK, detect key; CP, choice period; PT, project to target; R, reward. *B*: averaged results during the tactile categorization task of *A*. These data were collected during the study of the neuron shown in Fig. 2*A*. The data points indicate the percent trials in which the speed of the somesthetic stimuli was judged as higher. The curve is a logistic function fitted to these data points ($R^2 > 0.8$, $P < 0.001$).

RESULTS

General

During performance of the tactile categorization task, 522 neurons were recorded in the SMA contralateral to the moving arm; 328 of these responded in the task. Of these, 132 neurons responded in the period of skin indentation, 103 during the delay period, 176 during the period of skin stimulation, 195 during the reaction time, 108 during the movement time, 27 to the interruption of the target switches and 21 to the liquid reward. The sum of these classes exceeds the total number of reactive neurons because of the multiple relationships. We describe here those neurons that responded during the period of the stimuli, during the reaction time, movement time, and also those which showed differential responses to different speeds of the tactile stimuli.

Somesthetic responses

As indicated above, 176 neurons in SMA ipsilateral to the stimulated hand responded during the stimuli; 124 increased and 52 decreased their frequency of discharge with latencies of 162.487 ± 10.87 ms and 181.48 ± 29.7 ms (±SE), respectively. One hundred and forty-one of these neurons responded to all the speeds (Fig. 2*A*); 35 neurons responded differentially for higher (22 neurons) or lower (13 neurons) speeds (Fig. 3, *A* and *C*). A striking characteristic for these neurons is that few of them (3 of 58) discharged (although much weaker responses than in the tactile categorization task) when the same stimuli were delivered in the passive mode (Fig. 2*B*). In the passive mode the stimuli delivered were identical to those delivered in the categorization task, but the animal's key was removed and the arm movements were restricted. Also, in a visual control task, we tested 16 of the neurons that responded to all stimulus speeds and 11 of those neurons that responded differentially during the tactile categorization task. In this situation, each trial began as in the somesthetic categorization task, but one of the two target interrupt switches was illuminated after detection of the skin indentation, continued during the delay period, and turned off when the probe was lifted off from the skin. This condition instructed the animal which target interrupt switch was required to be pressed for reward. Those neurons that responded to all the speeds did not respond in the visual, control task, but the reaction time component was present (Fig. 2, *C* and *D*). None of the neurons that showed differential responses discharged in this task (Fig. 3*B*). None of the responses occurring during the stimuli were correlated with earlier EMG activations of muscles of the arm and forearm of the responding arm.

Arm responses

One hundred and ninety-five neurons responded during the RT of which 156 increased and 39 decreased their discharge rates. One hundred forty-four of these neurons discharged during the reaction time, in all classes, and 51 responded differentially during the reaction time, either after lower (21 neurons) or higher stimulus speeds (30 neurons). One hundred and eight neurons responded during the movement time of which 80 increased and 28 decreased their activity. Ninety-six of these neurons responded after all stimulus speeds; 12 did so differentially: 6 for lower speeds and 6 for higher. None of these units were tested in the visual control task.

DISCUSSION

We employed in this study a sensory task to investigate the processing of somesthetic information in the SMA ipsilateral to the stimulated hand. A striking finding was that a large number of neurons responded to the moving tactile stimuli. A second finding is that neurons of the SMA reflect differentially the categorization of the speeds of the moving tactile stimuli. We focus the discussion on these two issues.

Previous studies investigating the functional role of SMA have demonstrated that neurons in this cortical motor area discharge to sensory cues when the animal responds to those cues by performing a movement (Alexander and Crutcher 1990; Kurata and Tanji 1985; Romo and Schultz 1987, 1992; Tanji and Kurata 1985; Tanji et al. 1980). We have found in SMA ipsilateral to the stimulated hand many neurons responding to moving tactile stimuli but only during the categorization task. The fact that only a few SMA neurons responded to the somesthetic stimuli when the latter were delivered passively (3 of 58), suggests that the

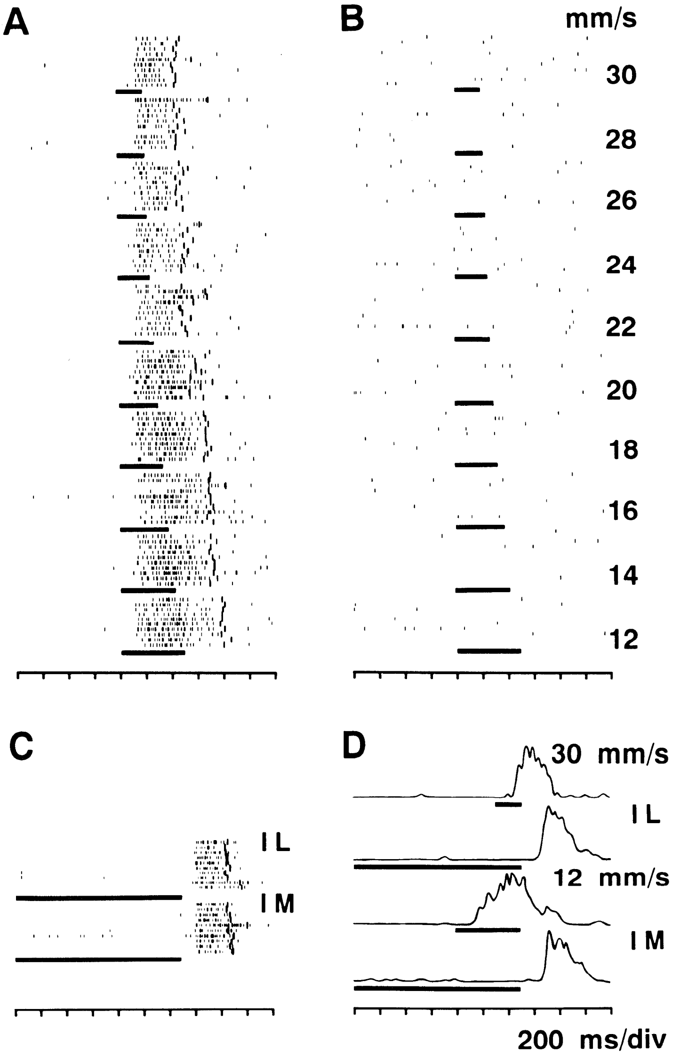

FIG. 2. *A*: responses of a supplementary motor area (SMA) neuron during the tactile categorization task of Fig. 1*A*. Horizontal lines represent the duration of the moving stimuli. Neuronal impulses indicated as vertical tics. Larger tics correspond to the moment the animal released the key to indicate categorization of the speed by projecting his free hand to 1 of 2 switches. Each line represents 1 trial; the 10 trials per class (speed) were presented randomly. *B*: same SMA neuron studied with the same classes of stimuli as in *A* but delivered in the passive, nonworking state. *C*: same SMA neuron was tested in a visual task, in which the animal was visually instructed which target interrupt switch had to be pressed for reward. Each trial began by illuminating 1 of the 2 target switches after detection of skin indentation and ending by lifting off the probe from the skin. IM and IL indicates illumination of medial or lateral interrupt target switches, respectively. Long horizontal lines indicates the period of the illumination of the target switch. *D*: spike density functions for the higher and lower speeds of *A* and the 2 classes of *C*. Horizontal lines indicate the period of the somesthetic stimuli and the instructed period. Vertical ticks correspond to neuronal impulses and larger vertical ticks the exact moment the animal released the key. Stimulus parameters: 6 mm of traverse distance, 10 gf of constant force; the scanning was from distal to proximal on the distal pad of D3 of the left hand.

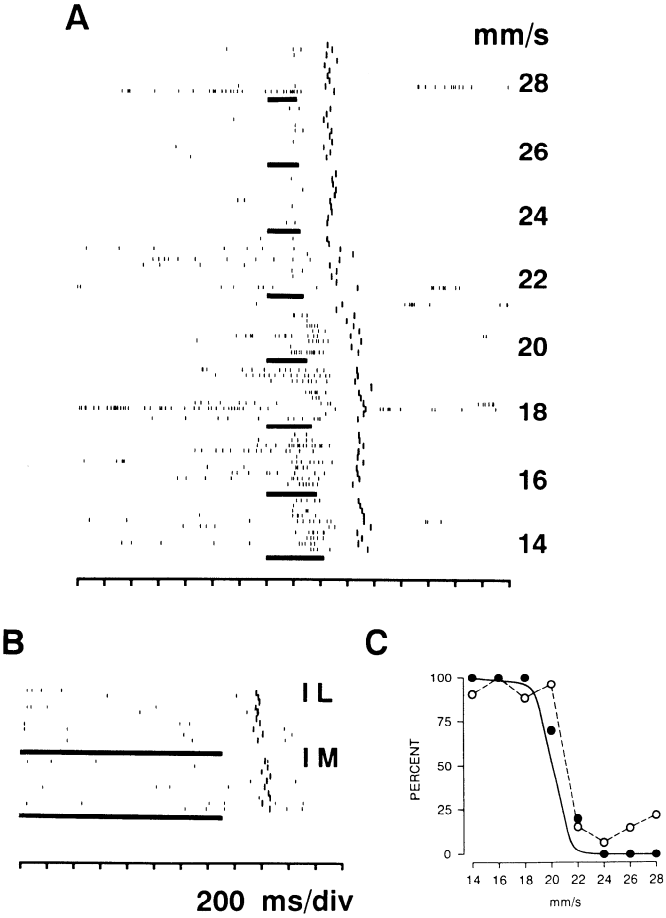

FIG. 3. Differential responses of a SMA neuron during the tactile categorization task of Fig. 1*A*. Horizontal bars indicate the duration of the moving tactile stimuli. Neuronal impulses indicated as vertical tics. Larger tics correspond to the moment the animal released the key to indicate categorization of the speed by projecting his free hand to 1 of 2 switches. *B*: same SMA neuron was tested in the visual control task, in which the animal was visually instructed which target interrupt switch had to be pressed for reward. Each trial began by illuminating 1 of the 2 target switches after detection of skin indentation and ended by lifting off the probe from the skin. IM and IL indicates illumination of medial or lateral interrupt target switches, respectively. Long horizontal lines signals the period of the illumination of the target switch, and the end of the lines indicates the end of skin indentation. Vertical ticks correspond to neuronal impulses and larger vertical ticks the exact moment the animal released the key, *C*. Averaged results during the tactile categorization task of *A*. Filled circles indicate the percent of trials in which the speed of the stimuli was judged lower and the open circles indicate the mean percent response of the neuron. Stimulus parameters: 6 mm of traverse distance, 10 gf of constant force; the scanning was from proximal to distal on the distal pad of D4 of the left hand.

SMA is engaged in the sensory processing mechanism of the present task. This is also supported by the fact that none of the SMA neurons, which responded to the somesthetic stimuli during the tactile categorization task, did so when the animal closed a target switch after previous visual instruction.

The second finding of interest in this study is that there are neurons in the SMA ipsilateral to the stimulated hand whose discharge reflects the categorization of the speed of the stimuli, for they discharge exclusively for lower or higher speeds during the stimuli or during the reaction time. A possible explanation for this finding is that these neurons reflect the intention of the animal to interrupt the left or right (medial and lateral in our experimental conditions) target switches (Alexander and Crutcher 1990; Matsuzaka et al. 1992) rather than the categorization of the speed of tactile stimuli. However, these neuronal discharges seem to be linked directly to the categorization of the tactile stimuli, since they did not discharge when the animal interrupted the target switches after previous visual instruction. This result suggests that the SMA is engaged in the sensory decision process of this learned somesthetic task.

Finally, we emphasize that in this task the SMA neuronal activity was recorded in the hemisphere ipsilateral to the stimulated hand and contralateral to the performing arm. This means that somesthetic information has to be transferred from the sensory somesthetic hemisphere to the motor one, very likely via the corpus callossum (reviewed by Mountcastle et al. 1992). This could occur by the well known connections between somesthetic parietal areas between the two hemispheres. Also the somesthetic areas have direct connections with the SMA (Jones 1984; Mountcastle et al. 1992; Wisendanger et al. 1987). Thus information processed by the sensory hemisphere could first be projected to the SMA in the sensory hemisphere (we have found similar results in a data base of 628 studied neurons in 2 monkeys) and then to the SMA contralateral to the responding arm via their reciprocal connections (McGuire et al. 1991). Experiments are in progress to elucidate the dynamic processing of somesthetic information during execution of this task in parietal and frontal motor areas of both hemispheres. This study extends and confirms the observation made by Mountcastle and colleagues in that it is possible to reveal the output or intermediary mechanisms associated with somatosensory discrimination in the brain (Mountcastle et al. 1992).

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Address for reprint requests: R. Romo, Instituto de Fisiología Celular, Universidad Nacional Autónoma de México, Apartado Postal 70-253, 04510 Mexico D. F., Mexico.

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