Categorical Perception of Somesthetic Stimuli: Psychophysical Measurements Correlated with Neuronal Events in Primate Medial Premotor Cortex

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In this paper we describe a type of neuron of the medial premotor cortex (MPC) that discharged differentially during a categorization task and reflected in their activity whether the speed of a tactile stimulus was low or high. The activity of these neurons was recorded in the MPC contralateral (right MPC, $n = 88$) and ipsilateral (left MPC, $n = 103$) to the stimulated hand of four monkeys performing this somesthetic task. Animals performed the task by pressing with the right hand one of two target switches to indicate whether the speed of probe movement across the skin of the left hand was low or high. Differential responses of MPC neurons occurred during the stimulus and reaction time period. We used an analysis based on signal detection theory to determine whether these differential responses were associated with the animal's decision. According to this analysis, 104 of the 191 neurons (right MPC, $n = 48$; left MPC, $n = 56$) coded the categorization of the stimulus speeds (categorical neurons). In a light instruction task, we tested the possibility that the categorical neurons ($n = 71$) were associated with the intention to press, or with the trajectory of the hand to one of the two target switches used to indicate categorization. In this situation, each trial began as in the somesthetic categorization task, but one of the two target switches was illuminated beginning with 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 switch was required to be pressed for reward. Very few neurons (14 of 71) maintained their differential responses observed in the categorization task. Some categorical neurons ($n = 6$) were also studied; the animal categorized the tactile stimulus speeds, but knew in advance whether the stimulus speed was low or high (categorization + light instruction). This was made by illuminating one of the two target switches which was associated with the stimulus speed. The categorical response was considerably attenuated in this condition. Interestingly, during the delay period, these neurons reflected in their activity whether the stimulus was low or high. A number of the categorical MPC neurons ($n = 30$) were studied when the same set of stimuli, used in the categorization, were delivered passively. None of these neurons responded in this condition. These results suggest that the MPC, apart from its well-known role in motor behavior, is also involved in the animal's decision during the execution of this learned somesthetic task.

Introduction

This study is part of a research program aimed at understanding the cortical processing of somesthetic information in behaving monkeys. With this purpose, we designed a sensory somesthetic task in which the neuronal events in somatic and motor cortical areas could be correlated with the sensory performance (Romo *et al.*, 1996). Animals performed the task by pressing one of two target switches to indicate whether one of ten speeds of probe movement across the glabrous skin of the hand was low or high. The sensory performance was evaluated with psychometric techniques, and the motor response was assessed by measuring the reaction (RT) and motor (MT) times. The results indicate that

the sensorimotor performance can be measured in a reliable manner in this task. Thus, this sensory task seems to be well suited for studying the coding of the parameters of the stimuli in the evoked activity of the somatosensory (SI) cortex, and the neural signals associated with the animal's decision.

We have recorded the responses of neurons of SI cortex with receptive fields on the finger tips during the categorization of the stimulus speeds (Romo *et al.*, 1996). The results indicate that a class of neurons of SI cortex respond by increasing their impulse rates as a function of the stimulus speeds. However, the same class of neurons of SI cortex also responded when the same stimuli were delivered passively. These findings suggest that the neural processes associated with the ability to categorize somesthetic stimuli must occur in more central areas linked to SI cortex. These central structures include the somesthetic areas of the posterior parietal lobe, motor areas of the frontal lobe, as well as subcortical structures . Thus, it would be interesting to study the flow of the somesthetic information processing from SI to those cortical and subcortical structures anatomically connected to it during the categorization of tactile stimuli.

We have focused our attention on the medial premotor cortex (MPC), a cortical motor area which may also be involved in the somesthetic categorization task. Anatomical studies have shown a rich connectivity between somesthetic areas of the parietal lobe and the MPC (Jones and Powell, 1969; Pandya and Kuypers, 1969; Jones *et al.*, 1978; Jürgens, 1984; Petrides and Pandya, 1984; Pons and Kass, 1986; Cavada and Goldman-Rakic, 1989; Luppino *et al.*, 1993). Interestingly, in a preliminary study (Romo *et al.*, 1993b), we recorded neurons in the MPC that responded during this categorization task. Of special interest was the recording of a type of neurons that reflected in their activity the categorization of the stimulus speeds.

We have pursued this problem by recording from the MPC in monkeys working in the somesthetic categorization task. In this paper, we analyze the activity of these neurons in terms of signal detection theory (Green and Sweets, 1966), to determine whether they encode the categorization process. The results indicate that this is true. In addition, we observe that most of these categorical neurons are not associated with the motor responses used by the animal to indicate categorization. Finally, we found that these categorical responses are context dependent, since they occurred exclusively during the categorization task. Therefore, these findings suggest that the MPC, apart from its well-known role in motor functions, is also involved in the sensory decision process in this learned somesthetic task.

Materials and Methods

Somesthetic task

Four monkeys (*Macaca mulatta*; 5.5 kg female and 4.5–5.5 kg males) were trained to perform a somesthetic task in which they were required to categorize the speed of a probe (2 mm round tip) moving across the
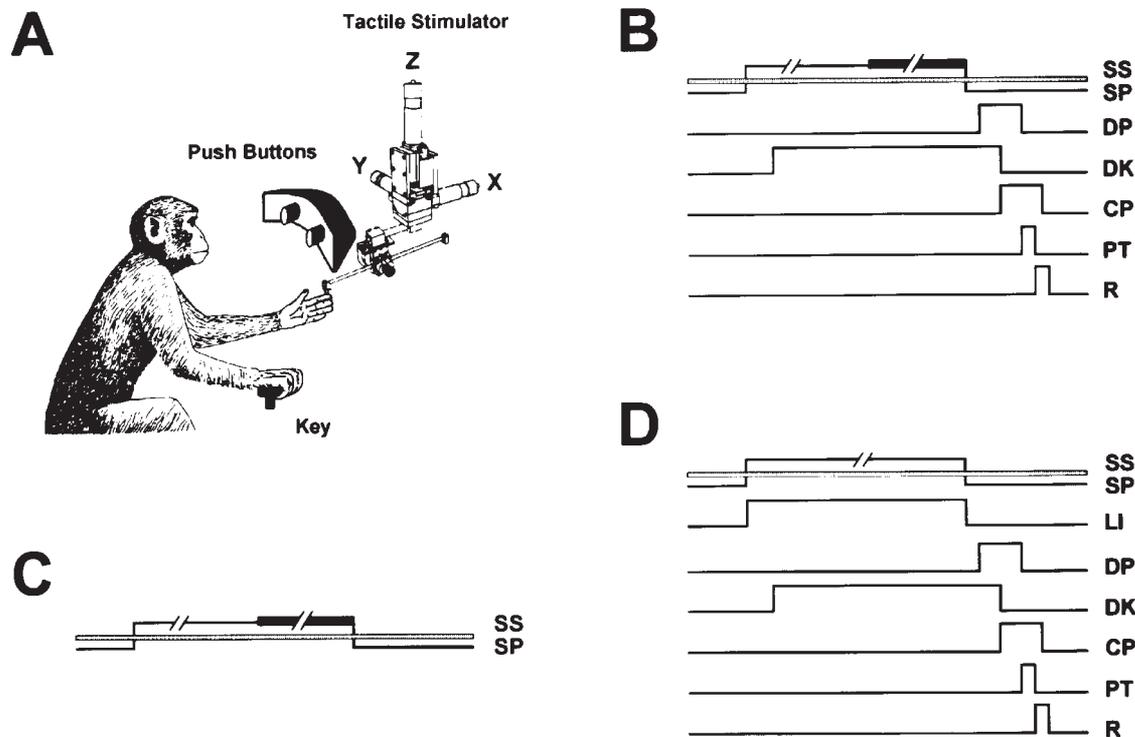
Figure 1. (A) Drawing of a monkey working on the tactile categorization task. (B) Schematic outline of the task. Bold broken line indicates variable speed movement of the stimulus probe across the glabrous skin. The broken line preceding the bold broken line means variable delay period (1.5–4.5 s). SS, skin surface; SP, stimulus probe; DP, detect period; DK, detect key; CP, choice period; PT, project to target; R, reward. (C) Passive delivery of the stimulus set. (D) Light instruction task, the same sequence as in (A), but without the moving tactile stimuli. Descriptions of the task sequences, stimulus set and sensory-motor performance are given in the text.

glabrous skin of one of the fingers of the left, restrained hand, and indicate the speed by interrupting with the right hand one of two target switches (Fig. 1A).

The left arm of the animal was secured in a half cast and maintained in a palm-up position (Romo *et al.*, 1993a). The right hand operated an immovable key (elbow joint at ~ 90°) and two target switches (the centers located at 70 and 90 mm to the right of the midsagittal plane) placed at reaching distance (250 mm from the animal's shoulder and at eye level). The stimuli consisted of a set of 10 speeds from 12 to 30 mm/s, in a fixed traverse distance (6 mm), direction and force (20 g) in which half of them were considered as low (12, 14, 16, 18 and 20 mm/s) and the rest as high (22, 24, 26, 28 and 30 mm/s). Stimuli were presented by a tactile stimulator built in our laboratory for studying motion processing in the somatosensory system of primates (Romo *et al.*, 1993a).

The trained monkey began a trial when he detected a step indentation of the skin of the left hand by placing his right hand into an immovable key in a period that did not exceed 1 s (Fig. 1B). He maintained this position through a variable delay period (1.5–4.5 s, beginning with detection of the indentation of the skin) until the probe moved at any of the 10 speeds. He indicated the detection of the end of the motion by removing his hand from the key within 600 ms, and whether the speed was low or high by projecting his right hand to one of the two switches within 1 s (the medial switch was used to indicate low speeds and the lateral one for high speeds). The animal was rewarded for correct categorization of the speed by a drop of water. The tactile stimuli were neither visible nor audible at any part of the task.

Passive Delivery of the Moving Tactile Stimuli
In this situation the stimuli were identical to those delivered during the categorization task, but the animal's key was removed and the right arm movements restricted (Fig. 1C).

Light Instruction Task
Animals were also required to execute movements from the key to the target switches in a light instruction task. In this situation, each trial

began as in the somesthetic task, but one of the two target switches was illuminated, beginning with the skin indentation, continued after detection of the skin indentation (variable delay period 1.5–4.5 s), and turned off when the probe was lifted off from the skin (stimulus triggers). This visual cue instructed the animal which target switch was required to be pressed for reward (Fig. 1D).

Surgery
After animals reached proficiency in the task (75–90% of correct responses), they were implanted with a stainless steel chamber to allow microelectrode penetrations for single neuron recording in the right and the left MPC, and with a head holder for head fixation. The center of the chamber was fitted to a rectangular hole (14 × 8 mm) made in the midline of the skull, exactly over the two MPCs. Stainless steel, Teflon-coated wires were chronically implanted into the extensor digitorum communis, biceps and triceps brachii muscles of the right arm for EMG recordings; the wires were brought to a connector fixed in the skull. The chamber, head holder and the connector were secured by screws and acrylic in the skull. All these procedures were carried out under aseptic conditions and sodium pentobarbital anesthesia (30 mg/kg).

Electrophysiological Recording
The activity of single neurons was recorded extracellularly with glass-coated platinum–iridium electrodes (2–3 MΩ), which were passed transdurally into the right or left MPC. Neuronal signals from the microelectrode were amplified, filtered and monitored with oscillo-scopes and earphones. Neuronal discharges were converted into digital pulses by means of a differential amplitude discriminator (DAD). A record was kept for the depth at which each neuron was isolated along the length of each penetration, from the first cell recorded after entering into the cortex. EMG from the forearm and arm muscles were recorded through the chronically implanted electrodes of the right moving arm in all recording sessions. In separate sessions, we recorded the EMG activity in different muscles of the shoulder, neck and dorsum during the categorization task (not shown; the behavior of these muscles during the
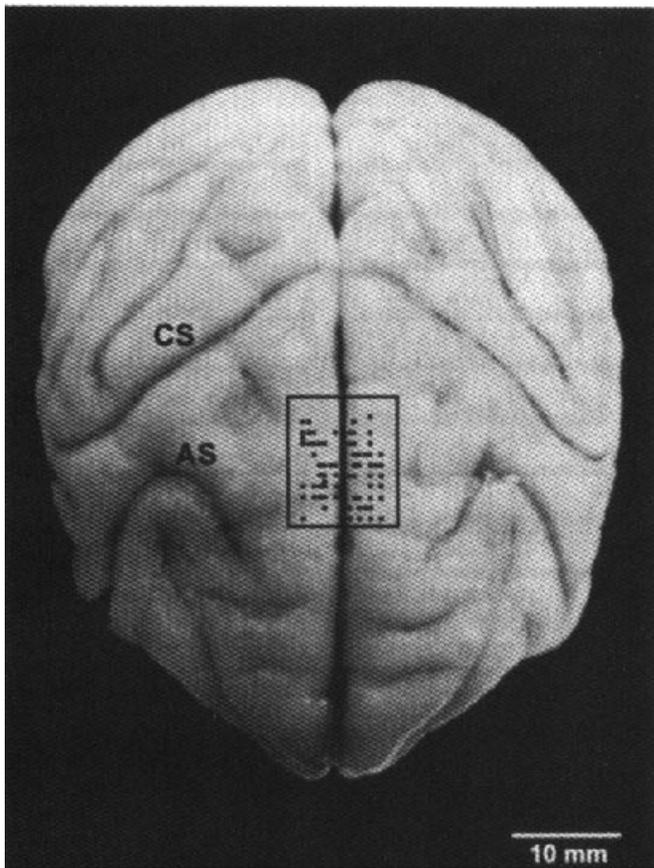
Figure 2. Top view of the medial premotor cortex surveyed in this study (monkey 4). Dots in the inset indicate microelectrode penetrations for the four animals in which categorical responses were recorded. AS, arcuate sulcus; CS, central sulcus.

Table 1

Differential responses of MPC neurons during the stimulus and arm movements in the categorization task

	Stimulus speeds		
	Low (12–20 mm/s)	High (22–30 mm/s)	Total
Right MPC			
Stimulus	21[a]	6	27
Stimulus + RT	16	5	21
RT	19	13	32
RT + MT	2	5	7
MT	0	1	1
Totals – right	58	30	88
Left MPC			
Stimulus	12[a]	11	23
Stimulus + RT	23	13	36
RT	8	25	33
RT + MT	1	5	6
MT	2	3	5
Totals – left	46	57	103
TOTALS	104	87	191

[a]Four neurons of the right MPC and three of the left MPC discharged selctively during the stimulus for low and during the reaction time (RT) for high stimulus speeds. The RT differential responses of these neurons are not included in the database. MT, movement time. These differential responses were determined according to the Kruskal–Wallis test (P < 0.05).

task are similar to those obtained in a delayed go–no go task in Schultz and Romo, 1992). Stimulus, behavioral control and data collection were carried out through a personal computer using standard interfaces. The time between neuronal events, 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. Computer data files were copied for off-line analysis.

Psychophysics of the Tactile Categorization Task
The number of correct and incorrect categorizations of the stimulus speeds during the study of the differential responsive neurons was used to construct psychometric functions. These psychometric functions were plotted as the probability of correct judgments of the stimulus speeds as >20 or <22 mm/s. We used the logistic Boltzmann equation to fit these data

$$p = \frac{A_1 - A_2}{1 + e^{(x - x_0)/dx}} + A_2 \tag{1}$$

where p is the probability of a correct judgment of the speed as >20 or <22 mm/s, A_1 is the initial p, A_2 is the final p, x_0 is the stimulus speed supporting the 0.5 of performance, and dx is the width of the function at the 0.367–0.632 of p interval. All regressions fitted significantly the data with a χ^2 of $P < 0.01$. Psychometric thresholds were computed as half of the sum of the stimulus speeds at the 0.25 plus 0.75 p of correct judgments of the tactile stimulus speeds (Fig. 7C).

Analysis of the Neuronal Responses
The statistically significant differences in impulse activity in two epochs [control (non-stimulus period) of identical duration to the suspected changes produced by the stimulus and RT–MT periods] were assessed with a sliding window procedure on the basis of the non-parametric one-tailed Wilcoxon matched-pairs signed rank test ($P < 0.05$). The non-parametric Kruskal–Wallis test and a test of multiple comparisons were used to determine significant differences ($P < 0.05$) between the neuronal responses occurring during the stimuli and during the RT–MT periods (Siegel and Castellan, 1988).

Anatomical Studies
In the final recording sessions, lesions (20 μA for 20 s) were placed in the MPC at different depths. Animals were anesthetized with ketamine (6 mg/kg) and intravenous sodium pentobarbital (40 mg/kg) and perfused though the carotids with PBS 0.1 M followed by 4% paraformadehyde in PB 0.1 M. Guide wires (125 μm) were inserted in the most anterior and posterior sectors of the recorded territory of the right and left MPC. The brain was removed and suspended in paraformaldehyde. A block of the right and left hemispheres containing the arcuate and central sulci was sectioned at 50 μm and these sections were stained with cresyl violet. We used the marks left by the guide wires and the microelectrode tracts and lesions, together with the micrometer readings during the experiments, to identify the neuronal recording sites in the MPC. The electrode penetrations were normalized against the posterior border of the arcuate sulcus by tracing a line to the MPC. This allowed correct location of the electrode penetrations in each of the eight hemispheres studied. However, given the chronic character of the study, it was impossible to carry out a precise electrode track reconstruction of cortical depths of neurons studied.
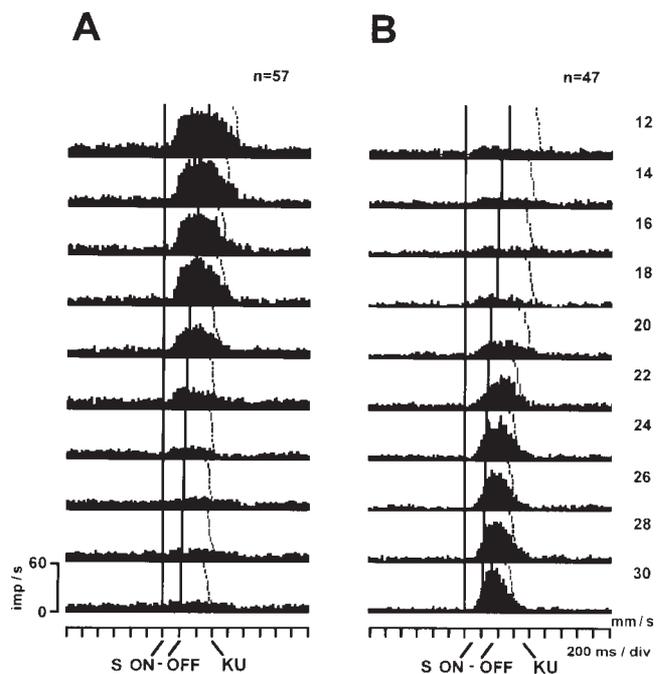
Results
We recorded single neurons in the wall of the two MPCs during the categorization task. The investigated area extended up to 3 mm lateral to the midline in the two hemispheres and 5 mm anterior and posterior to the posterior border of the arcuate sulcus (Fig. 2). This region comprises both pre-supplementary motor area (SMA) and SMA proper (Matsuzaka *et al.*, 1992; Luppino *et al.* 1993). Neurons were sampled from both subdivisions in approximately equal proportions and are
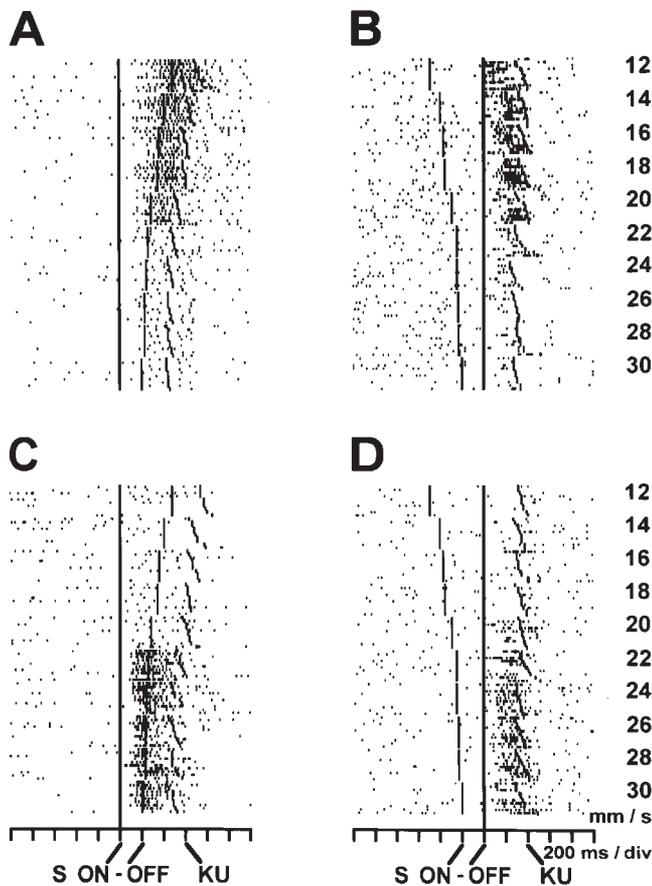
Figure 3. Discharges of four neurons of the MPC that had differential responses during the categorization task. Neurons in *A* and *C* began their differential responses at the end of the stimulus (S ON–OFF) and ended their discharges with the end of the reaction time (KU). Neurons in *B* and *C* responded selectively during the RT period. Large vertical lines indicate beginning of the scanning by the stimulus probe (S–ON). Vertical lines after the beginning of the stimulus indicate the end of the scanning (OFF). Small vertical lines indicate detection of the end of the stimulus (KU). These two events are shown in rank ordering of the reaction times (RT). Neuronal discharges are represented in the form of small ticks. Each line corresponds to one single trial. Stimuli were presented randomly in the glabrous skin of the distal segment of the third finger of the left hand. Stimulus parameters: traverse distance, 6 mm; direction, distal to proximal; constant force, 20 g; speeds, 12–30 mm/s.


Figure 4. Population response of all neurons of the MPC that discharged selectively for low (*A*) or high (*B*) stimulus speeds during the categorization. These neurons were selected according to an analysis made on the signal detection. Histograms for each neuron normalized from trial number were added and the resulting sum was divided by the number of neurons. Activity was aligned on the beginning of the moving tactile stimuli (S–ON), and according to the rank ordering of the reaction time (KU).

considered together because of similar activity during the categorization task.

Eighty eight (32 pre-SMA and 56 SMA proper) of 354 neurons of the right MPC, and 103 (47 pre-SMA and 56 SMA proper) of 391 of the left MPC discharged differentially during the categorization task, and reflected in their activity whether the stimulus speed was low or high (Kruskal–Wallis test, $P < 0.01$). These differential responses occurred mainly during the stimulus and RT periods (Table 1). Figure 3 shows four neurons that responded differentially during the categorization task. Two of them discharged during the end of the stimulus [with a mean average latency relative to the beginning of the moving tactile stimuli of 176.9 ± 10 ms (± SEM)], and continued discharging during the RT period (Fig. 3*A,C*). A number of these neurons also discharged differentially during the RT period (Fig. 3*B,D*). The histograms in Figure 4 show the population response of the MPC neurons that responded selectively for low or high stimulus speeds. These differential responses are not due to a bias in the RTs and MTs, since they were similar when the animal indicated

that the stimulus was low (RT: 345.0 ± 10.4 ms; MT: 186.4 ± 6.6 ms) or high (RT: 337.5 ± 10.8 ms; MT: 194.8 ± 8.8 ms). However, it may be possible that these MPC neurons were coding the intention to respond, or with the trajectory of the hand toward one of the two target switches to indicate categorization. We tested this possibility in a light instruction task (see the description of this task in Fig. 1*C*). Most of these neurons (57 of 71, 80%) did not show differential responses in this task (Fig. 5). In addition, some of the neurons which had differential responses were tested when the same stimuli were delivered passively ($n = 30$). None of these neurons discharged in this situation (Fig. 6).

Neurometric Functions of the Differential Discharges of MPC Neurons

Those neurons of the MPC that discharged selectively when the stimulus speed was low or high (according to the Kruskal–Wallis test, $P < 0.01$) were submitted to an analysis whose purpose was to produce a quantitative estimation that was comparable to the psychometric function. To this end, we employed an analysis based on signal detection theory to compute a neurometric function for each neuron (Green and Sweets, 1966; Britten *et al.*, 1992). These neurometric functions reflect the probability that an ideal observer could accurately report whether the stimulus speed was low or high, basing his judgments on the responses like those recorded from the neuron under study. Thus, these neurometric functions can be correlated to the psychometric functions.

To compute the neurometric function, we made the simplifying assumption that the neuronal threshold can be determined from two independent neural signals during the categorization task: that corresponding to the stimulus and RT
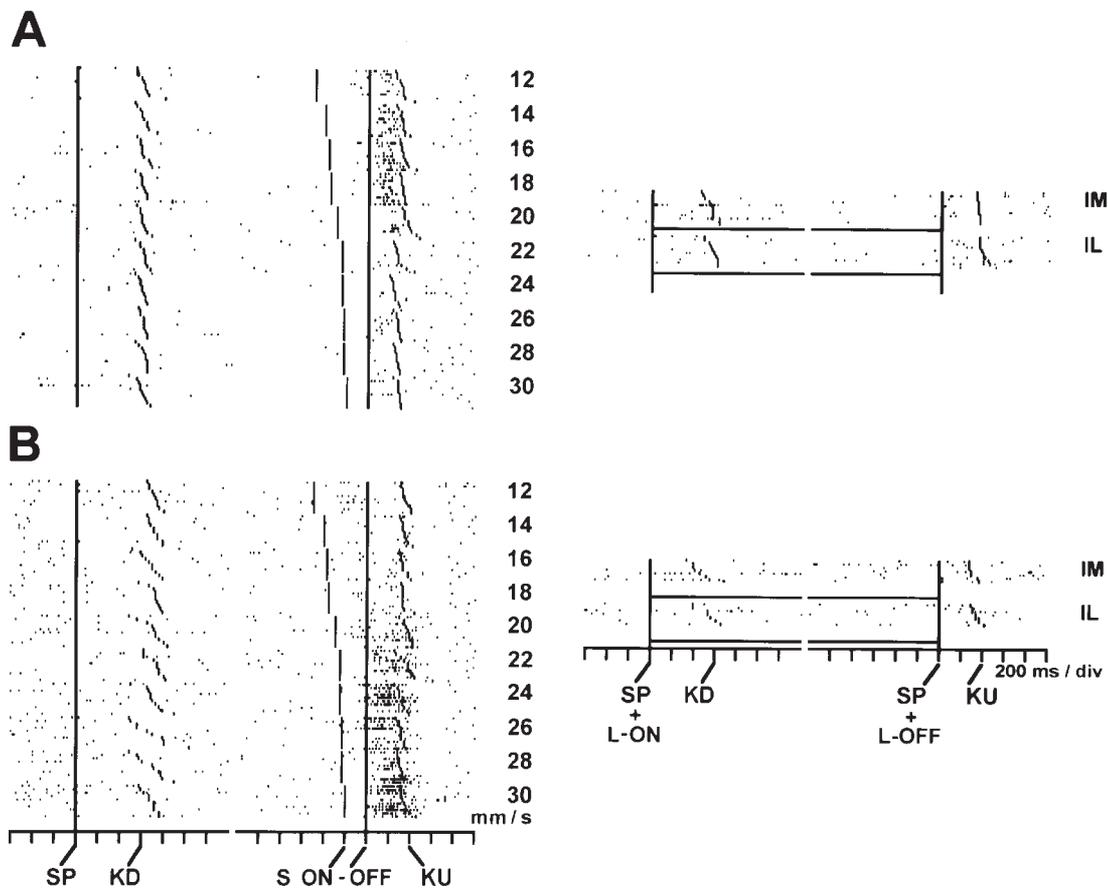
Figure 5. Differential responses of two neurons of the MPC (left side) that were tested in a light instruction task (right side). These two neurons were tested in the light instruction task to see whether these selective discharges were associated to the intention to press, or with the trajectory of the hand toward one of the two the target switches. In the light instruction task, trials were aligned relative to the indentation (SP) and to the probe up + light-off (SP + L-OFF), which served as triggers to indicate detection (KU) and button presses (IM, instruction for pressing medial push-button; IL, instruction for pressing lateral push-button). These examples illustrate that most of these categorical responses are not associated with the arm movements but with the categorization of the stimulus speeds.

periods, and that corresponding to an hypothetical anti-neuron [i.e. the same neuron's activity, using its control period (non-stimulus period preceding the beginning of the stimulus)]. This strategy has been used successfully by Britten *et al.* (1992) to compute neurometric functions that can be correlated with the sensory performance in a visual discrimination task. We then assumed that, on any given trial, the neuronal activity reflects the decision in favor of the stimulus categorization: low or high, with the larger response occurring during the stimulus–RT period. Finally, we assumed that the responses of the neuron and the anti-neuron are statistically independent. This is due to the fact that the neuronal activity during the control period was not significantly different (Wilcoxon test) to the spontaneous activity (the intertrial period).

Under these assumptions, a neuron that discharged selectively for low stimulus speeds (12–20 mm/s) during the categorization task will produce a correct categorization on a single trial, if the discharge rate during the stimulus–RT period is larger than the preceding control period (Fig. 7A). Conversely, the categorization is incorrect if the discharge rate is larger during the stimulus–RT period than the control period when the stimulus speed was high (22–30 mm/s). Performance was near chance (0.5 of *p*) if the neuron did not discharge for low stimulus speeds. The same criteria was applied for those neurons that contribute to the categorization of the high stimulus speeds.

Performance was computed trial by trial by compiling a receiver operating characteristic (ROC) for each pair of discharge rates (stimulus–RT period against the discharge rates during the control period). Each ROC curve (Fig. 7B) was generated by plotting the proportion of trials in which the response during the stimulus–RT period exceeded a criterion against the proportion of trials in which the control period exceeded the same criterion. We used 42 criterion levels, beginning at 0 spikes/s/trial, and increased the criterion in steps of 0.5 until 40 spikes/s/trial. Thus, for neurons that discharged differentially during the categorization of low stimulus speeds, for example, all trials during the both stimulus–RT and control periods exceeded a criterion of 0.5 spikes/s/trial, and the resulting points of the ROC curve fell in the upper right corner of the plot. As the criterion increased to 20 spikes/s/trial, the proportion of responses during the control period fell nearly to 0, while the proportion of responses during the stimulus–RT period exceeded the criterion with a *p* near to 1. As the criterion increased further to 40 spikes/s/trial, the responses during the stimulus–RT period that exceeded the criterion also fell toward 0. Thus, for a neuron that discharged at low stimulus speeds, 12–18 mm/s, its values fell along the upper and left margins of the plot. In contrast, the ROCs for speeds between 24 and 30 mm/s fell near to the diagonal line bisecting the plot, since the distributions of responses exceeding the criterion during the
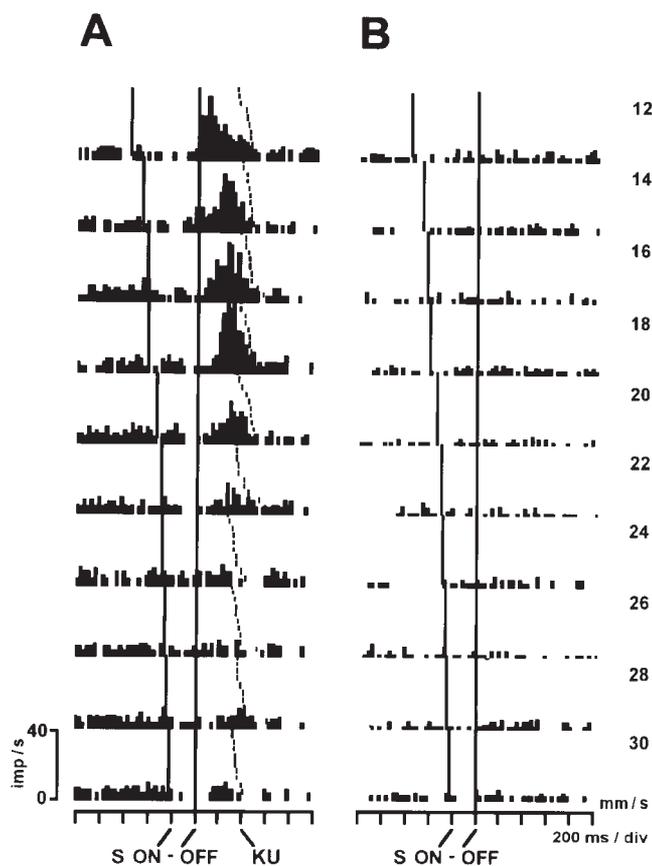
Figure 6. (A) Response of a neuron of the MPC that discharged selectively for low stimulus speeds. (B) Responses of the same neuron when the same set of stimuli as used in the categorization task were delivered passively. The activity shown in the form of histograms was normalized according to the maximum discharge rates during the stimuli in one of the ten classes of stimuli.

stimulus–RT period were very similar to the responses exceeding the criterion during the control period. In general, the curvature of the ROC away from the diagonal indicates the separation of the response distribution of the stimulus–RT period from the control period.

It has been shown formally that the normalized area under the ROC's curve corresponds to an ideal observer in a two-alternative, forced-choice psychophysical paradigm (Green and Sweets, 1966), as in the present categorization task. Thus, for a neuron that fires selectively for low stimulus speeds, the area under the ROC's curve for high stimulus speeds was ~0.5 of p. Therefore, the area under the curve is ~1 of p when the stimulus speed is low. The same applies when the discharge of a neuron is associated with the categorization of the high stimulus speeds. Thus, for each stimulus speed, we used this method to compute the probability that the decision rule would yield a correct response. As for the psychometric data, we fitted the neurometric data with sigmoidal curves of the form described in equation (1). This function provided an excellent description of the neurometric data (chi-square test, $P < 0.01$; Table 2). The neurometric thresholds were computed as the stimulus speed at 0.75 p of correct judgments (Fig. 7C).

Relations between the Psychometric and Neurometric Functions

We computed the threshold ratio of each pair of psychometric

Table 2

MPC neurons with neurometric functions that coded whether the stimulus speed was low or high

	Stimulus speeds		
	Low (12–20 mm/s)	High (22–30 mm/s)	Total
Right MPC			
Stimulus	1	1	2
Stimulus + RT	16	5	21
RT	15	10	25
Totals – right	32	16	48
Left MPC			
Stimulus	1	0	1
Stimulus + RT	18	8	26
RT	8	21	29
Totals – left	27	29	56
TOTALS	59	45	104

All these neurons fitted the Boltzmann equation with a chi-square of $P < 0.001$.

RT, reaction time.

and neurometric functions. This was determined by dividing the neurometric threshold by the psychometric threshold. It is shown in Figure 8 that sometimes these neurons, which had differential responses, are more sensitive, equal, or less sensitive than the psychometric threshold, for either neurons that fired selectively for low or high stimulus speeds. However, the threshold ratio of the neuronal population was close to 1 (Fig. 9). The threshold ratios of the two populations that coded that the stimulus speed was low (20.73 mm/s) or high (20.7 mm/s) were almost identical to the threshold ratios of the psychometric functions when the animal decided that the stimulus speed was low (20.73 mm/s) or high (20.7 mm/s). Figure 10 shows the neurometric population functions that decided whether the speed of the stimulus was low (Fig. 10A) or high (Fig. 10B), together with their corresponding psychometric functions. This was made by plotting the total probability of the population that the response during the stimulus–RT period exceeded the same criterion. We used the 42 criterion levels described above. With these ROC curves, we computed the neurometric functions of these two independent neuronal populations and obtained the profiles shown in Figure 10.

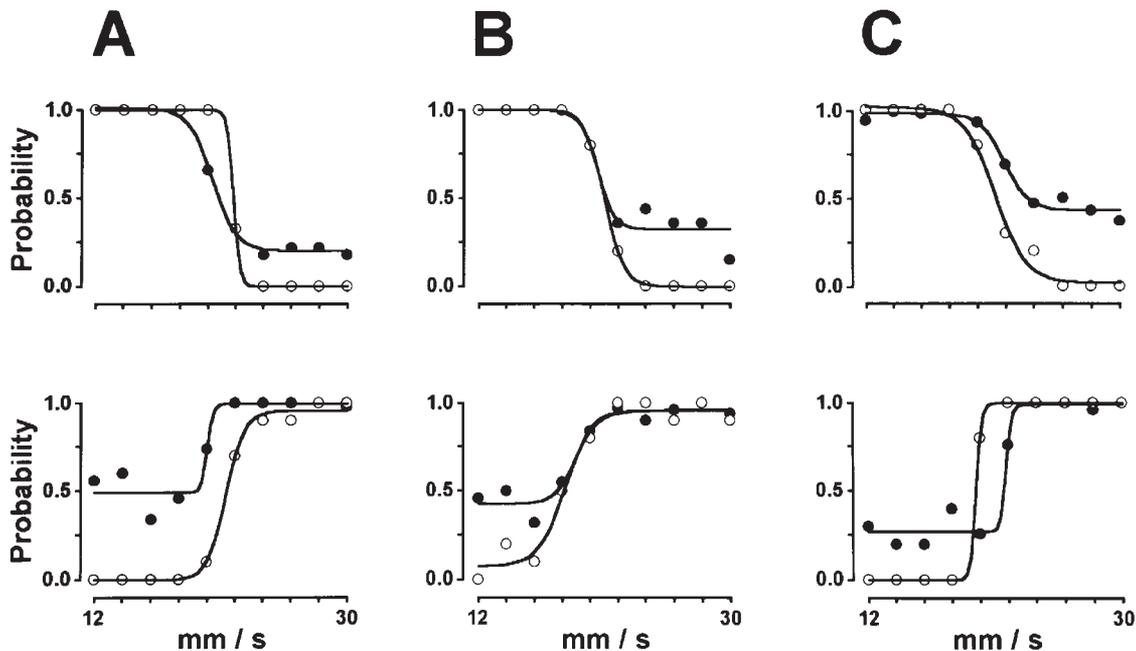### *Modulation of the Neurometric Function*

Six categorical neurons of the right MPC (contralateral to the stimulated hand) were tested when the animal categorized the moving tactile stimulus, but knew in advance whether the moving tactile stimulus was low or high. This was done by illuminating one of the two push-buttons which was associated with the stimulus speed. Figure 11 gives an example of one neuron studied in this condition. The neuron in Figure 11A shows strong responses during the stimulus–RT period for low stimulus speeds. This categorical response (Fig. 11C), for low speeds, was considerably attenuated when the animal was visually instructed about the forthcoming stimulus speed (Fig. 11B,D). Interestingly, this neuron developed a differential delay response during the visual instruction (Fig. 11B).

Discussion

We recorded neurons in the MPC that had differential responses during the categorization task, predicting whether the stimulus speed was low or high. We made an analysis of these differential responses in terms of signal detection theory to see whether these MPC neurons coded the animal's decision (Green and
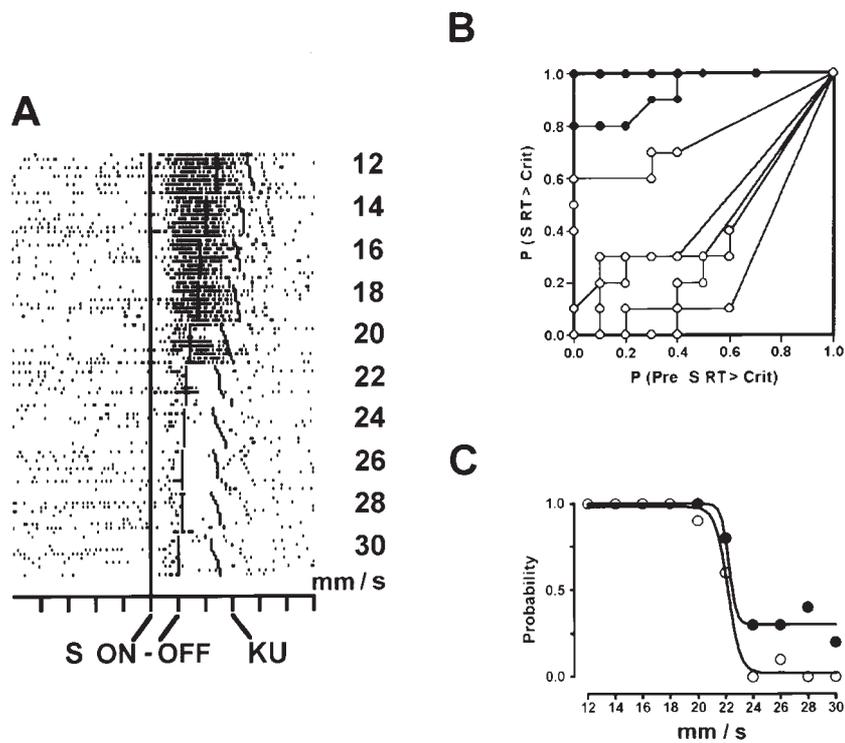
Figure 7. (*A*) Categorical neuron of the MPC. (*B*) Receiver operating characteristic (ROC) for the 10 pairs of discharge rates of the stimulus–ration time versus control periods. Each point in the ROC curve represents the proportion of trials on which the neuronal response exceeded a criterion level plotted against the proportion of trials on which the control period (non-stimulus period) preceding the stimulus exceeded a criterion level. Each ROC was generated by increasing the criterion level from 0 to 42 spikes/s/trial, in 0.5 increments. Increased separation of the selective response from the control period in *A* leads to an increase in the deflection of the ROC away from the diagonal (filled circles correspond to low classes and open to high classes of stimulus speeds). (*C*) Neurometric function (filled circles) that describes the selectivity of the categorical process shown in open circles as the probability that animal judged correctly that the stimulus speed was <22 mm/s. Neurometric and psychometric functions were fitted with sigmoidal curves of the form of the Boltzmann equation (described in the text). Neurometric threshold is 22.09 mm/s; psychometric threshold 22.09 mm/s.

Figure 8. Different types of correlation between neurometric (filled circles) and psychometric (open circles) functions for those neurons that discharged selectively during the categorization of low or high stimulus speeds. In *A*, the neurometric threshold (top, 19.66 mm/s; bottom, 20.0 mm/s) is more sensitive than the psychometric threshold (top, 21.8 mm/s; bottom, 21.4 mm/s). In *B*, both thresholds are almost identical (neurometric: top, 20.8 mm/s; bottom, 19.3 mm/s; psychometric: top, 20.99 mm/s; bottom, 18.1 mm/s). In *C*, the psychometric threshold (top, 21.2 mm/s; bottom, 19.7 mm/s) is more sensitive than the neurometric threshold (top, 21.6 mm/s; bottom, 21.99 mm/s).
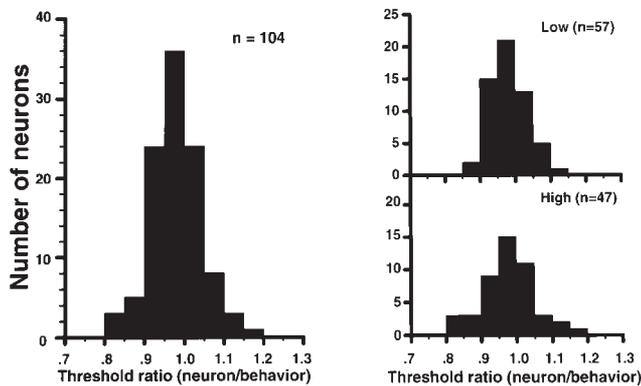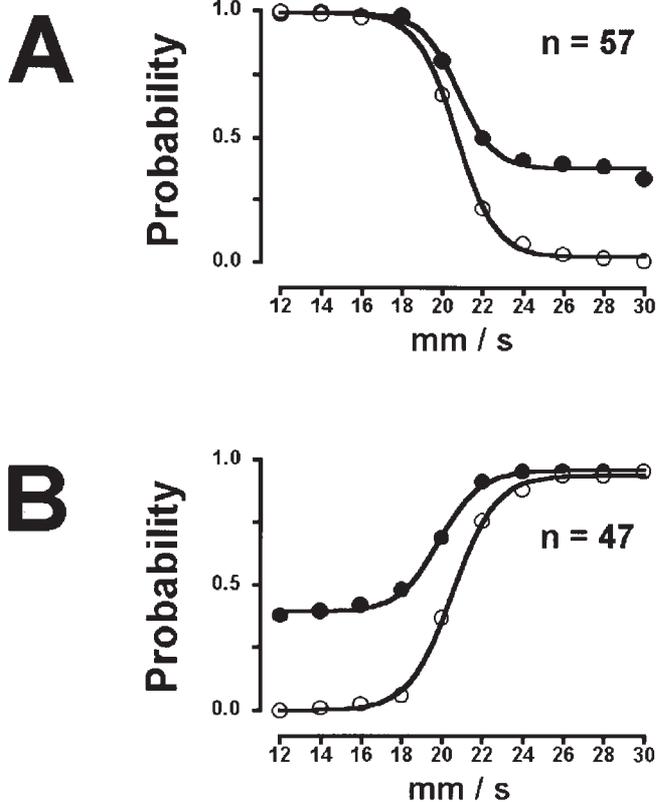
Figure 9. Threshold ratios of the whole population of neurons of the MPC that coded the categorization process (left side). On the right side are the threshold ratios of the population of neurons that coded whether the stimulus speed was low (top) or high (bottom).

Figure 10. Correlation between the population of neurons that coded whether the stimulus was low (A) or high (B) and the psychometric functions. In A, the neurometric threshold is 20.38 mm/s and the psychometric threshold is 20.73 mm/s. In B, the neurometric threshold is 20.38 mm/s, and the psychometric threshold is 20.7 mm/s. Filled circles represent the neurometric functions, and open circles represent the psychometric functions.

Sweets, 1966; Britten *et al.*, 1992). Psychometric and neurometric thresholds were highly correlated. Therefore, these neural signals may be associated with the categorization of the stimulus speed. Categorical responses occurred during the stimulus and RT periods. Thus, it appears that there exists a continuum in the construction of the categorization process, beginning during the stimulus period, and ending with an output selective signal which reflects the animal's decision. These categorical responses occur exclusively during the categorization task, since none of them occurred during the passive delivery of the same set of stimuli used in the categorization task. Therefore, these findings suggest that the MPC possesses a neural apparatus which is engaged in the animal's decision process in the present somesthetic task. We focus the discussion on this issue.

MPC neurons that had differential responses began their discharges during the stimulus period with a mean average latency of 176.9 ± 10 ms. These neurons respond with similar latencies to those MPC neurons with invariant stimulus responses (Romo *et al.*, 1993b). Considering the response latencies between these two populations of neurons, it could be interpreted that two independent neural processes were operating in the MPC during the execution of this sensory task. The first as a sensory-motor neural process associated with the general behavioral motor reaction, and the second as a stimulus-movement-related neural process which predicts whether the stimulus speed was low or high.

Animals categorized the stimulus speeds by pressing with the right hand one of two target switches (medial for low speeds and lateral for high speeds). It is possible, therefore, that the MPC neurons with differential responses, instead of coding the stimulus speed in their activity, were associated with the intention to press, or with encoding the trajectory of the hand toward the target switches to indicate categorization (Alexander and Crutcher, 1990; Matsuzaka, *et al.*, 1992, for results in different motor paradigms). However, most of these neurons seem to be associated with the categorization of the speed of the tactile stimuli. This is supported by the fact that most of them (80%) did not discharge differentially when the animal interrupted the target switches after visual instruction. Therefore, most of these neurons code in their activity the categorization task.

This finding raises the question whether these MPC neurons are entirely specialized in the categorization of the stimulus speeds. We studied the responses of some MPC neurons in a combination of light instruction task and tactile categorization. In this condition, the animal is instructed about the forthcoming stimulus speed. All differential responses are considerably attenuated in this situation. Interestingly, neurons studied in this condition responded selectively during the delay period associated with the differential response occurring during the stimulus, although the selective response during the stimuli almost disappeared. It is likely that the categorical neural response is considerably attenuated, since the differential motor response was already specified by the visual instruction. This finding indicates that neurons of the MPC are not necessarily specialized in one single function. Indeed, these categorical neurons displayed the selection of the categorization of the stimulus speed during the delay period. Therefore, these results are consistent with previous investigations showing that the MPC is involved in the planning of the forthcoming behavioral reaction (Kurata and Tanji, 1985; Tanji and Kurata, 1985; Alexander and Crutcher, 1990; Kurata and Wise, 1988; Romo and Schultz, 1987; Schall,1991; Romo *et al.*, 1992).

One important question raised by these results is the possible role of the MPC in sensory decision processes. We believe that the MPC is only one of several structures which may be associated with this function. Indeed, in the present task, we have described similar differential responses in the neostriatum (Romo *et al.*, 1995) and, in preliminary results, observed these neural signals in the lateral premotor cortex (unpublished results). Mountcastle *et al.* (1992) have recorded neurons in MI
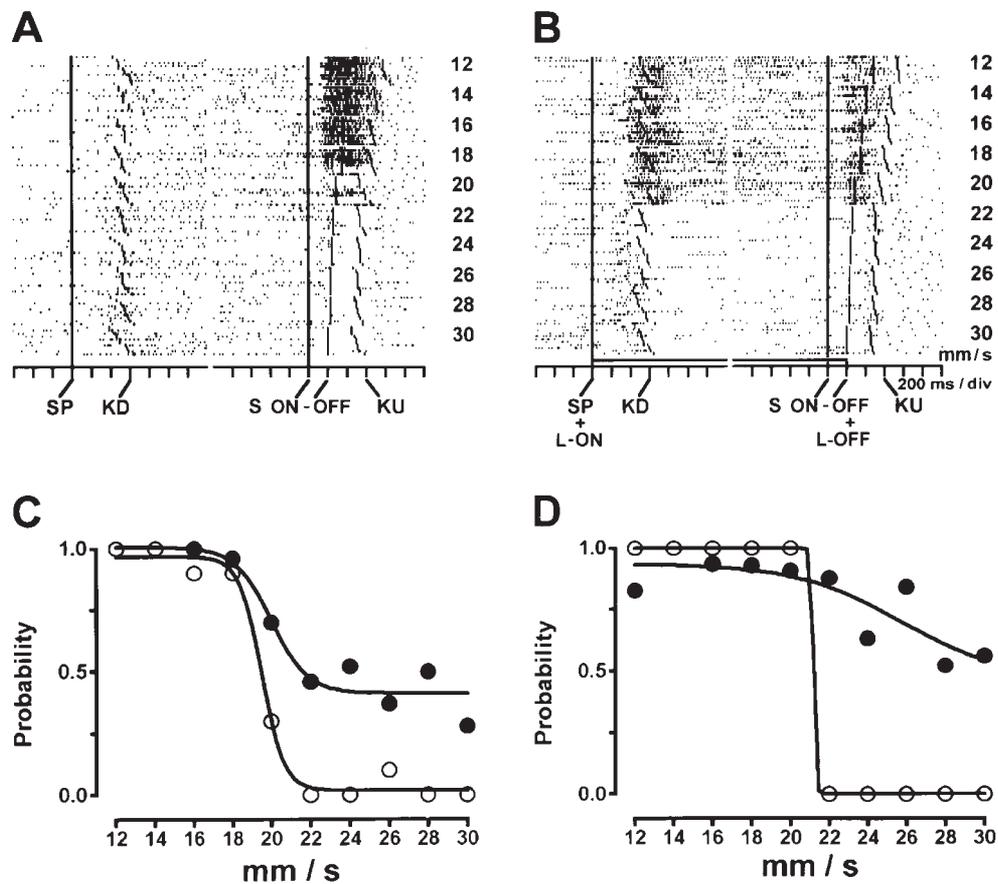
Figure 11. Modulation of the neurometric function. (*A*) Neuronal response associated selectively with the categorization of low stimulus speeds. (*C*) Psychometric (open circles, threshold 19.4 mm/s) and neurometric functions (filled circles, neurometric threshold 19.4 mm/s). In (*B*) this neuron was studied when the animal categorized the stimulus speed but knew in advance whether the stimulus speed was low or high. This was done by combining the categorization task with a visual instruction task (see legend of Fig. 5 for description of the light instruction task). It is seen in (*B*) that the categorical response was considerably attenuated. Interestingly, this neuron discharged during the instruction period associated with low stimulus speeds. (*D*) The relation between the psychometric and neurometric functions obtained from (*B*).

cortex that reflect in their activity the discrimination process in a somesthetic discrimination task. This is in contrast to the fact that SI cortex neurons do not code in their activity the sensory decision (Romo *et al.*, 1996). A similar observation was made by Mountcastle *et al.* (1990) in a different sensory somesthetic task. Thus, if SI cortex neurons do not reflect in their activity the animal's decision, the alternative is that the construction of the sensory decision process begins in those somesthetic areas of the parietal lobe linked to SI. However, experiments remain to be done to see the contribution of somesthetic areas of the parietal lobe in this function.

The role of MPC in motor functions is well established. This cortical region is connected with the spinal cord (Dum and Strick, 1991) and with a number of subcortical structures that subserve motor functions (Wiesendanger and Wiesendanger, 1985; McGuire *et al.*, 1991). On the other hand, the large number of afferent projections to the MPC from such structures as the parietal lobe makes the MPC an important node for associating the sensory with the motor processing in this categorization task (Jones and Powell, 1969; Petrides and Pandya, 1984; Pons and Kass, 1986; Cavada and Goldman-Rakic, 1989; Luppino *et al.*, 1993). Our study has shown how the processing of sensory information reaches a motor area of the frontal lobe, very likely associated with the output of the perceptual process.

In a series of elegant studies made in the middle temporal

area, Newsome and colleagues have demonstrated that few neurons of this cortical region are necessary for monkeys to be capable of discriminating visual motion (Newsome *et al.*, 1990; Britten *et al.*, 1992). In this sensory task, animals use the eyes to indicate discrimination. The discriminative visual neural signal recorded in the middle temporal area must be projected to the oculomotor regions of the brain to move the eyes to indicate discrimination. The question is whether in the neuronal discharges of these oculomotor regions is also observed the animal's decision. The same problem is posed by our paradigm, although we have no evidence of a tactile motion area in the parietal lobe similar to the visual motion area of the middle temporal lobe. The results obtained in our study suggest that the output of the animal's decision is reflected in a type of neuron of the MPC during the execution of the tactile categorization task. Thus, this study presents evidence that the decision-making process is also represented in motor areas of the brain.

Notes

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