Functional Properties of Primate Putamen Neurons During the Categorization of Tactile Stimuli

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Merchant, Hugo, Antonio Zainos, Adrián Hernández, Emilio Salinas, and Ranulfo Romo. Functional properties of primate putamen neurons during the categorization of tactile stimuli. *J. Neurophysiol.* 77: 1132–1154, 1997. We used psychometric techniques and neurophysiological recordings to study the role of the putamen in somesthetic perception. Four monkeys were trained to categorize the speed of moving tactile stimuli. Animals performed a task in which one of two target switches had to be pressed with the right hand to indicate whether the speed of probe movement across the glabrous skin of the left, restrained hand was low or high. During the task we recorded the activity of neurons in the putamen contralateral (right) and ipsilateral (left) to the stimulated hand. We found different types of neuronal responses, all present in the right and left putamen. Some neurons responded during the stimulus period, others responded during the hand-arm movement used to indicate categorization, and others responded during both of these periods. The responses of many neurons did not vary either with the speed of the stimuli or in relation to the categorization process. In contrast, neurons of a particular type responded differentially: their activity reflected whether the stimulus speed was low or high. These differential responses occurred during the stimulus and hand-arm motion periods. A number of the nondifferential and differential neurons were studied when the same stimuli used in the categorization task were delivered passively. Few neurons with nondifferential discharges, and none of the differential neurons, responded in this condition. In a visually cued control task we studied the possibility that the differential responses were associated with the intention to press or with the trajectory of the hand to one of the target switches. In this condition, a light turned on instructed the animal which target switch to press for a reward. Very few neurons in both hemispheres maintained the differential responses observed during the categorization task. Those neurons that discharged selectively for low or high speeds were analyzed quantitatively to produce a measure comparable with the psychometric function. The thresholds of the resulting neurometric curves for the neuronal populations were very similar to the psychometric thresholds. The activity of a large fraction of these neurons could be used to accurately predict whether the stimulus speed was low or high. The results indicate that the putamen, both contralateral and ipsilateral to the stimulated hand, contains neurons that discharge in response to the somesthetic stimuli during the categorization task. Those neurons that respond irrespective of the stimulus speed appear to be involved in the general sensorimotor behavior of the animal during the execution of the task. The results suggest that the putamen may play a role in bimanual tasks. The recording of neurons in the right and left putamen whose activities correlate with the speed categories suggests that this region of the basal ganglia, in addition to its role in motor functions, is also involved in the animal's decision process.

INTRODUCTION

Anatomic studies have shown a cortical input to the putamen from the primary somatosensory (SI) cortex (Flaherty and Graybiel 1991; Jones et al. 1978; Künzle 1977). Although this was not tested during a sensory task, recordings of single neurons in the putamen have revealed somesthetic input (Alexander and DeLong 1985; Crutcher and DeLong 1984; Gardiner and Nelson 1992). In addition to this input from SI cortex, bilateral input to the putamen from the primary motor (MI) cortex and supplementary motor area (SMA) has been demonstrated (Künzle 1975; McGuire et al. 1991). It has been shown that SMA neurons respond to somesthetic stimuli during a somesthetic categorization task (Romo et al. 1993b). Interestingly, a portion of the SMA neurons reflect in their activity the animal's decision during the categorization task (Romo et al. 1993b). In the same task, neurons of SI cortex contralateral to the stimulated hand respond to the tactile stimuli; however, their responses are independent of the categorization process (Romo et al. 1996).

In view of these anatomic and neurophysiological results, we decided to explore the possibility that the putamen is involved in processing somesthetic information. To this end, we trained monkeys in a somesthetic task (Romo et al. 1996). Animals performed the task by pressing one of two push buttons with the right hand to indicate whether the stimulus speed across the left, restrained hand was low or high. Sensory performance was evaluated with psychometric techniques, and motor responses were monitored by measuring the reaction time (RT) and movement time (MT). Because of the bimanual nature of the task, we made the simplifying assumption that the right putamen (contralateral to the stimulated hand), could be considered as ''sensory,'' whereas the left putamen (contralateral to the responding hand-arm), could be considered as ''motor.'' To demonstrate the possible sensory input to the putamen, we analyzed the neuronal responses in terms of their response latencies and discharge rates associated with the somesthetic stimuli. We also analyzed the correlations between the neuronal discharges and the categorization process. We were particularly interested in revealing any difference between the sensory and the motor putamen, and in exploring whether this region of the striatum is involved in the animal's decision. The results indicate that there is neuronal activity in the putamen that is time locked to the somesthetic stimuli and that some of these neurons also discharge during the responding hand-arm motion. These neuronal responses were found in both hemispheres, suggesting a role in bimanual sensorimotor tasks. However, the most interesting finding was that the activity of neurons in the right and left putamen predicted

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the animal's decision. We suggest that the putamen, in addition to its role in sensorimotor functions, is also involved in the decision making process. A preliminary report of this work has appeared elsewhere (Romo et al. 1995).

METHODS

General

The study was performed on four male monkeys (*Macaca mulatta*, 4.5–6 kg). Animals performed 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. They indicated the corresponding category by pressing one of two target switches with the right hand. The activity of single neurons was recorded with movable microelectrodes in the right and left putamen during performance of the task. Sensory performance was measured with psychometric techniques, and motor performance was evaluated by measuring the RTs and MTs in the same trials. We also monitored the electromyographic (EMG) activity of the extensor digitorum communis (EDC), biceps brachii (BIC), and triceps brachii (TRI) of the responding arm through chronically implanted electrodes during all recording sessions. In separate sessions we also recorded from muscles of the left, restrained arm and the shoulder, neck, and trunk. Recording locations were reconstructed from histological sections at the end of the experiment.

Somesthetic task

The left arm of the animal was secured in a half cast and maintained in a palm-up position (Fig. 1*A*). 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 and placed at reaching distance, 250 mm away from the animal's shoulder and at eye level. The round tip delivering the stimuli moved at any of 10 speeds, from 12 to 30 mm/s. It covered a fixed traverse distance (6 mm), always in the same direction (distal to proximal), and applied a constant force (20 g). Half of the speeds 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). The tactile stimulator was custom built in our laboratory to study motion processing in the somatosensory system of primates (Romo et al. 1993a).

The trained monkey began a trial when it detected a step indentation of the skin of the left hand (SP). The monkey indicated detection by placing the right hand on an immovable key (DK) in a period not exceeding 1 s (Fig. 1*B*). The monkey maintained this position throughout a variable delay period (1.5–4.5 s) beginning with detection of the SP (KD), until the probe moved at 1 of the 10 speeds. The monkey indicated detection of the end of the scanning by removing the hand from the key within 600 ms (DP), and indicated whether the speed was low or high (CP) by projecting the right hand (PT) to one of the two target switches within 1 s. The medial switch was used for low speeds and the lateral one for high speeds. The animal was rewarded for correct categorization with a drop of water (R). Throughout the task the tactile stimuli were neither visible nor audible.

Light instruction task

In this case, animals had to execute movements from the key to the target switches, but guided by visual cues (Fig. 1*C*). Each trial began with the probe touching the skin, as in the somesthetic task, but one of the two target switches was illuminated the moment the SP occurred. It was kept on after detection (variable delay period of 1.5–4.5 s) and turned off when the probe was lifted off. Because the probe did not move across the skin, the visual trigger signals alone instructed the animal which target switch to press for a reward.

Surgery

After animals reached proficiency in the task (75–90% correct responses), two stainless steel chambers tilted 30° laterally were implanted to allow microelectrode penetrations for single-neuron recording in the right (3 monkeys) and left (4 monkeys) putamen. A head holder for head fixation was also implanted. Stainless steel Teflon-coated wires were chronically implanted into the EDC, BIC, and TRI of the right arm for EMG recordings; the wires were brought to a connector fixed to the skull. The chambers, head holder, and connector were secured to the skull with screws and acrylic. All procedures were carried out aseptically under pentobarbital sodium anesthesia (30 mg/kg). Postoperative infections and pain were prevented by administration of penicillin G and acetaminophen for 1 wk after surgery.

Electrophysiological recording

The activity of single neurons was recorded extracellularly with glass-insulated tungsten electrodes (1.5–2.0 MΩ), which were passed into the brain each day inside a rigid guiding cannula (0.6 mm OD). The cannula was advanced 3 mm below the surface of the dura and the penetrations were alternated in the right and left hemispheres. Neuronal signals from the microelectrode were amplified and filtered, and monitored with oscilloscopes and earphones. Neuronal discharges were converted into digital pulses by means of a differential amplitude discriminator. A record was kept of the depth at which each neuron was isolated along the length of each penetration. EMGs from the forearm and arm muscles were recorded through the chronically implanted electrodes of the right moving arm during all recording sessions. In separate sessions, EMGs from the forearm and arm muscles of the left, restrained hand and from muscles of the shoulder, neck, and trunk were also recorded. EMG activity was filtered, rectified, and converted into digital pulses by means of a differential amplitude discriminator. Stimulation, behavioral control, and data collection were carried out through a personal computer with the use of standard interfaces. The times between neuronal events, EMGs, and 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 analyzed off-line.

Analysis of the sensory-motor behavior

The numbers of correct and incorrect categorizations in a run, which consisted of 10 trials per class (speed) presented randomly, were used to construct psychometric functions. These were plotted as the probability p of correctly judging the stimulus speed as >20 mm/s, as a function of speed x. Curves were also calculated for the probability of correctly judging the speed as <22 mm/s. We used logistic Boltzmann equations to fit these data

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

where A_1 and A_2 determine the minimum and maximum values, respectively, of p; x_0 is the stimulus speed for which $P = (A_1 + A_2)/2$; and dx determines the width of the function. All regressions fitted the data significantly, with a χ^2 of $P < 0.01$. Psychometric thresholds were computed as the average of the speeds at which $P = 0.25$ and $P = 0.75$.

We also measured RT and MT during the categorization of speeds. The nonparametric Kruskal-Wallis test and a test of multiple comparisons (Siegel and Castellan 1988) were used to deter-

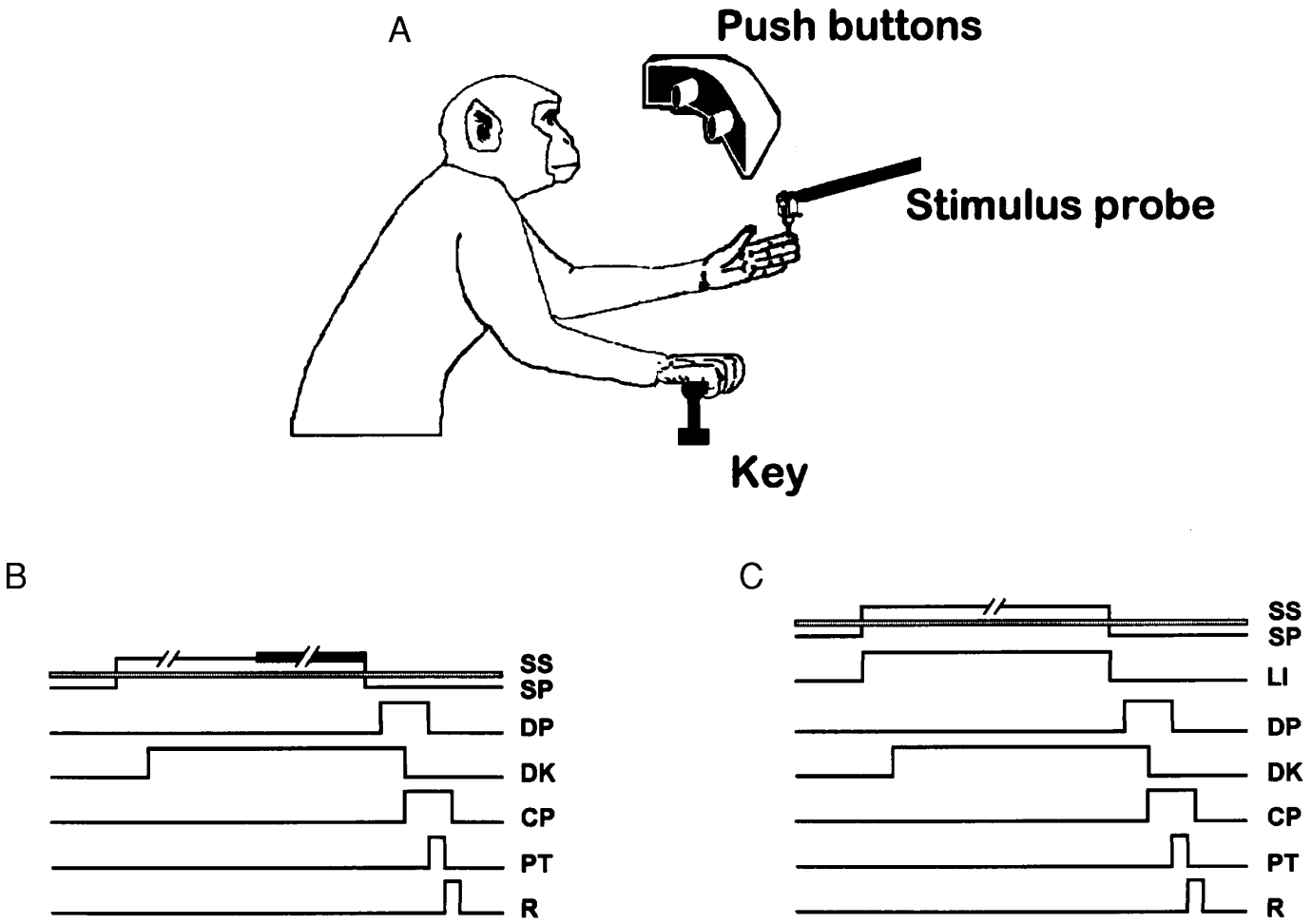

FIG. 1. *A*: drawing of a monkey working in the somesthetic categorization task. *B*: schematic outline of the task. Broken line preceding the bold broken line: variable delay period (1.5 to 4–5 s). Bold broken line: period of variable length during which the stimulus probe moves at different speeds (12–30 mm/s) across the glabrous skin of 1 of the fingers of the left, restrained hand. SS, skin surface; SP, skin indentation; DP, detect period; DK, detect key; CP, choice period; PT, project to target; R, reward. *C*: light instruction (LI) task. Same sequence as in *A*, but without motion of the SP across the skin.

mine significant differences ($P < 0.05$) in the RTs and MTs across presented stimuli (all classes).

Analysis of the neuronal responses

Off-line inspection of the data for each neuron was performed on the basis of raster plots and in reference to each of the behavioral events: SP, KD, beginning and end of the moving tactile stimulus, key release marking the end of the RT, and pressing of the target switches marking the end of the MT. Neurons were classified according to their responses in the intervals between each of these events. We assessed the statistical significance of differences in impulse activity during these intervals and during control epochs of identical duration taken from the nonstimulus period immediately preceding movement of the stimulus probe. Differences were assessed with a sliding window procedure based on the nonparametric, one-tailed Wilcoxon matched-pairs signed-rank test ($P < 0.05$). Because a class of putamen neurons responded by increasing their impulse activity during stimulation, we analyzed the period comprising the beginning of the discharges (after a latency) to the end of the stimulation; we did this for those cells with tonic responses. However, some neurons had phasic responses during the stimulus period. For these, we considered a fixed-length interval of 210 ms as a stimulus period for all speeds. We used a period of 210 ms as poststimulus period. This period corresponds to the RT during the tactile categorization task and the light instruction task, and to the poststimulus period during passive stimulation. The Wilcoxon and Kruskal-Wallis tests and a test of multiple comparisons were used to determine significant differences ($P < 0.05$) between the neuronal responses occurring during the stimulus versus the prestimulus periods, and during the RT-MT versus the stimulus or prestimulus periods (Siegel and Castellan 1988).

Neural response latency

An analysis of the latencies of the neuronal discharges relative to the beginning of the moving tactile stimuli was carried out by means of signal detection methods. Briefly, the spike trains were transformed into functions expressing the actual density of spikes in time (Richmond et al. 1987; Ruiz et al. 1995). Having generated the individual spike density functions for each neuron and each speed, we identified significant nonstationary or driven activity and quantified its latency and variability (Mcpherson and Aldridge 1979) with the use of statistical bootstrapping techniques (Diaconis and Efron 1983; Efron 1982). For each neuron, the 10 classes (stimulus speeds) of spike density functions were shuffled bin by bin with the use of a random number generator (Press et al. 1988) to construct a mean spike density. This mean density is a binned

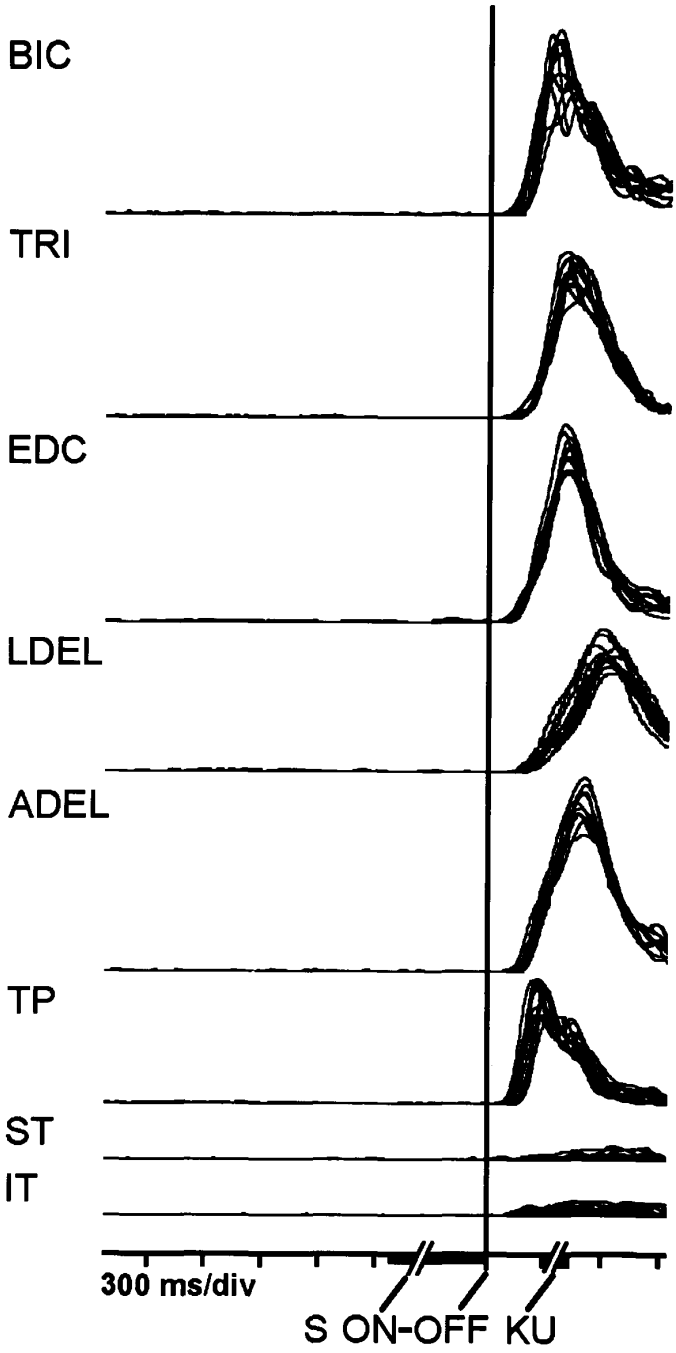

FIG. 2. Spike density functions of the electromyograms (EMGs) of the extensor digitorum communis (EDC), biceps (BIC), and triceps (TRI) of the right arm during the categorization of stimulus speeds. The shoulder muscles lateral deltoid (LDEL) and anterior deltoid (ADEL) and the trunk muscles thoracic paraspinal (TP), suprascapular (ST), and infrascapular trapezius (IT) ipsilateral to the responding arm were also active during the task. The spike density function (Ruiz et al. 1995) of each muscle was calculated during the categorization of each stimulus speed during a run, which included 10 speeds (10 trials per speed). Long vertical line: end of the stimulus. Broken horizontal bars: stimulus period (S-ON to S-OFF) and detection of the end of the stimulus (KU). The reaction time (RT) was measured from stimulus off to KU.

estimated background that was used to test the significance of the changes in the individual spike density functions. This test was performed 1,000 times for each neuron and each speed, computing 1,000 different mean densities, to obtain final values for the significance. The advantage is that instead of determining exactly the components needed to calculate the background, this method uses the data themselves to generate it, thereby offsetting any local biases. Finally, the mean latency was calculated as the first bin in which a significant change ($P < 0.05$) in the spike density occurred after the stimulus onset.

Neurometric functions

An analysis based on signal detection theory (Green and Swets 1966) was used to compute neurometric functions for a class of putamen neurons whose activity reflected whether the stimulus speed was low or high (see RESULTS). The neurometric functions reflect the probability of an ideal observer accurately reporting whether the stimulus speed was low or high, basing that judgment on the activity pattern of the neuron under study. Thus the neurometric functions can be compared with the psychometric functions. To this end, we made the following simplifying assumptions. First, the neuronal threshold can be determined from two independent neural signals: the response during the stimulus-movement period, and the same neuron's activity during the control, prestimulus period. Activity during the prestimulus period can be thought of as the response of a hypothetical antineuron. This strategy has been used successfully by Britten et al. (1992) and by us (Romo et al. 1997) to compute neurometric functions that can be correlated with sensory performance. Second, on a given trial, the neuronal activity reflects the decision corresponding to the presented stimulus speed: low or high, with the larger response occurring during the stimulus and arm movement period. Third, the responses of the neuron and the antineuron are statistically independent.

Neuronal performance was evaluated trial by trial by computing a receiver operating characteristic (ROC) curve for each speed with the use of pairs of discharge rates, the responses during the stimulus-movement period and the responses during the control period. Each ROC curve was generated by calculating the proportion of trials in which the response exceeded a prespecified discharge rate called the criterion level. The proportion of trials in which the criterion level was exceeded during the stimulus-movement period is plotted versus the proportion of trials in which the same criterion was exceeded during the control period; each criterion level produces a point in the plot. We used 42 criterion levels, from 0 to 40 spikes/s per trial in steps of 0.5 spikes/s per trial. Neurons that discharged differentially during the categorization of low speeds, for example, exceeded a criterion of 0.5 spikes/s per trial in both periods, and the resulting points of the ROC curve fell in the top right corner of the plot (Romo et al. 1997). As the criterion increased to 20 spikes/s per trial, the proportion of responses exceeding it during the control period fell nearly to 0, whereas the proportion of responses exceeding the criterion during

TABLE 1. *Data base of putamen*

Monkeys Hemispheres	Penetrations	Neurons Studied		
		Tested	Responsive	Analysis
M1-R	18	393	240	127
M2-R	23	361	168	86
M3-R	14	266	179	93
Total-r	55	1,020	587	306
M1-L	29	548	287	158
M2-L	18	359	156	56
M3-L	23	386	156	75
M4-L	18	367	179	100
Total-l	88	1,660	778	389
Total	143	2,680	1,365	695

R, right; L, left.

TABLE 2. *Type of responses of putamen neurons during the categorization task*

Monkeys Hemispheres	Stimulus Related		Stimulus-Movement Related	Differential	Preparatory	Movement Related
	Activations	Suppressions				
M1-R	22	11	12	40	15	27
M2-R	25	13	5	12	15	16
M3-R	14	7	12	33	17	10
Total-r	61 (19.9)	31 (10.1)	29 (9.5)	85 (27.8)	47 (15.4)	53 (17.3)
M1-L	11	16	26	37	13	55
M2-L	10	5	11	3	10	17
M3-L	13	11	17	7	10	17
M4-L	10	8	8	31	18	25
Total-l	44 (11.3)	40 (10.3)	62 (15.9)	78 (20.0)	51 (13.1)	114 (29.4)
Total	105 (15.1)	71 (10.2)	91 (13.1)	163 (23.5)	98 (14.1)	167 (24.0)

Number in parentheses corresponds to the % of neurons associated with the different types of responses. R, right; L, left.

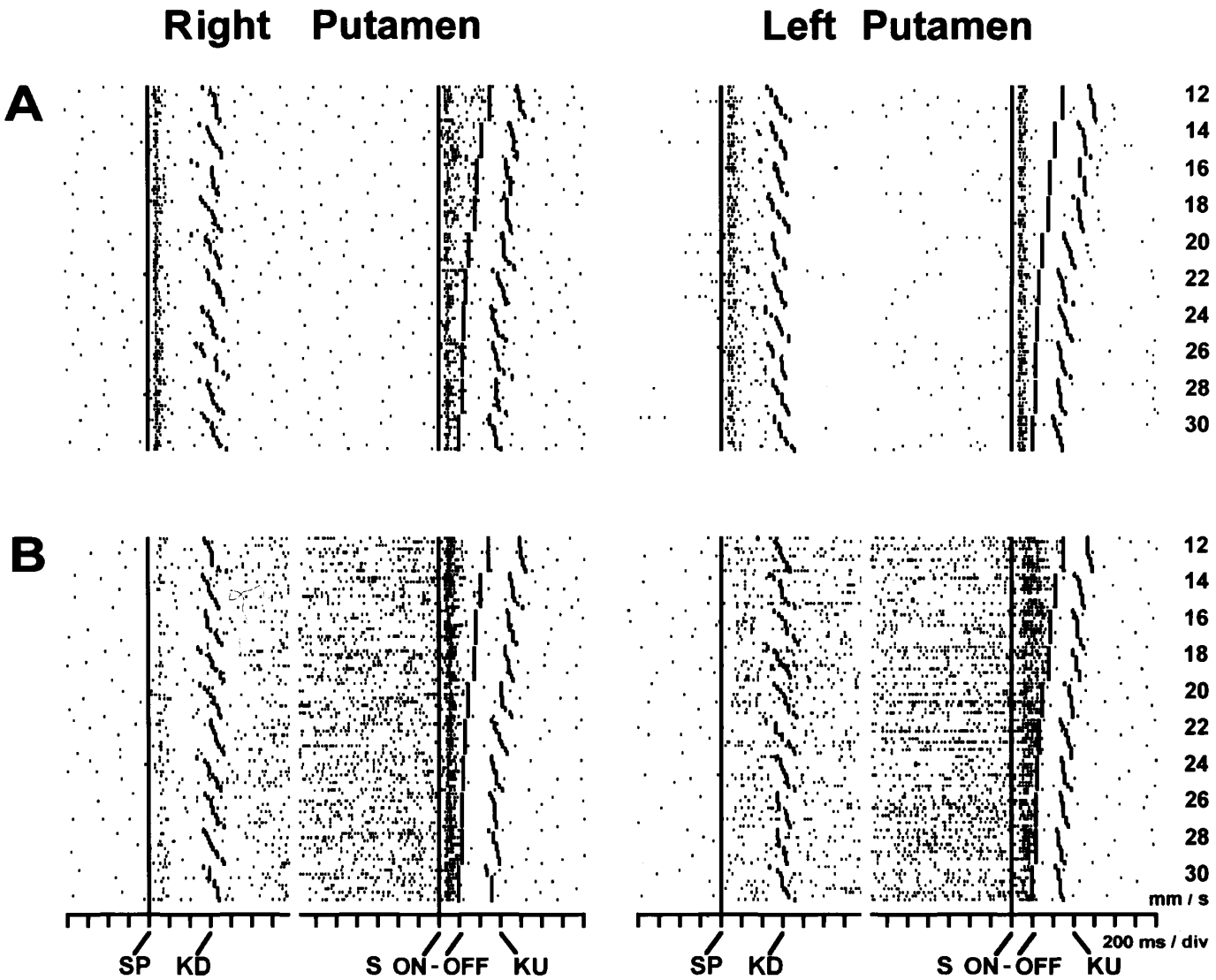

FIG. 3. Discharges of 4 putamen neurons responding exclusively during movement of the stimulus probe (type S), which had stimulus-related responses during the categorization task. Long vertical lines: beginning of SP, and beginning of the scanning. Medium vertical lines after the stimulus onset: end of the scanning. Small vertical lines: detection of indentation (KD) and end of tactile stimulation KU. These 2 events, KD and KU, are shown in rank order according to the RTs. Each line in the rasters corresponds to a single trial. *A*: 2 neurons that responded to the SP and to the moving tactile stimuli. *B*: 2 neurons that had stimulus-related responses preceded by preparatory activity developed during the delay period.

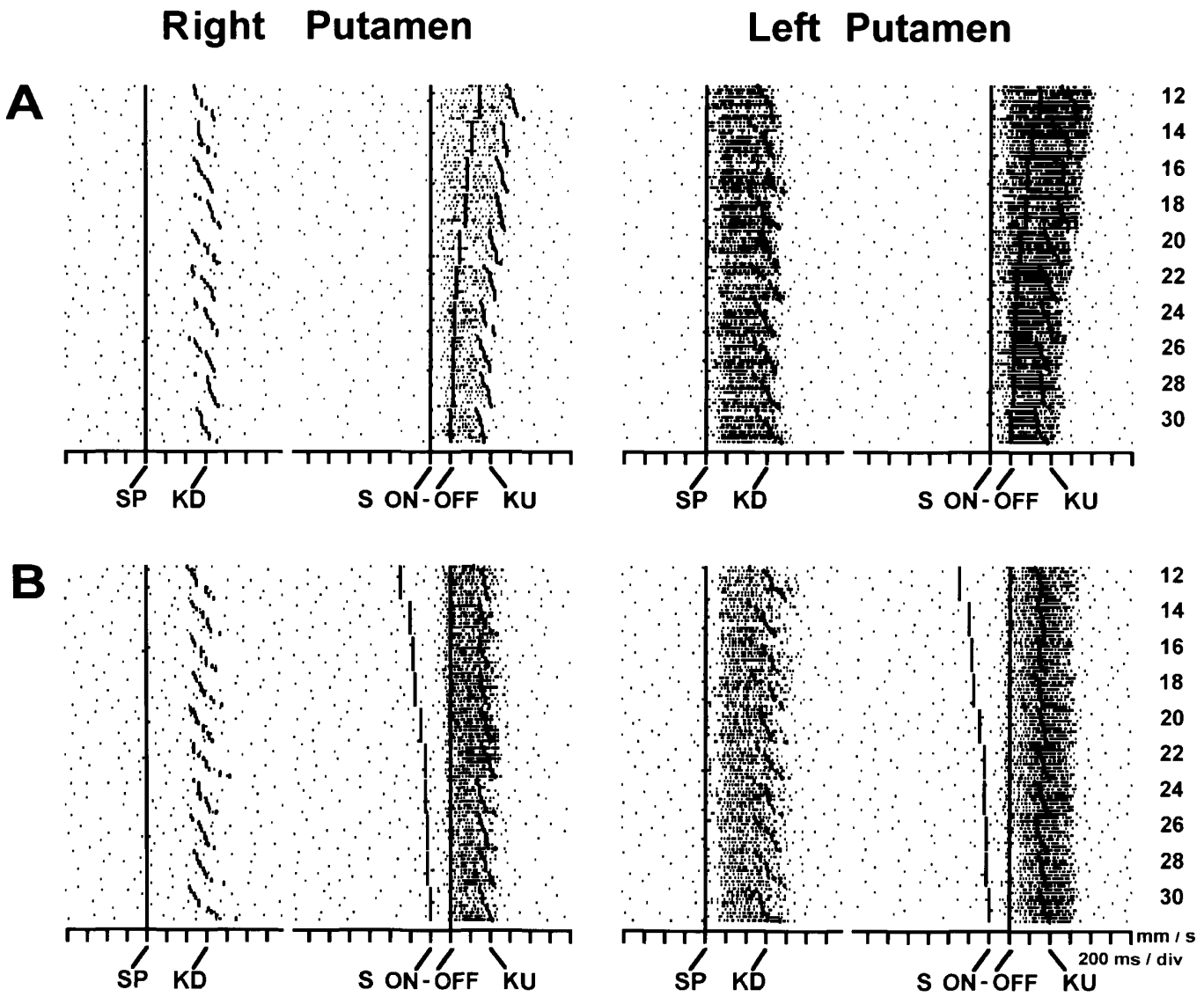

FIG. 4. *A*: discharges of 2 neurons (type SM) that responded during the stimulus period and continued discharging until the end of the RT (from stimulus on-off to KU). *B*: responses of 2 neurons (type M) that were active during the RT period. Neurons of the left putamen in *A* and *B* responded also to the SP and continued discharging until KD.

the stimulus-movement period remained close to 1. As the criterion increased further toward 40 spikes/s per trial, the proportion of responses that exceeded the criterion during the stimulus-movement period also decreased to 0. Thus, for neurons selective for low speeds, the curves corresponding to 12–18 mm/s were composed of points falling along the top and left margins of the plot. In contrast, the ROCs for speeds between 24–30 mm/s were close to the diagonal line bisecting the plot, because in this case the distributions of responses exceeding the criterion were very similar for both periods. In general, the curvature of the ROC away from the diagonal indicates the separation of the response distributions during the two periods.

It has been shown formally that the normalized area under the ROC curve corresponds to the probability with which an ideal observer can discriminate correctly in a two-alternative, forced-choice psychophysical paradigm (Green and Swets 1966), as in the present task. For a neuron selective for low speeds, the area under the ROC curves is around $P = 1$ for low speeds and around $P = 0.5$ for high speeds. The opposite is true when the neuronal discharge is associated with the categorization of high speeds. For each stimulus speed, we used this method to compute a neuron-specific value of p equal to the probability of predicting the correct choice given the cell's response. Comparisons with the psychometric data were made by fitting the resulting neurometric data with sigmoidal curves of the form described by *Eq. 1*. This function provided an excellent description of the neurometric data (χ^2 test, $P < 0.01$). The neurometric threshold was defined as the stimulus speed for which $P = 0.75$.

Histological reconstruction

Toward the end of the experiment, neuronal recording sites were marked with small electrolytic lesions by passing negative current (10 μA for 20 s) through the microelectrode at a few positions in each of several tracks. Monkeys were killed after 18–47 days of consecutive recording sessions; animals were anesthetized with ketamine (6 mg/kg) and intravenous pentobarbital sodium (40 mg/kg) and perfused through the carotids with 0.1 M phosphate-buffered saline followed by 4% paraformaldehyde in 0.1 M phosphate buffer. The brain was removed and suspended in paraformal-

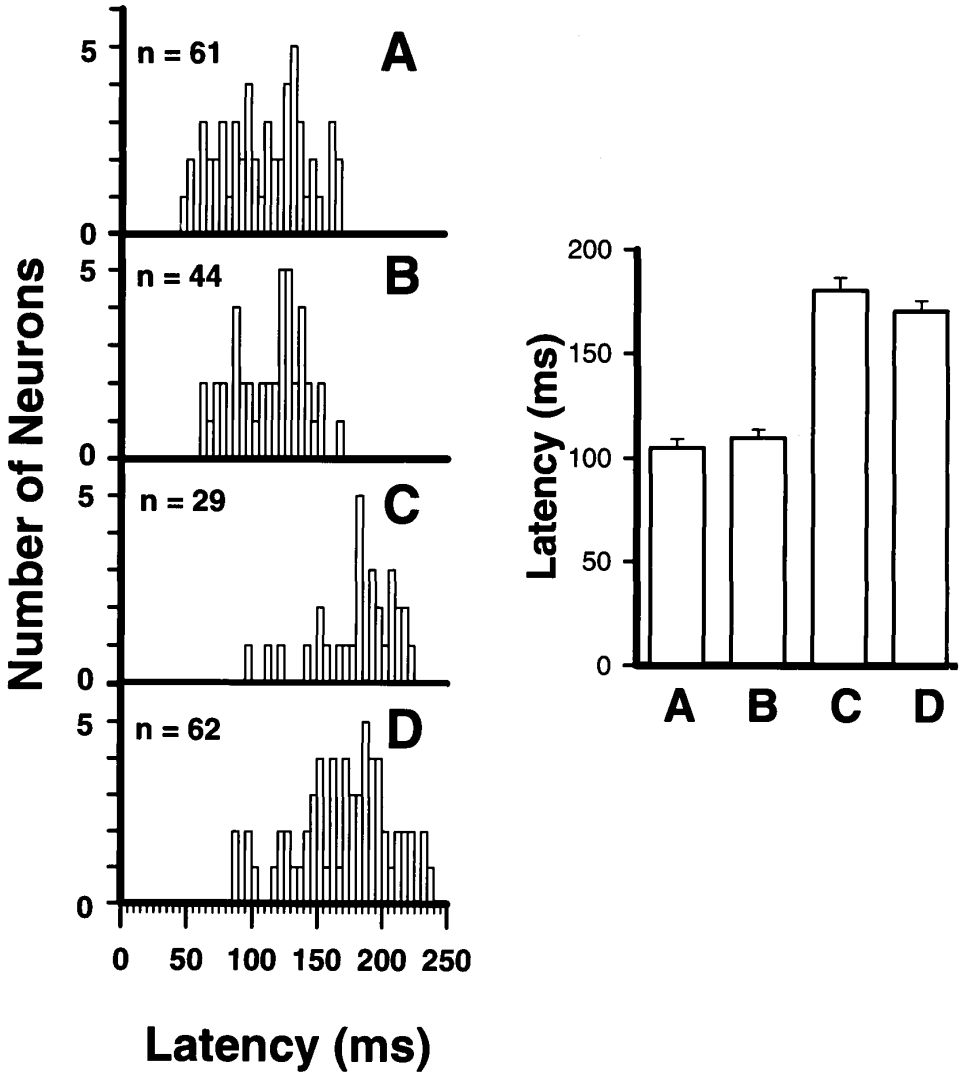

FIG. 5. *Left*: distributions of response latencies of neurons of the right (*A*) and left (*B*) putamen that had stimulus-related responses (type S), and distributions of response latencies for those neurons of the right (*C*) and left (*D*) putamen that had stimulus and movement-related responses (type SM). *Right*: response latencies (means ± SE) of the same groups shown at *left.*

dehyde. A block of the right and left hemispheres containing the neostriatum was sectioned at 50 μm and these sections were stained with cresyl violet. Neuronal positions were reconstructed with the use of the micrometer readings with reference to the microlesion marks.

RESULTS

General

The purpose of this study was to examine the responses of single neurons of the ipsilateral and contralateral putamen as monkeys categorized the speed of tactile stimuli. This was done by determining the response latencies and the magnitude and selectivity of the discharge rates relative to the stimulus speeds. Sensorimotor performance was evaluated with psychometric techniques and by measuring RT and MT during the task. In addition, we monitored the EMG activity of the EDC, BIC, and TRI of the responding arm during the categorization of the moving tactile stimuli in all neuronal recordings. In separate sessions, we recorded the EMG activity from the EDC, BIC, and TRI from the left, restrained arm and from shoulder, neck, and trunk muscles, both contralateral and ipsilateral to the moving arm. This was done to detect any phasic or tonic EMG activity in these muscles during the delay and stimulus periods. Muscles of the right arm responded after the stimuli and not during the delay period (Fig. 2). Less consistent activity was observed in the shoulder and trunk muscles both contralateral and ipsilateral to the responding arm after the stimuli. No tonic or phasic EMG activity was observed in the forearm and arm muscles of the left, restrained arm during the task. Psychometric curves were very similar throughout the study. The same was observed for motor behavior, as measured by the RTs, MTs, and EMGs.

Data base

During the somesthetic task, we recorded 1,020 neurons in the putamen contralateral to the stimulated hand (right hemisphere of 3 monkeys) and 1,660 neurons in the putamen ipsilateral to the stimuli (left hemisphere of 4 monkeys). Responses of 587 neurons of the right putamen (57.5%) and 778 neurons of the left putamen (46.8%) were associated with at least one of the behavioral events during the task. We selected 306 neurons of the right putamen and 389 of the left putamen for quantitative analysis (see Table 1). The

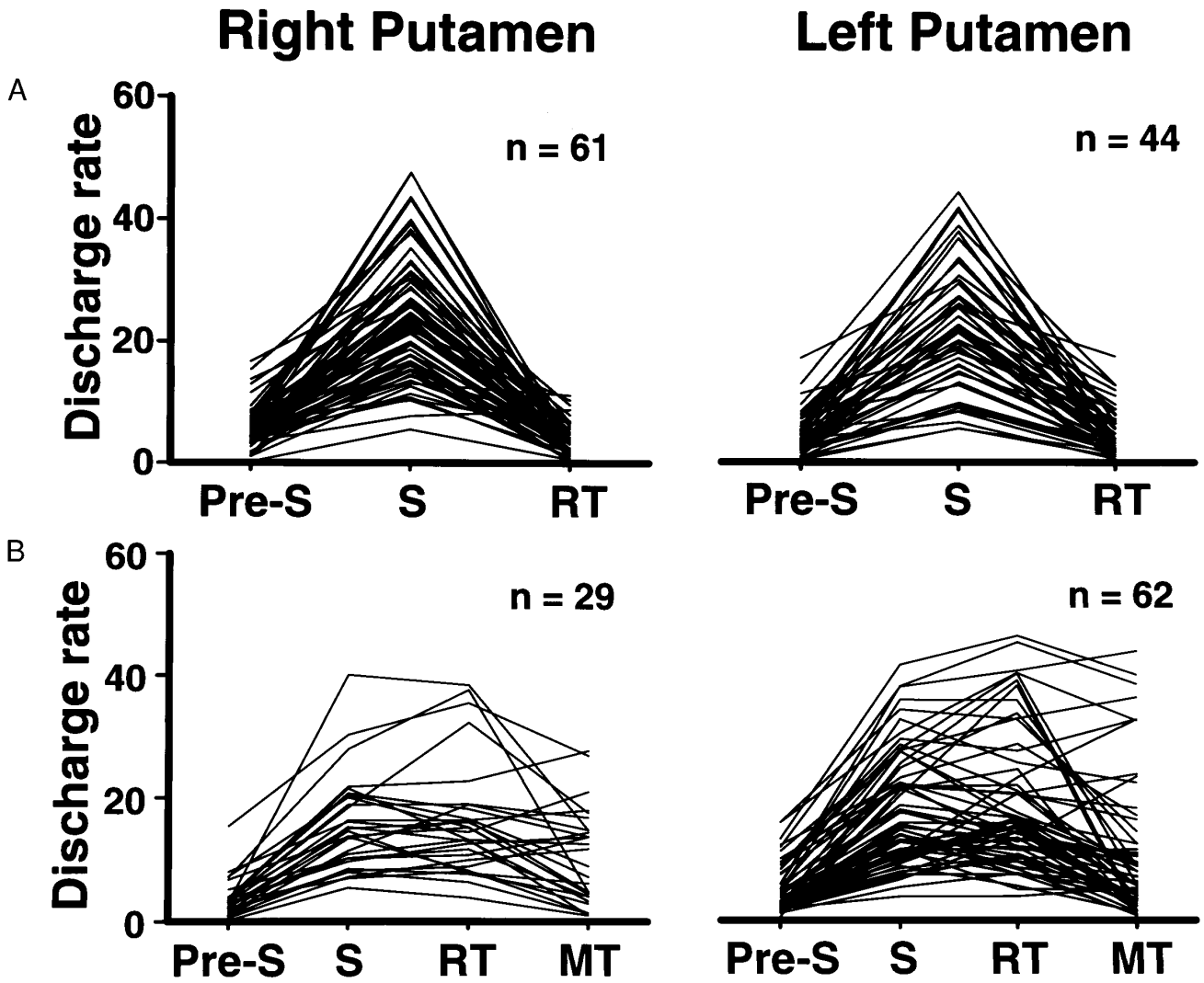

FIG. 6. Discharge rates of all type S (*A*) and type SM (*B*) neurons studied during the tactile categorization task. Pre-S: prestimulus period; S: stimulus period; RT: reaction time period; MT: movement time period.

selection criterion was that sufficient data had been collected to analyze the neuronal responses associated with any event of the task. We refer exclusively to these two selected populations of neurons.

Table 2 shows the number of neurons and the different types of neural responses recorded in the right and left putamen during the categorization task. We focused the analysis on those neurons of both hemispheres whose responses appeared related to the stimulus and to the categorization process. One type of neuron (S) responded exclusively during movement of the stimulus probe. A second type (SM) also responded during stimulation but continued discharging during the hand-arm movement. A third type of neuron (M) discharged only during the hand-arm movement, after the end of the probe sweep. These three types of neurons did not vary their response latencies and discharge rates either as functions of the stimulus speed or in relation to the differential hand-arm movements used to indicate categorization (Kruskal-Wallis test). A fourth type of neuron responded differentially and reflected whether the stimulus speed was low or high; we term these categorical or differential neurons. These were active at the same times in the trials as SM and M neurons, but were classified as differential because their responses changed with stimulus speed. There was no ambiguity in the classification, because no neurons were found with discharge rates that varied smoothly with speed, as in SI cortex (Romo et al. 1996); those putamen neurons whose activity changed as a function of speed were selective for either low or high speeds, responding similarly to speeds within the same category. We also recorded responses from a population of neurons that discharged during the delay period preceding the stimuli. These neurons with preparatory activity did not discharge during the stimulus or the hand-arm movement periods. A number of the S and SM responses were preceded by preparatory activity; these were not included in the group of neurons with preparatory activity alone (see Fig. 3*B*). Finally, we also found a number of neurons that decreased their impulse rates during the stimulus period; they will be reported elsewhere. In the present paper we refer to the analysis of the S, SM, M, and the categorical responses.

We explored the possible presence of cutaneous and deep

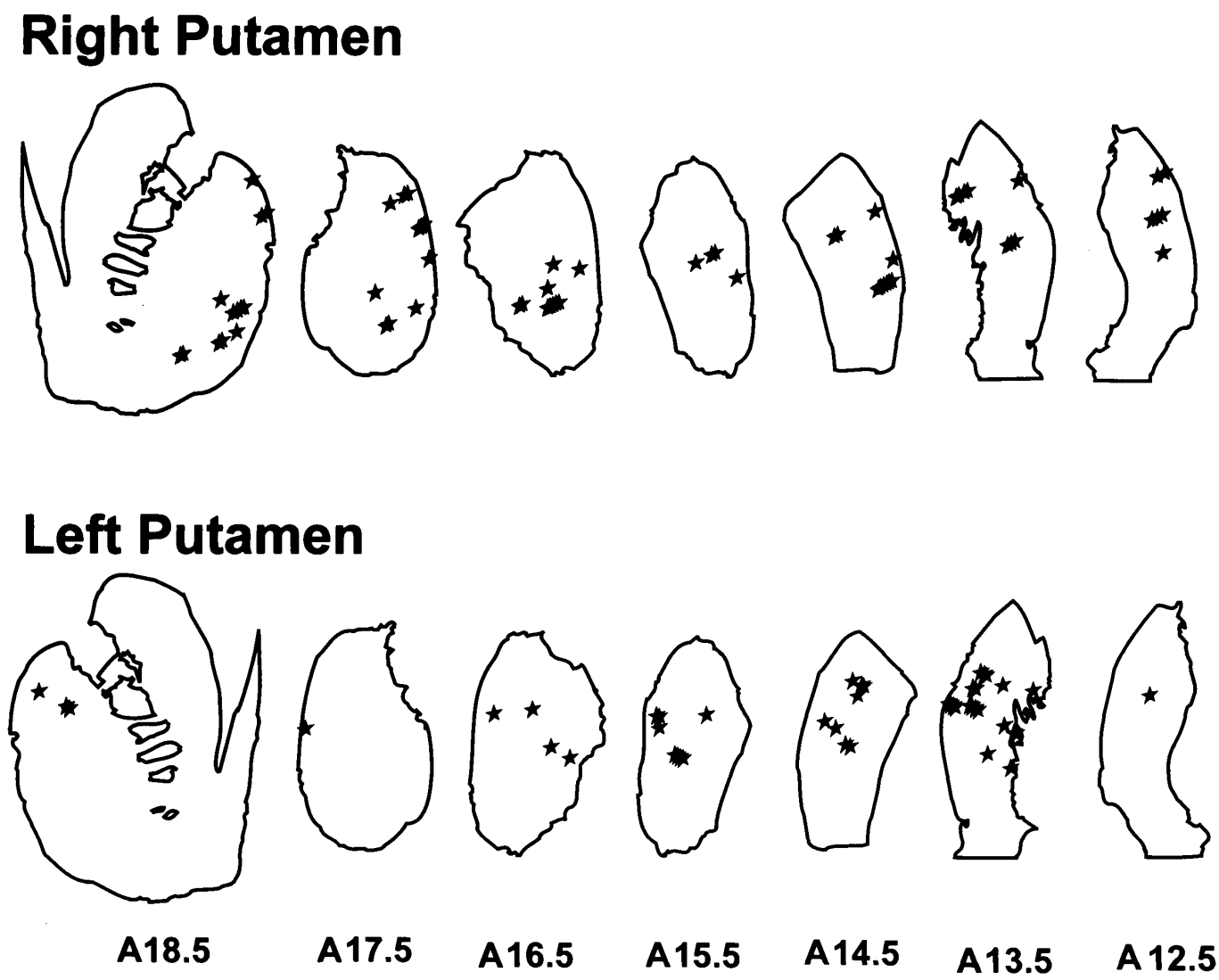

FIG. 7. Positions of type S neurons (⋆), which had stimulus-related responses during the categorization task. Data from all monkeys (3 for the right and 4 for the left putamen) are drawn on representative coronal sections labeled in stereotaxic planes (A12.5–A18.5).

receptive fields for those putamen neurons of types S and SM. This was done by listening through earphones to the activity of these neurons during manual stimulation of the skin and deep tissues of the left, restrained hand and of the free hand. We were unable to reveal cutaneous or deep receptive fields as we have described in single neurons of SI cortex (Mountcastle et al. 1990; Romo et al. 1996; Ruiz et al. 1995). If neurons of the putamen possess cutaneous receptive fields, they are very weak. For example, some S and SM neurons responded to the first touch and manipulation of the deep tissues, but repetitions failed to drive them consistently. These neurons were recorded in the territory of the putamen corresponding to the sites of projections from SI cortex (Flaherty and Graybiel 1991; Jones et al. 1978; Künzle 1977), MI cortex (Künzle 1975), and SMA (McGuire et al. 1991).

Responses to somesthetic stimuli during the categorization task

Sixty-one of the 306 neurons of the right putamen and 44 of the 389 neurons of the left putamen were classified as S, increasing their impulse rates during the stimulus period for all speeds (Fig. 3*A*). Twenty-nine neurons of the right putamen and 62 neurons of the left putamen responded similarly, but continued discharging until the end of the RT or MT period, being classified as SM (Fig. 4*A*).

S neurons of the right and left putamen had latencies of 105.8 ± 4.3 (SE) ms and 109.9 ± 4.1 ms, respectively (Fig. 5, *A* and *B*), whereas SM neurons responded later, with latencies of 180.3 ± 6.1 ms for the right putamen and 170.3 ± 4.9 ms for the left putamen (Fig. 5, *C* and *D*). The discharge rates for all S and SM neurons of the right and left putamen are shown in Fig. 6. The Wilcoxon test ($P < 0.001$) revealed significant differences in the mean impulse rates during tactile stimulation for S and SM neurons, and during the RT period for the SM neurons, compared with the control (nonstimulus) period. Thus these results reveal the presence of neurons in the putamen contralateral and ipsilateral to the stimulated hand, with responses related to the somesthetic stimuli (Figs. 7 and 8).

Visual inspection of the impulse activity revealed that a

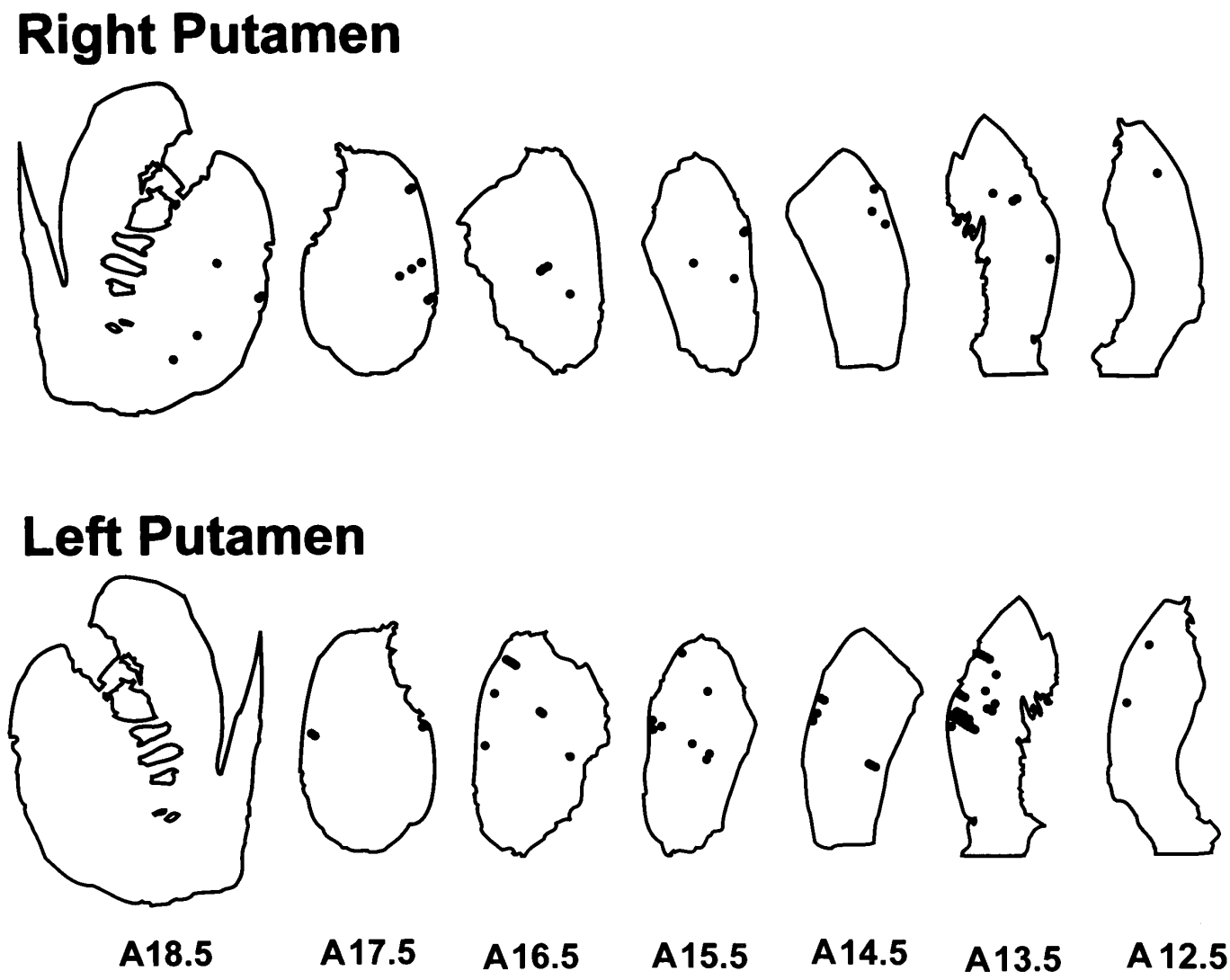

FIG. 8. Positions of type SM putamen neurons (●), which had stimulus- and movement-related responses during the categorization task.

number of S neurons of the right putamen (37 of 61) and left putamen (13 of 44) had preparatory activity during the delay period (Fig. 3*B*). Neurons in this subclass were different from those that only developed preparatory activity and did not discharge during tactile stimulation. Of these we found 47 in the right putamen and 51 in the left putamen. The response latency of the S neurons with preparatory activity was slightly shorter (right putamen: 96 ± 5.6 ms; left putamen: 93.7 ± 7.5 ms) than the response latency of those neurons with responses alone (right putamen: 122.4 ± 6.3 ms; left putamen: 116.9 ± 4.4 ms). The Mann-Whitney *U* test revealed that this difference was significant ($P < 0.001$) for both the right and left putamen. The discharge rates of the two populations were similar. Very few SM neurons of the right ($n = 2$) and left ($n = 5$) putamen were preceded by preparatory activity, precluding any further analysis.

A number of S and SM neurons of the right and left putamen also responded to the SP at the beginning of a trial. We found 40 S and 5 SM neurons in the right putamen, and 20 S and 27 SM neurons in the left putamen, with this characteristic. Figure 3 shows two S neurons and Fig. 4*A* shows one SM neuron that responded to the SP. Of these neurons, those of type S had a latency after SP (104 ± 5.3 ms for the right putamen and 100.3 ± 6.4 ms for the left putamen) similar to the response latency beginning with the moving tactile stimuli (96.7 ± 4.6 ms for the right putamen and 107.2 ± 5 ms for the left putamen). For SM neurons, the latency after SP (145.5 ± 31 ms for the right putamen and 159.4 ± 8.5 ms for the left putamen) was also similar to the latency beginning with the moving tactile stimuli (148.7 ± 23 ms for the right putamen and 164.7 ± 8.1 ms for the left putamen). These responses were time locked to the SP, because there was no relation between the response latencies and the detection of the SP, determined by KD ($r < 0.53$, where r represents the average correlation for the population responding to the SP). A similar result was found for the neural responses elicited by the moving tactile stimuli:

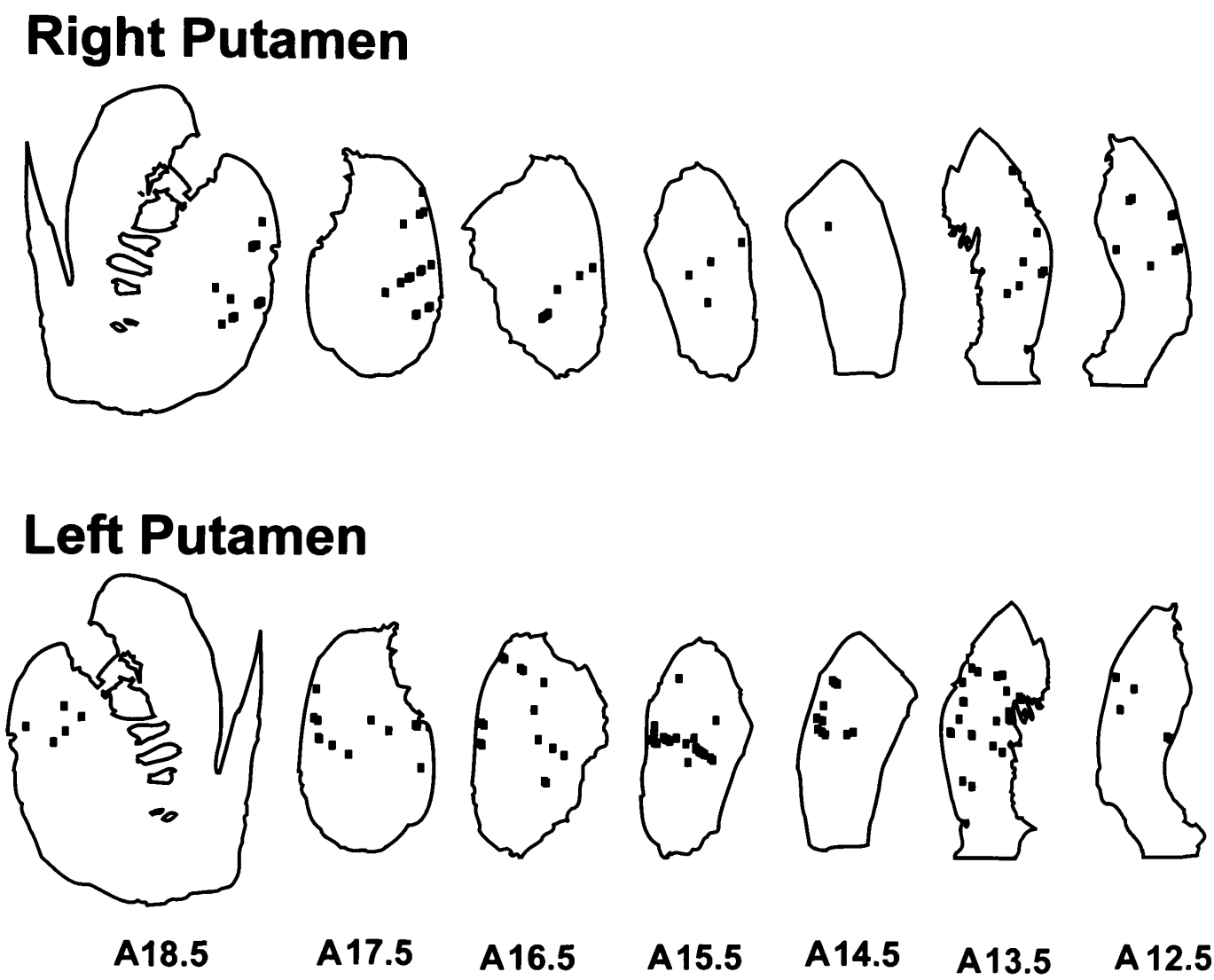

FIG. 9. Positions of type M putamen neurons (squares), which had movement-related responses during the categorization task.

the latencies were time locked to the beginning of the stimuli and not to the detection of the end of the stimuli, determined by key release ($r < 0.58$).

Responses to the hand-arm movement during the categorization task

During the categorization task, 53 of the 306 neurons of the right putamen and 114 of the 389 neurons of the left putamen were classified as type M, discharging during the movement of the right hand-arm made in response to the tactile stimuli (Fig. 4*B*). This type of response was found in both hemispheres, despite the fact that the movement indicating the speed category was made with the right hand-arm (Fig. 9). Passive movements of the right hand-arm by the experimenter from the key to the target switches modulated the impulse activity of all these neurons.

Categorical responses

We found 85 of 306 neurons in the right putamen and 78 of 389 in the left putamen that discharged differentially (Fig. 10) for low or high stimulus speeds. These responses, which we term categorical, were determined by the statistical differences in the discharge rates obtained during the categorization of low and high speeds (Kruskal-Wallis test, $P < 0.05$). We found no differences in discharge rate for speeds belonging to the same category. The differential responses occurred at the end of the stimulus period and during the hand movement period (see Table 3). We determined the response latencies for those neurons that started discharging differentially at the end of the tactile stimulation. Neurons of the right putamen had a latency of 224.01 ± 5.3 ms and those of the left putamen had a latency of 203 ± 6.5 ms. These numbers were measured with respect to the beginning of probe movement, and take into account neurons selective for low speeds as well as neurons selective for high speeds; we found no significant differences in latency between them. Thus the activity of some neurons in the putamen contralateral and ipsilateral to the stimulus reflected whether the stimulus speed was low or high, correlating with the speed categories involved in the task (Fig. 11).

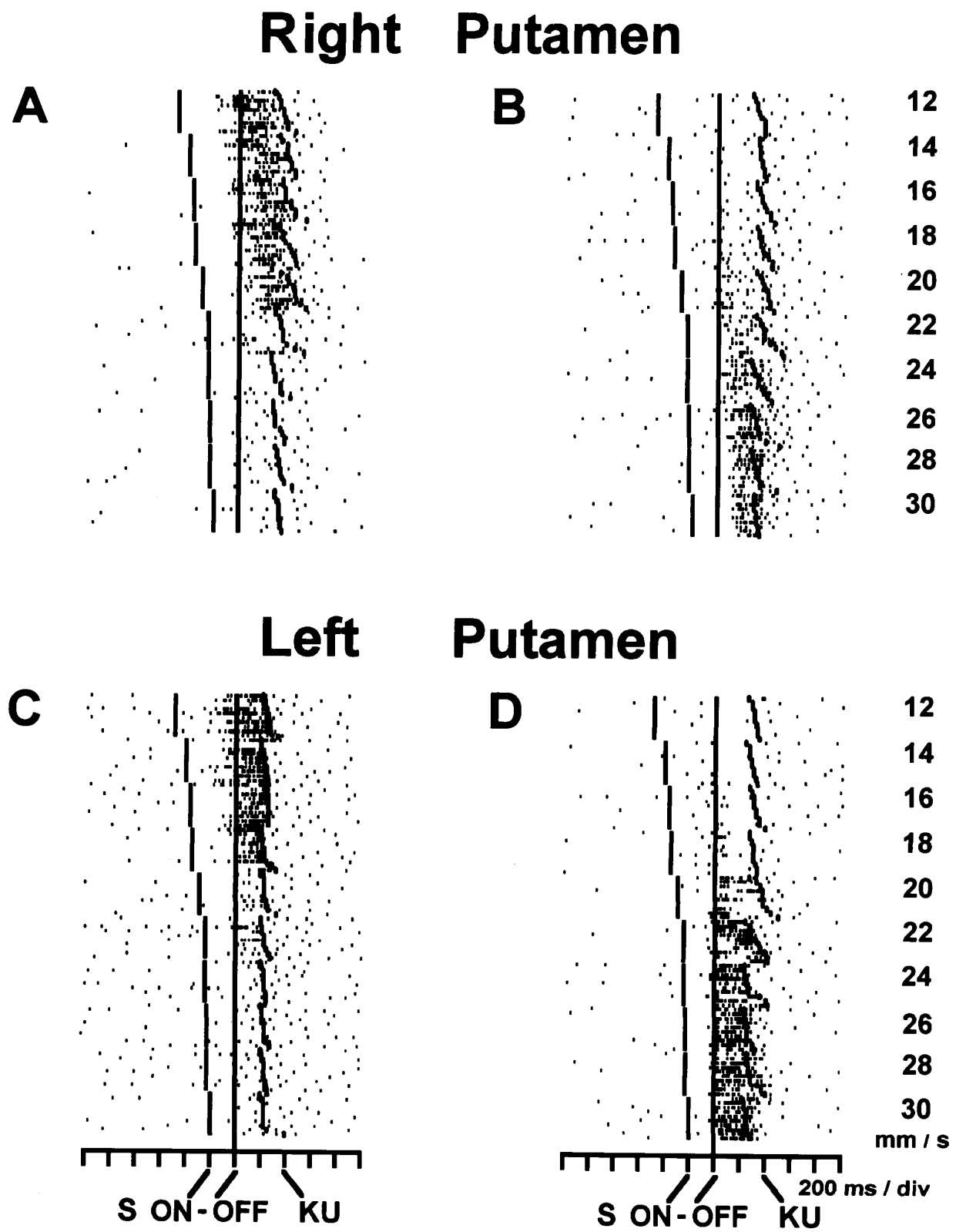

FIG. 10. Discharges of 4 categorical neurons of the right and left putamen, which showed differential responses during the categorization task. *A* and *C*: examples of responses selective for low-speed stimuli. *B* and *D*: examples of responses selective for high-speed stimuli.

TABLE 3. *Putamen neurons with differential responses during the stimulus and arm movement in the categorization task*

	Stimulus Speeds		
	Low (12–20 mm/s)	High (22–30 mm/s)	Total
Right putamen			
SM	37	2	39
M	26	20	46
Totals-r	63	22	85
Left putamen			
SM	7	2	9
M	32	37	69
Totals-l	39	39	78
Totals	102	61	163

These differential responses were determined according to the Kruskal Wallis test ($P < 0.05$). SM, stimulus-movement; M, movement.

Comparison between correct and incorrect categorizations

As shown in Table 4, the mean values of the RTs and MTs for the S, SM, M, and categorical neurons remained constant in the study. According to these measurements, the motor behavior of the animals was very regular throughout the experimentation period. When we examined the motor behavior during correct and incorrect categorizations, we found that the RTs for trials in which categorization was incorrect were longer than those for trials in which categorization was correct. However, the MTs during correct and incorrect categorization remained constant.

When the response latencies were analyzed for S and SM neurons, we found no substantial differences between correct and incorrect categorizations in the right putamen (S: 105.8 ± 4.3 ms for correct and 111.3 ± 5.4 ms for incorrect categorizations; SM: 180.1 ± 6.7 ms for correct and 179.9 ± 9 ms for incorrect categorizations). However, S neurons of the left putamen delayed their responses, from 109.9 ± 4.1 ms for correct to 149.5 ± 8.1 ms for incorrect categorizations (Wilcoxon test, $P < 0.002$). The latencies of SM neurons of the left putamen remained constant (169.7 ± 5.5 ms for correct and 169.9 ± 6.1 ms for incorrect categorizations). Therefore only the S neurons of the left putamen, ipsilateral to the stimuli and contralateral to the responding arm, delayed the onset of their discharges when the animal made incorrect categorizations of the stimulus speeds. No substantial changes in the discharge rates of the S and SM neurons were detected in either hemisphere between correct and incorrect categorizations.

Responses during the passive delivery of stimuli

We compared the responses of 36 neurons of the right putamen (19 S, 6 SM, and 11 categorical) and 30 neurons of the left putamen (8 S, 13 SM, and 9 categorical) in two conditions: during categorization and when the same set of stimuli was delivered passively. In this situation the stimuli were identical to those delivered during the categorization task, but the animal's key was removed and the right hand-arm movements were restricted; the movement speeds were chosen from the same set used for the categorization task. Of the S neurons, 12 of 19 from the right putamen and 4 of 8 from the left putamen responded to passive delivery of stimuli (Fig. 12, *A* and *B*). This was not the case for the SM neurons (Fig. 12*C*) and the categorical neurons (Fig. 13, *A* and *B*), because none of them, in either hemisphere, responded in the passive condition. The discharge rates of those S neurons that were active during passive stimulation were smaller than during the categorization task (Figs. 12*A*). Interestingly, the neurons that responded in both conditions had shorter latencies during categorization (84.5 ± 7.8 ms for the right putamen and 86.5 ± 10 ms for the left putamen) than during passive stimulation (108.1 ± 9.3 ms for the right putamen and 112.6 ± 9.4 ms for the left putamen). These results demonstrate that about half of the S neurons, but none of the SM and categorical neurons, respond to passive stimulation.

Responses during the light instruction task

We tested, in the light instruction task, 99 neurons of the right putamen (28 S, 14 SM, 16 M, and 41 categorical) and a total of 106 neurons of the left putamen (14 S, 23 SM, 31 M, and 38 categorical) that also responded in the categorization task. The neuronal discharges occurred after the light was turned off and the skin probe was lifted; these were the trigger stimuli for initiation of the arm movement toward the target switches. Twenty-three of 28 S neurons from right putamen and 10 of 14 neurons from the left putamen responded to the trigger stimuli (Fig. 14), with latencies of 104.9 ± 5.9 ms and 121.1 ± 11.1 ms, respectively. No statistically significant differences were found compared with the response latencies occurring during the categorization task (right putamen: 97.5 ± 7.2 ms; left putamen: 109.3 ± 9 ms). For SM neurons, 7 of 14 from the right putamen and 13 of 23 from the left putamen responded to the trigger stimuli (Fig. 15), with latencies of 174.2 ± 14.6 ms and 162.2 ± 14.4 ms, respectively. These latencies were also similar to those occurring during the categorization task (189.7 ± 7.9 ms for the right putamen and 151 ± 12.8 ms for the left putamen). For the M neurons, 13 of 16 from the left putamen and 28 of 31 from the right putamen responded during the RT-MT. In contrast, only 5 of 41 differential neurons in the right putamen, and 13 of 38 in the left putamen, maintained their differential responses during the light instruction test (Figs. 16 and 17). The discharge rates of the S, SM, M, and categorical neurons in both hemispheres were similar in the two tasks. According to these results, a considerable number of neurons in the putamen respond exclusively during the categorization task.

Neural coding of speed categories

Those neurons of the right and left putamen that discharged selectively for low or high stimulus speeds were reanalyzed to produce a quantitative measure comparable with the psychometric function (see METHODS). A neurometric curve was thus computed for each categorical neuron. The individual neurometric curves were averaged among cells with the same selectivity. Table 5 specifies the numbers of categorical neurons of each type. Figure 18 compares the resulting population average neurometric curves with the psychometric curves describing the animals' behavior. In each plot there is considerable

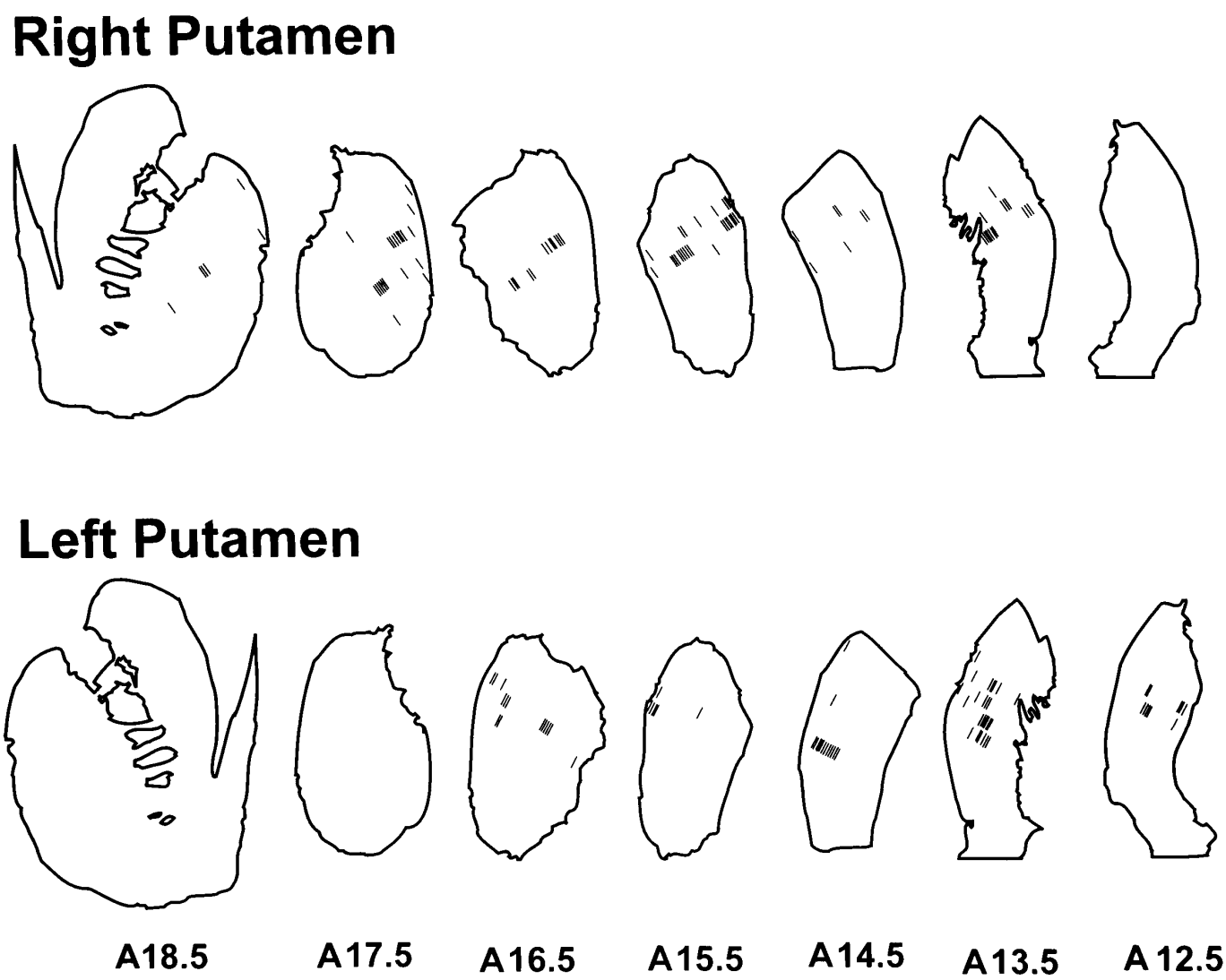

FIG. 11. Positions of the categorical neurons (bars) in the putamen.

TABLE 4. *Reaction and movement times during the study of the stimulus, stimulus-movement, movement related, and categorical related neurons of putamen*

	RT		MT	
	Correct	Incorrect	Correct	Incorrect
Right putamen				
S	340.0 ± 6.1	370.6 ± 7.8*	216.7 ± 3.4	224.6 ± 5.9
SM	358.6 ± 7.5	418.6 ± 14.8*	217.9 ± 5.1	218.9 ± 6.8
M	353.6 ± 3.3	404.0 ± 5.8*	225.0 ± 4.2	232.0 ± 7.6
Categorical	368.6 ± 3.9	403.9 ± 7.0*	224.7 ± 3.9	230.5 ± 4.6
Left putamen				
S	360.5 ± 5.5	415.2 ± 10.5*	216.0 ± 4.3	218.1 ± 5.2
SM	358.9 ± 5.2	400.7 ± 9.9*	224.4 ± 4.2	232.2 ± 7.0
M	353.6 ± 3.3	404.0 ± 8.8*	230.0 ± 3.2	232.0 ± 5.6
Categorical	368.7 ± 4.7	419.7 ± 8.3*	246.5 ± 5.8	244.1 ± 6.2

Values are mean ± SE. RT, reaction time; MT, movement time; S, stimulus; SM, stimulus movement; M, movement. * Means statistical significant differences between correct and incorrect categorizations ($P < 0.05$, Mann-Whitney U test).

overlap between the two kinds of curves in the range of speeds each subpopulation of neurons was selective for. Because the populations responding to low and high speeds were analyzed separately, in the plots the two curves agree with each other for about half of the total range of speeds used. We also computed, for each neuron from a given monkey, the ratio between the threshold of its neurometric curve and the threshold of the psychometric curve of the monkey obtained during the recording session. Figure 19 shows the resulting distributions of threshold ratios; they are centered around values that are close to 1. The mean threshold values calculated from these distributions confirm the agreement between neuronal and behavioral data: in the right putamen we found, for low and high speeds, 20.77 and 20.33 mm/s, respectively, very close to the 20.32 mm/s for low and 20.74 mm/s for high speeds found psychometrically. Similar results were obtained in the left putamen: the neurometric thresholds for low and high speeds were 19.89 and 20.81 mm/s, respectively, and the psychometric thresholds were 20.64 and 20.68 mm/s.

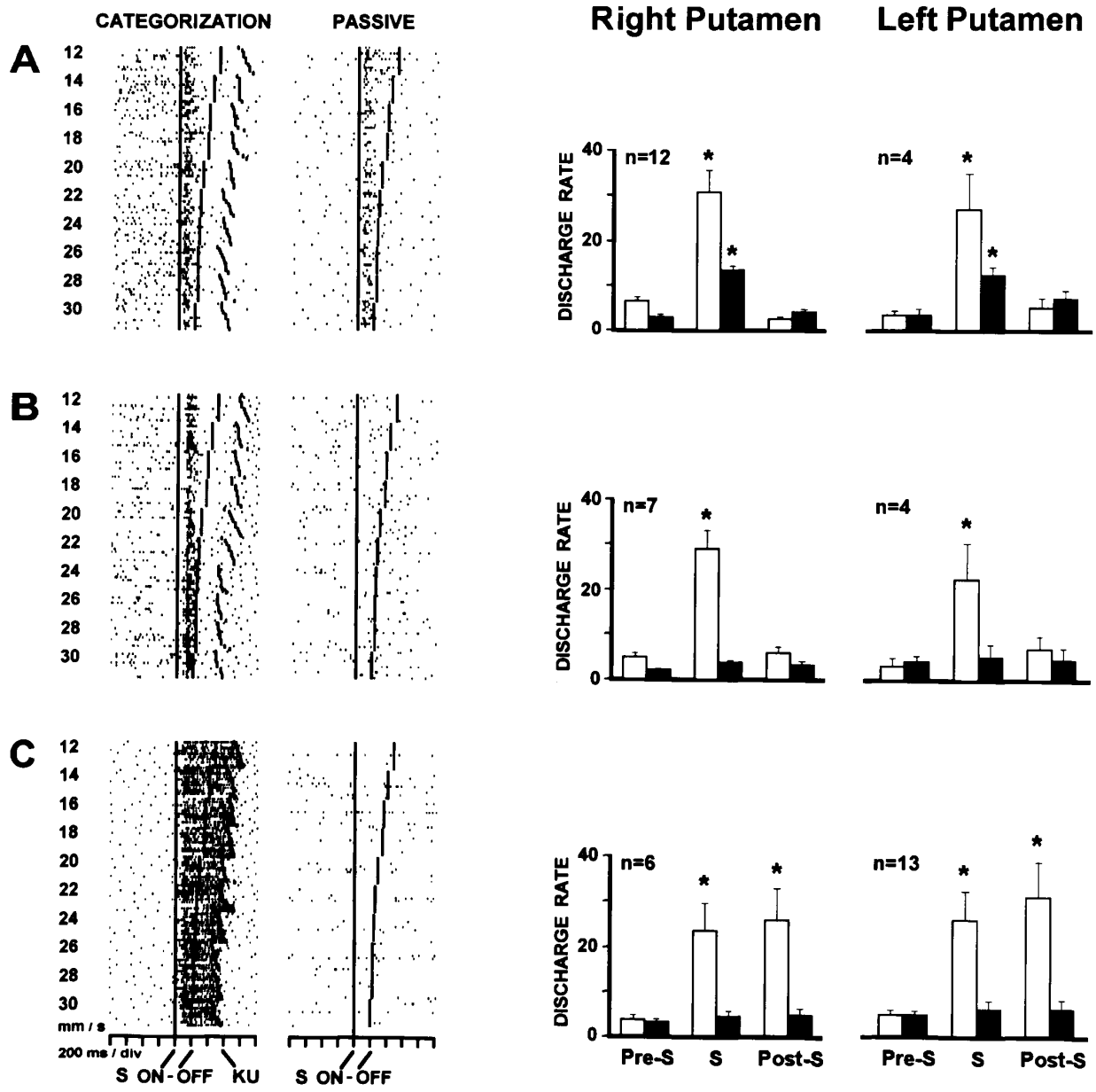

FIG. 12. *Left*: responses of 3 neurons studied during the categorization of stimulus speeds and when the same stimuli were delivered passively. *A*: S neuron that responded both during categorization and during passive stimulation. *B*: S neuron that responded during the categorization task but did not respond during passive stimulation. *C*: SM neuron that responded during the categorization task but did not respond in the passive mode. *Right*: discharge rates (means ± SE) of the 3 types of neurons shown from *A* to *C*. Open bars: responses during the categorization task. Black bars: responses during passive stimulation. Pre-S: prestimulus period; S: stimulus period; Post-S: poststimulus period. Asterisk: statistically significant differences between the prestimulus and stimulus or poststimulus periods (Wilcoxon test, $P < 0.001$).

DISCUSSION

This study addresses whether the putamen is involved in somesthetic perception. We assumed that somesthetic processing had to be investigated not only in SI cortex, but also in those cortical and subcortical structures anatomically linked to SI cortex, which include sensory and motor areas as well. Three major observations were made in the present study. First, we recorded a number of neurons in the putamen whose activities are associated with the sensory stimuli and/or with the behavioral motor reaction, although they encode neither the physical characteristics of the stimuli (i.e., the speed) nor the categorization process. Second, we also found neurons whose activity reflects the categorization of the stimulus speeds, suggesting that the putamen is involved in the animal's decision making process. Third, both kinds of neuronal responses were detected bilaterally, suggesting that this region of the striatum may be involved in bimanual sensorimotor tasks. We focus the discussion on these three issues.

Nature of the stimulus and movement-related responses

Single-neuron recordings in the putamen contralateral (right) and ipsilateral (left) to the stimulated hand during the

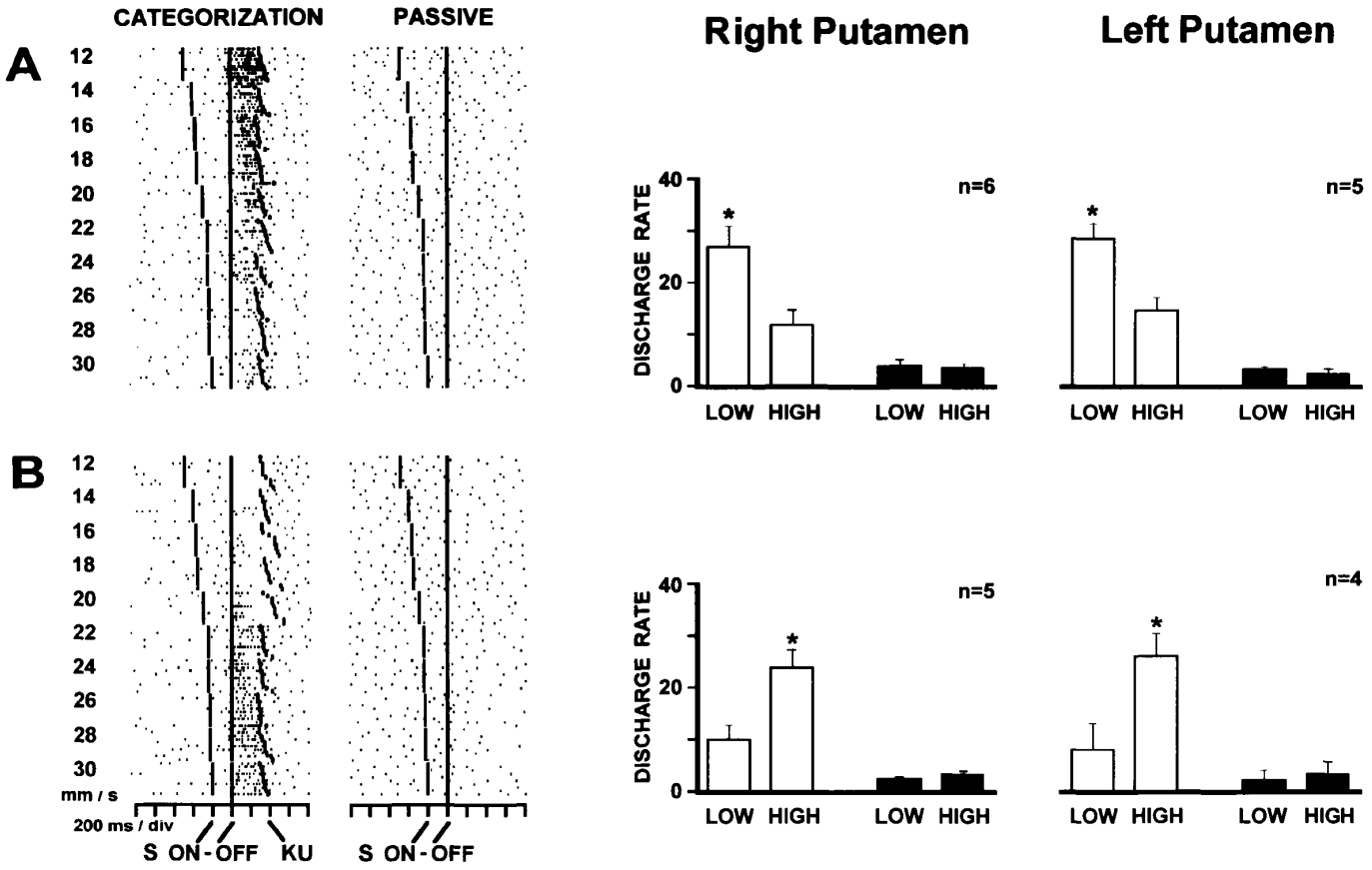

FIG. 13. *Left*: responses of 2 categorical neurons that were studied during the categorization of stimulus speeds and when the same stimuli were delivered passively. *A*: responses of a neuron activated during the RT period and selective for low-speed stimuli. This cell is unresponsive during passive stimulation. *B*: responses of a neuron also active during the RT period but selective for high-speed stimuli. This cell did not respond during the passive stimulation either. *Right*: discharge rates (means ± SE) of the categorical neurons that were tested in the passive mode. Open bars: responses during the categorization task. Black bars: responses during passive stimulation. Asterisk: statistically significant differences between the neuronal discharges during low vs. high speeds (Wilcoxon test, $P < 0.01$).

categorization task revealed a type of neuron that responded during the stimulus period (S neurons). A second type behaved similarly but continued discharging until the end of the behavioral motor reaction (SM neurons). S neurons of the right and left putamen began their responses, on average, almost simultaneously (105.8 ± 4.3 ms and 109.9 ± 4.1 ms), despite a wide variability in the individual response latencies. SM neurons also showed similar latencies in both hemispheres (right putamen: 180.3 ± 6.1 ms; left putamen: 170.3 ± 4.9 ms), although they began their discharges after the S neurons. According to these numbers, S neurons discharge before SM neurons. This suggests, in this somesthetic task, the presence of a sensorimotor continuum of activity initiated with the stimulus and ending with the behavioral motor reaction.

Considering these neural responses, one wonders what is the input that drives these putamen neurons. We can exclude the somesthetic input from SI cortex, because neurons in this area tested in the same task respond to the contralateral stimulus with a mean response latency of 25.8 ± 0.6 ms (Romo et al. 1996), and this cortical region does not send bilateral projections to the putamen (Flaherty and Graybiel 1991; Jones et al. 1978; Künzle 1977). The input to the putamen may come from the SMA or MI cortex; it has been shown that both areas send bilateral projections to the putamen (Künzle 1975; McGuire et al. 1991). Interestingly, we have recorded neurons in the SMA with the use of the same task (unpublished data), and found the same repertoire of responses found in the right and left putamen. However, from the response latencies we found that the S neurons of the putamen responded slightly before the S neurons of the SMA (123 ms), whereas the SM neurons of the putamen respond slightly after the SM neurons of the SMA (right SMA: 152.4 ± 2.9 ms; left SMA: 145.7 ± 3.5 ms). Although these measurements indicate small differences in the response latencies of these two areas, there is a considerable overlap in the individual latency distributions.

The discharge rates of the S and SM neurons of the putamen did not vary as functions of the stimulus speed during the categorization task. Thus this activity does not encode the physical properties of the stimuli or the categorization process. Similar neuronal responses were found in the SMA in the same task (unpublished data). This similarity suggests that the putamen and SMA contain neurons that share the same functional properties. Interestingly, similarities in the response patterns of SMA and putamen neurons have been described in different motor paradigms (Alexander and Crutcher 1990a,b; Crutcher and Alexander 1990; Romo and

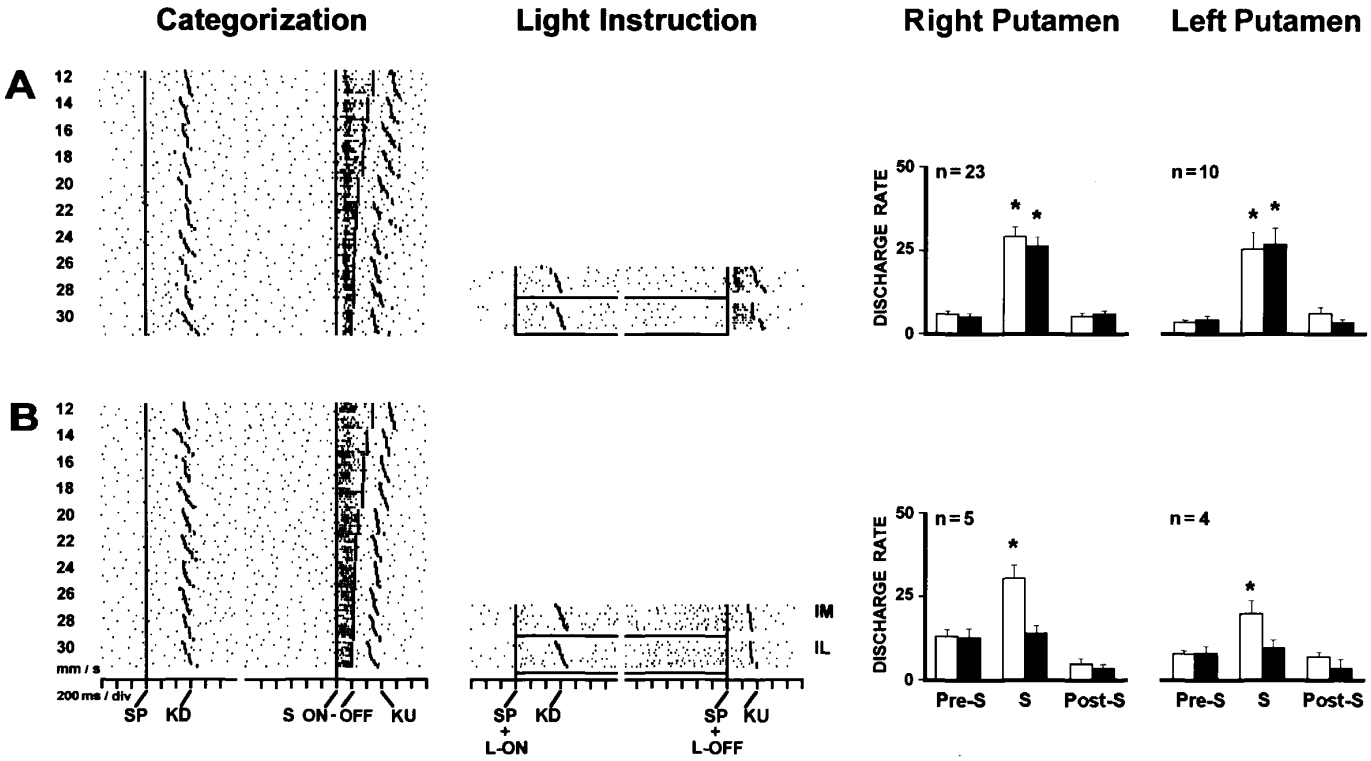

FIG. 14. *Left*: rasters from 2 type S neurons that responded (*A*) or did not respond (*B*) in the light instruction task, in which visual stimuli indicated initiation of the hand-arm movement toward 1 of the 2 target switches. In the light instruction task, trials were aligned with the SP, simultaneous with turning the target light on (SP + L-ON), and with retraction of the probe, simultaneous with turning the light off (SP + L-OFF). IM, instruction for pressing the medial push button; IL, instruction for pressing the lateral push button. *Right*: histograms showing discharge rates (means ± SE) of the populations represented in *A* and *B*. Open bars: responses during the categorization task. Black bars: responses during passive stimulation. Asterisk: statistically significant differences between the prestimulus vs. stimulus or poststimulus periods (Wilcoxon test, $P < 0.01$).

Schultz 1992; Romo et al. 1992; Schultz and Romo 1992). However, in these studies recordings were always made contralateral to the responding arm. Our findings demonstrate bilateral processing in the putamen and SMA during the sensory somesthetic task. This similarity suggests that both areas are important for sensorimotor transformations, such as the conversion of a sensory signal into a neural motor signal that may contribute to the initiation of a behavioral motor reaction. On the other hand, these sensorimotor transformations may be relevant for the bimanual manipulation of objects. Indeed, neurophysiological and lesion studies suggest that the SMA is involved in bimanual tasks (Brinkman 1984; Tanji et al. 1987).

The observed motor activity in the putamen could depend on the bilateral inputs from MI cortex or from the SMA (Künzle 1975; McGuire et al. 1991). Indeed, in this task the left MI cortex (unpublished results) and the right and left SMA (unpublished data) discharge during the right hand-arm movement toward the target switches, whereas the right SI cortex responds to the left, stimulated hand (Romo et al. 1996). This suggests that in this task, sensory processing begins in SI cortex contralateral to the stimulated hand and the output of the motor process occurs in the MI cortex contralateral to the responding arm. However, between SI and MI cortex there is bilateral sensorimotor activity in the SMA and putamen. Further experiments are needed to unravel the functional meaning of these bilateral neural responses in the present task.

Half of the S neurons responded during the passive delivery of the somesthetic stimuli used in the categorization task. This was not the case for the SM neurons, because none of them discharged in this situation. It would seem as if S neurons were closer to the cortical somesthetic input than the SM neurons. However, a majority of the observed responses were task dependent. The fact that there are neurons of S and SM types in the putamen suggests that they are associated with the hand-arm movement triggered by the stimulus, contributing to the initiation of the motor response that follows. In fact, previous studies performed in the putamen have also shown single-neuron responses to sensory cues when the animal uses the cues to perform hand-arm movements (Gardiner and Nelson 1992; Kimura 1990; Romo et al. 1992; Schultz and Romo 1988). Therefore the S and SM responses may be interpreted as produced by movement-triggering neurons.

To test this possibility, we studied some of the S and SM neurons in a light instruction task, in which the animal had to perform exactly the same hand-arm movements as in the somesthetic task, but following a visual trigger signal. Half of the S and SM neurons responded to the visual trigger, which is consistent with the idea that these neurons play a role in the initiation of behavioral motor reactions. However,

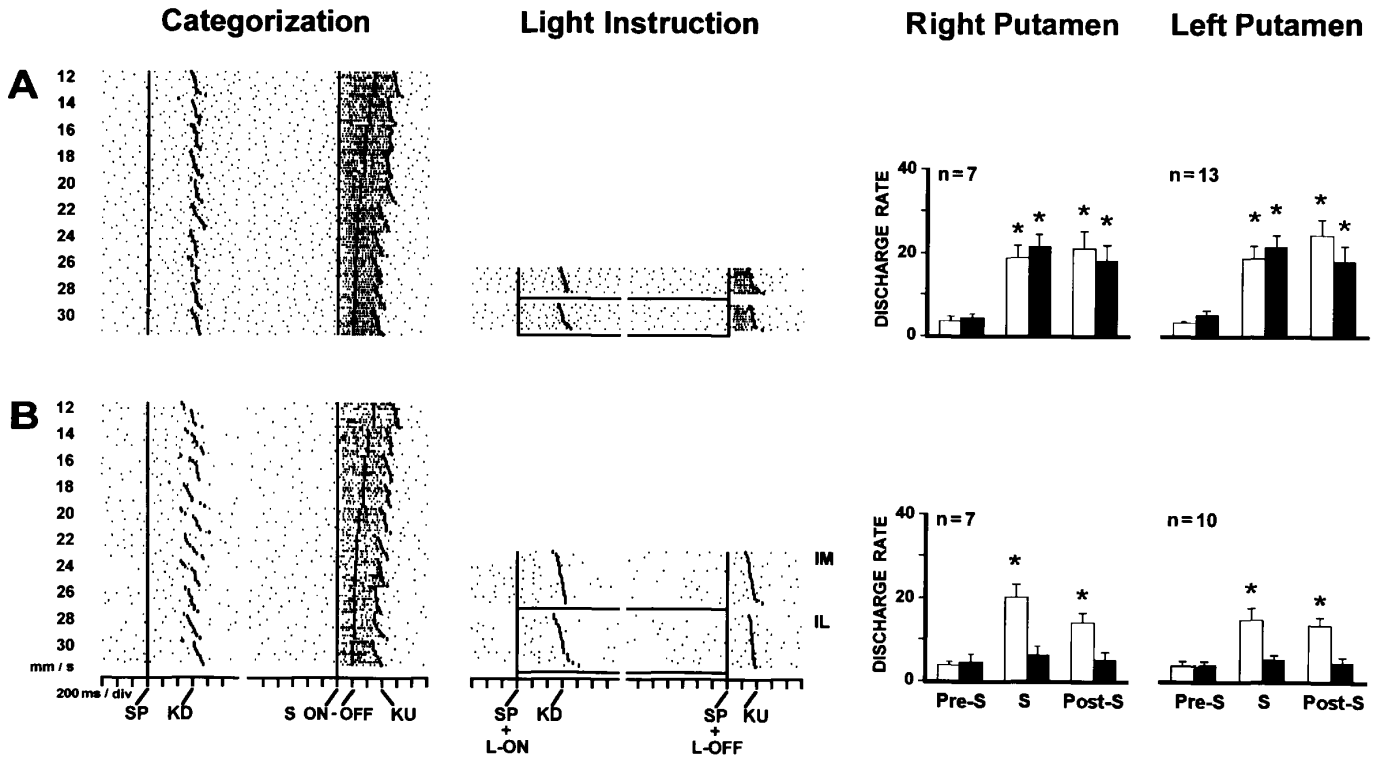

FIG. 15. Rasters from 2 type SM neurons that responded (*A*) or did not respond (*B*) in the light instruction task. Asterisk: statistically significant differences between the prestimulus vs. stimulus or poststimulus periods (Wilcoxon test, $P < 0.001$). All other symbols as in Fig. 14.

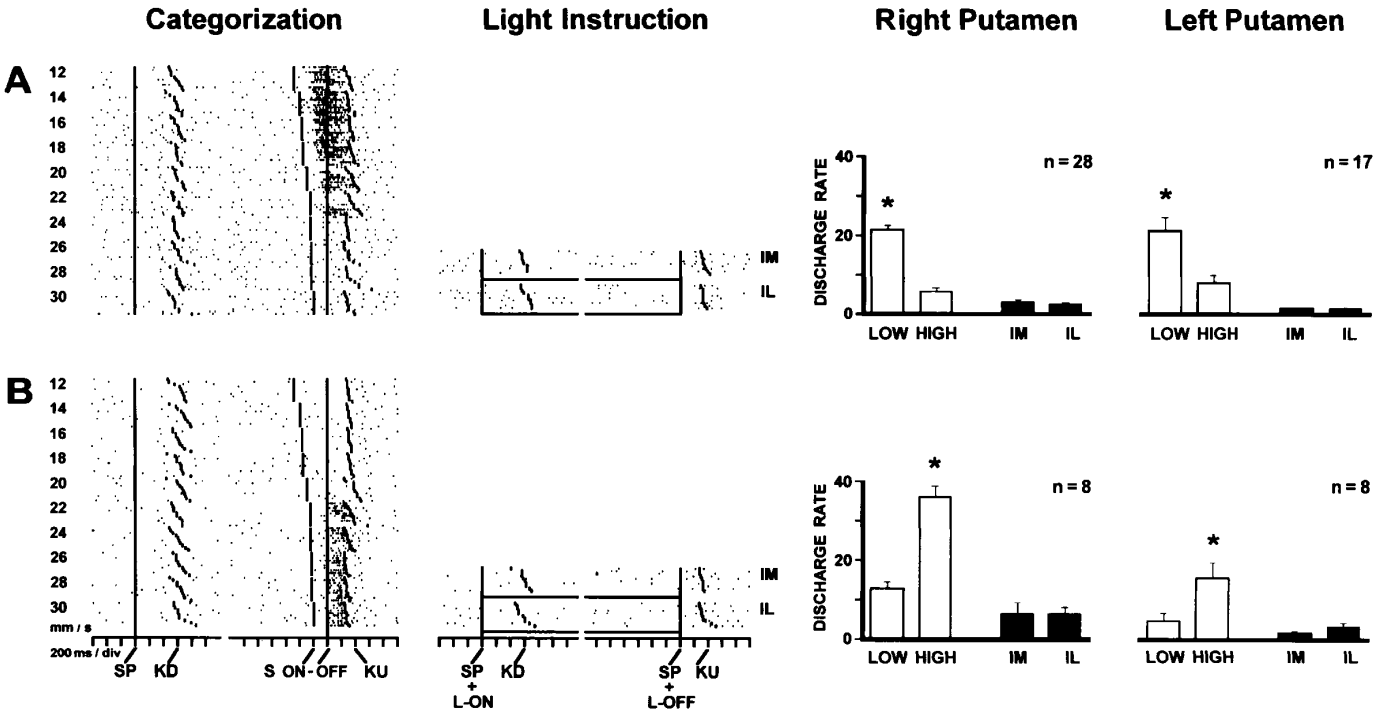

FIG. 16. Rasters from 2 categorical neurons that did not respond in the light instruction task. The cell in *A* is selective for low speeds and the cell in *B* is selective for high speeds. Asterisk: statistically significant differences between the neuronal discharges during low vs. high speeds (Wilcoxon test, $P < 0.01$). All other symbols as in Fig. 14.

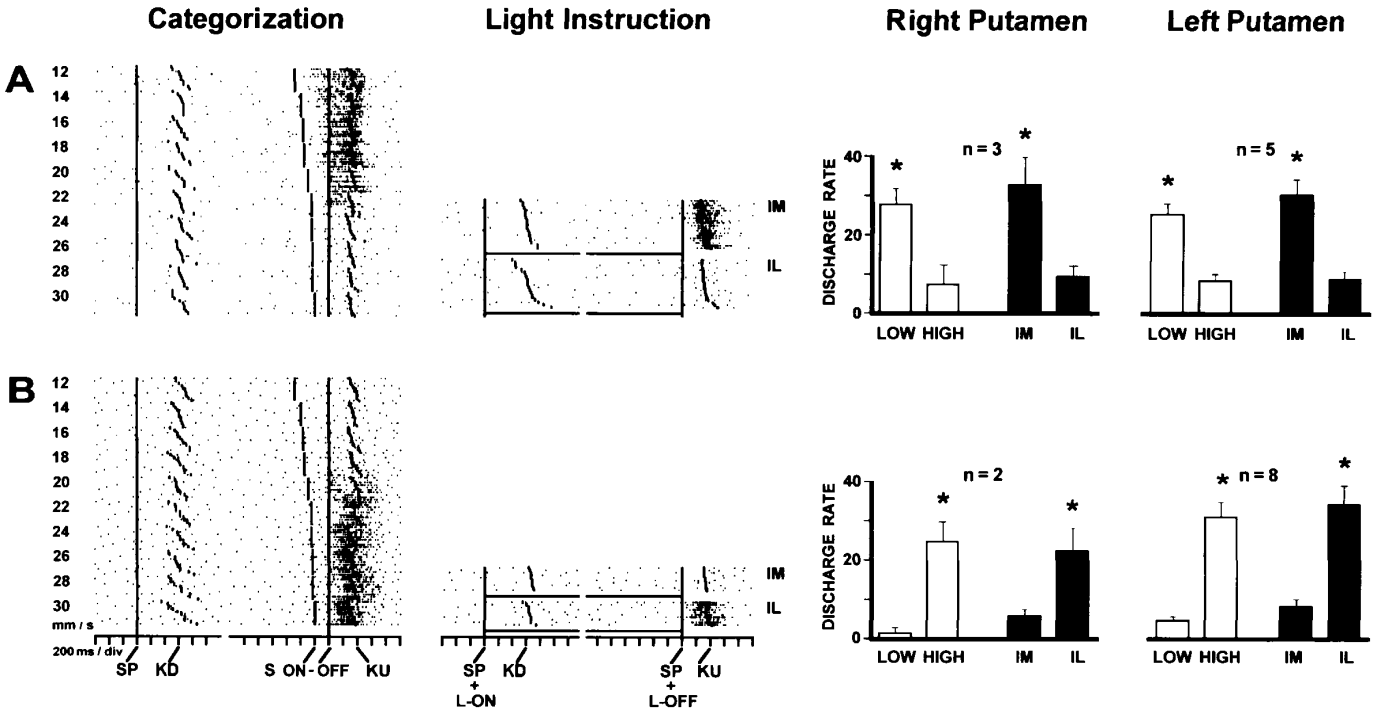

FIG. 17. Rasters from 2 categorical neurons that responded in the light instruction task. The cell in *A* is selective for low speeds and the cell in *B* is selective for high speeds. Asterisk: statistically significant differences between the neuronal discharges during low vs. high speeds (Wilcoxon test, $P < 0.05$). All other symbols as in Fig. 14.

Kimura (1990, 1992) has shown that some putamen neurons stop responding to the sensory trigger when an instruction cue precedes the stimulus, suggesting that they may not be unconditionally involved in movement initiation. Furthermore, the fact that some S and SM neurons did not respond to the visual cue triggering the movement suggests that these neurons are specifically related to the tactile stimulus triggering the behavioral motor reaction. In general, our findings are congruent with those studies of the putamen demonstrating sensory cue-related responses in motor paradigms (Gardiner and Nelson 1992; Kimura 1990; Romo et al. 1992; Schultz and Romo 1988). Similar results have also been found in the SMA (Romo et al. 1993b and unpublished data), again suggesting a similar role for these structures in this learned somesthetic task.

TABLE 5. *Putamen neurons that coded whether the stimulus speed was low or high*

	Stimulus Speeds		
	Low (12–20 mm/s)	High (22–30 mm/s)	Total
Right putamen			
SM	26	1	27
M	14	18	32
Totals-r	40	19	59
Left putamen			
SM	6	2	8
M	20	30	50
Totals-l	26	32	58
Totals	66	51	117

All these neurons fitted the Boltzmann equation with a χ^2 of $P < 0.001$. SM, Stimulus-movement; M, movement.

Some neurons of S type in the right and left putamen were preceded by preparatory activity. In delayed instruction paradigms, preparatory activity for movement execution has been revealed (Alexander and Crutcher 1990a; Jaeger et al. 1993; Schultz and Romo 1992). We would like to suggest that a component of the preparatory activity found in the putamen reflects preparation for the arrival of the somesthetic signal triggered by tactile stimulation. This preparatory activity ended during stimulation, while the probe was still moving, whereas preparatory activity for movement execution ended with the beginning of the arm movement (we recorded few SM neurons with preparatory activity). We also found that the response latencies of S neurons with preparatory activity were shorter than those of S neurons without preparatory activity. These results suggest that preparatory activity in the putamen may be associated with the somesthetic stimulus set. Similar processes have been observed in the SMA (unpublished data), again suggesting that these two brain structures share very similar functional properties during the execution of this task.

We were not able to find reliable receptive fields for the S and SM putamen neurons during passive stimulation. Their responses in this condition were very inconsistent; no somesthetic fields could be determined like those of SI cortex (Mountcastle et al. 1990; Romo et al. 1996; Ruiz et al. 1995). We are certain, however, that during the categorization task most of the responses in the putamen depend on the presentation of the stimulus. Studies in the putamen of naive animals revealed that very few neurons in this region

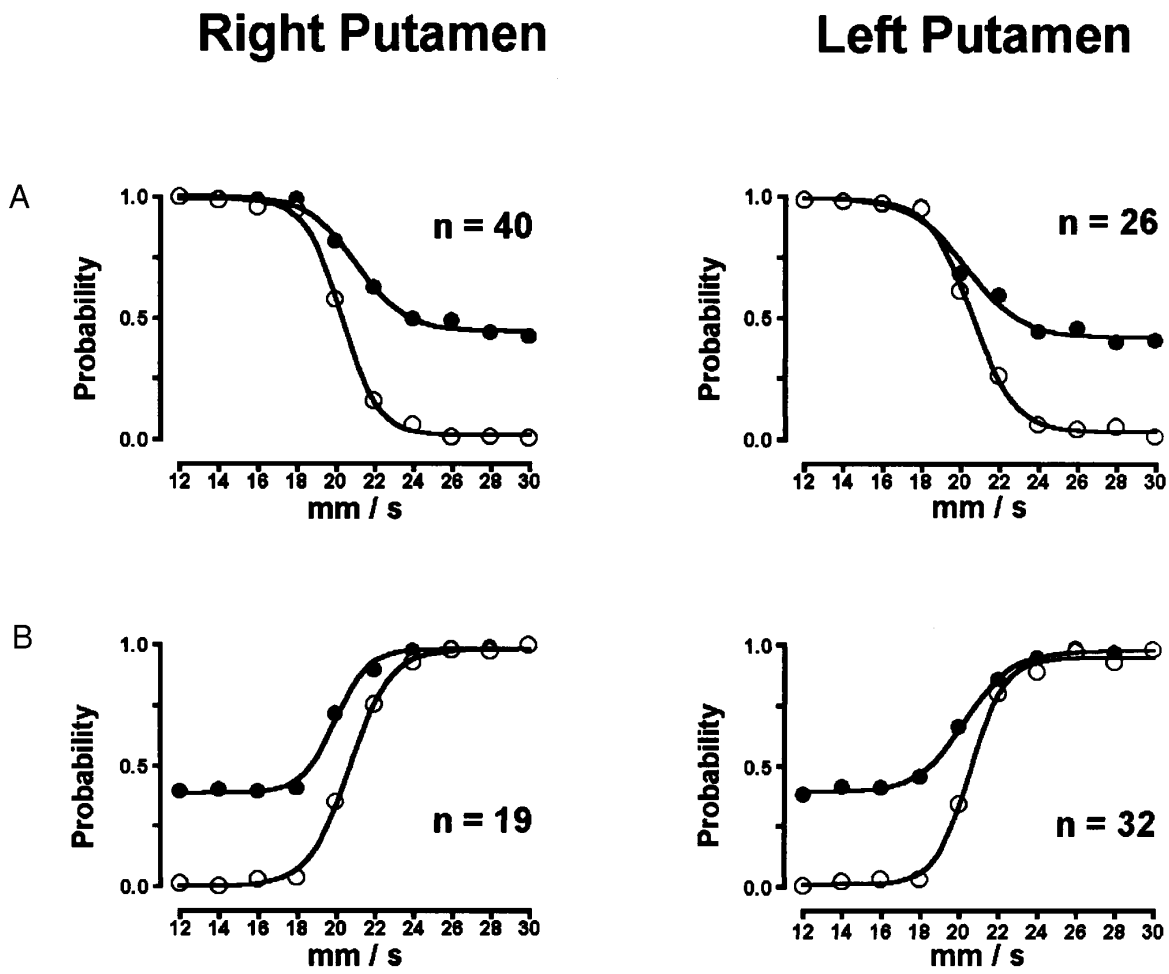

FIG. 18. Comparison between the neurometric curves (●) computed from the neurophysiological data and the psychometric curves (○) obtained from the animals' behavioral performance. *A*: graphs showing, for each speed at which the stimuli were presented, the probability of correctly categorizing the stimulus speed as low, on the basis of the psychometric measurements (○) and of the recorded responses of differential neurons selective for slow speeds (●). *B*: graphs showing the probability of correctly categorizing the stimulus speed as high, on the basis of the psychometric measurements and of the recorded responses of differential neurons selective for high speeds. Neurometric curves are population averages; the numbers of cells included are indicated in each plot. The neuronal data account for the behavioral responses, as seen by the agreement between both types of curve in the range of speeds for which each population is selective.

possess cutaneous receptive fields (Alexander and DeLong 1985; Crutcher and DeLong 1984). Nevertheless, we cannot rule out direct somesthetic input to the S and SM neurons; indeed, a more recent report has shown large cutaneous receptive fields in putamen neurons of anesthetized monkeys (Graziano and Gross 1993). It is recognized that in awake animals the exploration of somesthetic receptive fields is more difficult than in an anesthetized preparation, particularly when the fields are large and weak or when they contain more than one submodality. On the other hand, these cutaneous and deep receptive fields might be masked by the motor behavior of the animal.

The results obtained on the functional properties of S and SM neurons suggest that they do not process somesthetic information like SI cortex does (Mountcastle et al. 1990; Phillips et al. 1988; Romo et al. 1996; Ruiz et al. 1995). Most of these stimulus-related responses occur during the task, suggesting a dependence on the behavioral motor reaction. The activity of S and SM neurons is related to the beginning of the stimulus and to the initiation of the hand-arm movement, whereas the activity of M neurons correlates with the execution of the hand-arm movement. This suggests the presence of a neural sensorimotor continuum in the putamen that may be relevant for the general execution of the task. Interestingly, these neural responses are very similar to those described previously in different motor paradigms in which a sensory cue determines the initiation of the behavioral motor response (Gardiner and Nelson 1992; Kimura 1990; Romo et al. 1992; Schultz and Romo 1988). The fact that these neural responses occurred in the right and left putamen suggests that this region of the striatum may be involved in bimanual tasks.

Nature of the categorical responses

A major finding of this study is the discovery of neurons in the putamen whose responses correlate with the speed categories used, low or high. Their activity did not vary with

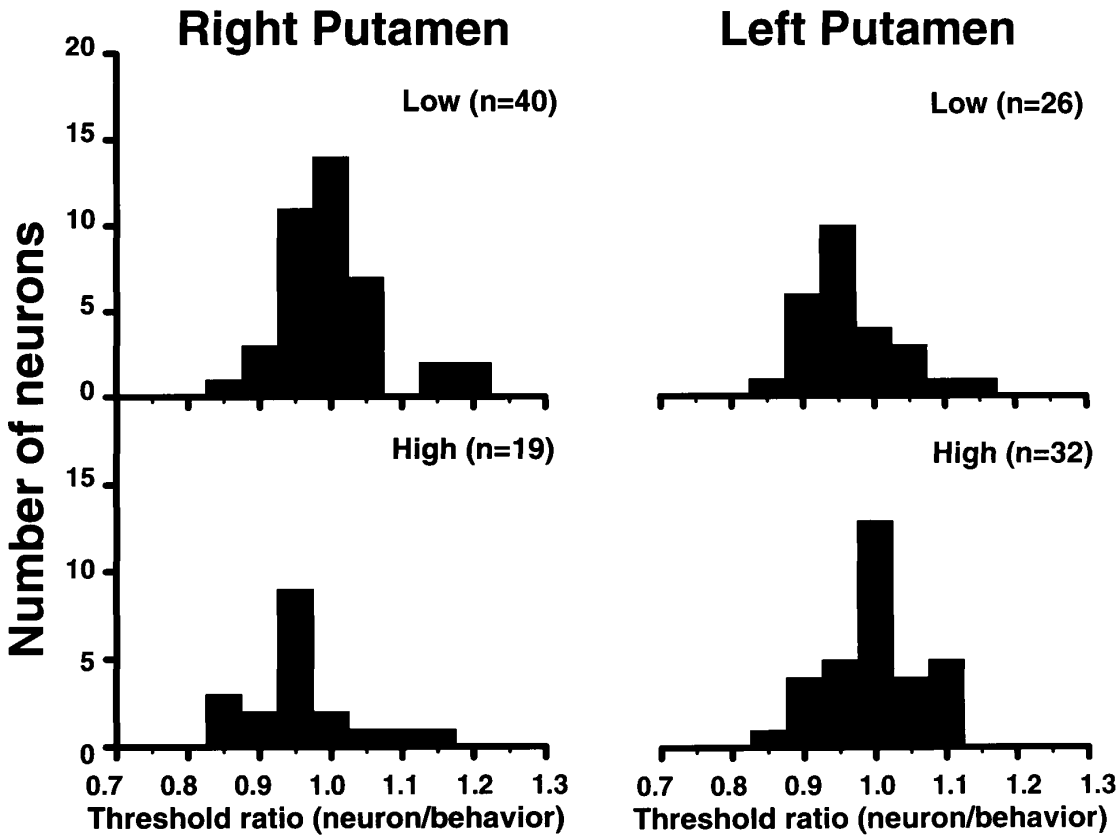

FIG. 19. Distributions of the ratio between the neurometric and psychometric thresholds. The neurometric threshold is defined as the speed at which the probability of correct categorization equals 0.75. It is read out from the neurometric curve of each neuron. The psychometric threshold is equal to the average of the speeds for which the probability of correct categorization equals 0.25 and 0.75. It is read out from the psychometric curve.

speeds within the same category. This type of neuron was found in both hemispheres. Most of these categorical responses appeared at the end of the stimulation period and continued discharging during the hand-arm movement. This suggests that the decision process begins during stimulation and ends with an output signal that is directly associated with the motor response. These categorical responses were conditional on the categorization task, because they disappeared during passive stimulation.

Animals categorized the stimulus speeds by pressing with the right hand one of two target switches, the medial for low speeds and the lateral for high speeds. Thus there is the possibility that the differential responses, instead of being involved in the categorization process, were associated with the intention to press, or with the trajectory of the hand toward the target switches. In a motor paradigm it was shown that the activities of some putamen neurons reflect the intention to move or the trajectory of the arm in one direction but not in the other (Alexander and Crutcher 1990a). In the somesthetic task, however, the differential neurons seem to be associated with the categorization itself, because most of them did not discharge differentially when the animal pressed the target switches after visual instruction, despite the fact that the hand-arm trajectories were the same in both conditions. A few of these neurons might simply have reflected the differential motor response, but most of them specifically coded the speed categories.

Signal detection methods were used to reveal whether the categorical responses carried information about the animal's decision (Britten et al. 1992; Green and Swets 1966; Romo et al. 1997). The neurometric curves derived from neurophysiological data predicted the psychometric behavior of the animals. The psychometric behavior for the two categories utilized was explained independently by two neuronal populations. However, we do not know whether these two groups of neurons interact in the putamen, or whether their responses are generated by local circuits or are imposed by cortical inputs driving them. In the same task, we have recorded neuronal activity in the SMA coding the speed categories (Romo et al. 1993b, 1997), and in preliminary experiments we have observed similar neural signals in the lateral premotor cortex (unpublished observations). Mountcastle et al. (1992) have recorded in MI cortex neurons that reflect the discrimination process in a different somesthetic discrimination task. All these neural signals recorded in cortical motor areas and in the putamen appear to be associated with the animal's decision. This is in contrast to what is found in SI cortex, where cells show no sign of the sensory decision process (Mountcastle et al. 1990; Romo et al. 1996). Thus, if SI cortex does not participate in it, an alternative is that the construction of such decision is initiated in those somesthetic areas of the parietal lobe linked to SI cortex. Experiments remain to be done to reveal the role of the posterior parietal somesthetic areas in these learned somesthetic tasks (Mountcastle et al. 1990; Romo et al. 1996).

Neurons of the frontal motor areas and the putamen share some functional properties; why are the same neural signals present in these interconnected structures? We believe that this redundant replication of neural activity assures a reliable coding of the animal's decision, made by the frontal motor areas. In this sense the role of the basal ganglia is to enhance the probability that the frontal motor areas generate an output neural signal that is consistent with the animal's decision. This would be achieved through the thalamic inputs to the frontal motor areas (Inase and Tanji 1995; Nambu et al. 1988; Schell and Strick 1984).

Neuronal activity in the putamen has been tested in a number of paradigms: delayed instruction tasks (Alexander and Crutcher 1990a,b; Schultz and Romo 1992), stimulus-triggered arm movements (Kimura 1990, 1992; Romo et al. 1992), and self-initiated arm movements as well (Schultz and Romo 1992). Most of these studies came to the conclusion that neurons in the putamen participate in different aspects of the planning and execution of voluntary movements, because neurons respond in tasks involving these elements. We believe that the results obtained in this study are compatible with those reported previously: the putamen must be considered as part of a large system that is engaged not only in the planning and execution of voluntary motor behavior, but also in decision making processes.

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