

WE have studied neuronal activity in the putamen of two monkeys trained to discriminate the speed of moving tactile stimuli. Animals pressed one of two target switches to indicate whether the speed of the probe across the skin was low or high. The activity of single neurones was recorded in the putamen ipsilateral to the glabrous skin of the stimulated hand and contralateral to the responding arm. During the task, we recorded neurones in the putamen that showed responses confined exclusively to the stimulus period of all speeds. A second class of putamen neurones responded during the stimulus period but continued discharging during the reaction and movement time period. None of these two classes of putamen neurones discharged when the same set of stimuli were delivered passively. A third class of putamen neurones responded differentially in the discrimination task and predicted whether the speed of the stimulus was low or high. A number of these neurones, which responded differentially during the categorization task, were tested in a light instruction task. This tested the possibility that these differential responses were associated with the intention to move the arm to one of the two target switches. Few neurones responded in this situation. These results indicate that the putamen, in addition to its role in motor regulation, is also involved in higher order aspects of sensory–motor behaviour and in the sensory decision process in this learned somesthetic task.

Key words: Primate putamen; Tactile categorization

Neuronal activity of primate putamen during categorical perception of somesthetic stimuli

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Introduction

Neurophysiological studies in primate putamen suggest that this region of the striatum is involved in the preparation and execution of movements.^{1–8} Most of the neuronal responses in the putamen are similar to those recorded in the frontal motor areas of the cerebral cortex.^{1–3,9–12} Indeed, anatomical studies have demonstrated that frontal motor areas of the cerebral cortex send bilateral projections to the putamen.^{13–16} Although these data support a role for putamen in different aspects of motor behaviour, somatic sensory areas of the parietal lobe also send projections to this region of the neostriatum.^{13,17,18} Neurones in the putamen respond to deep stimulation of body parts, while very few neurones respond to cutaneous stimulation.¹⁹ According to these results, it is reasonable to suggest that the putamen may be also involved in sensory processing at the sensory–motor transition. This is very likely, since in a recent study, we showed that a large number of neurones of the supplementary motor area (SMA), which sends bilateral projections to the putamen,^{13,17,18} responded in a sensory task in which monkeys are required to determine the speed of the tactile stimuli.²⁰ A second finding was that SMA neurones responded differentially in this categorization task and predicted its outcome.²⁰ Therefore, this study addressed the question whether the putamen is also involved in processing tactile stimuli. The results

suggest a role for putamen in higher order aspects of sensory–motor behaviour in this learned somesthetic task.

Materials and Methods

Animals and somesthetic task: Two monkeys (*Macaca mulatta*; 5.5 kg female and 4.5 kg male) were trained to perform a somesthetic task in which they were required to classify the speed of a probe (2 mm round tip) moving across the glabrous skin of one of the fingers of the left, restrained hand, and to indicate the speed by interrupting with the free hand one of two target switches (the centres 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 eye level). The stimuli consisted of a set of 10 speeds from 12 to 30 mm s⁻¹, in a fixed traverse distance of 6 mm, direction and force (20 g) half of which were considered as slow (12, 14, 16, 18 and 20 mm s⁻¹) and the rest as fast (22, 24, 26, 28 and 30 mm s⁻¹). Stimuli were presented by a tactile stimulator built in our laboratory for studying motion processing in the somatosensory system of primates.^{21,22}

The trained monkey began a trial when he detected a step indentation of the skin by placing his free hand into an immovable key in a period of time which did not exceed 1 s. He maintained this interruption 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 fast or slow by projecting his free hand to one of the two switches within 1 s (medial switch was used to indicate lower speeds and the lateral one for higher speeds). Animal was rewarded for correct categorization of the speed by a drop of water. The tactile stimuli were neither visible nor audible in any part of the task. The number of correct and wrong categorizations in a run [which consisted of 10 trials per class (speeds) presented randomly] was used to construct psychometric functions. These psychometric functions were plotted as the percentage of judgements of the speed as $> 20 \text{ mm s}^{-1}$ (Fig. 1C), or $< 22 \text{ mm s}^{-1}$ (Fig. 2B).

Visual control 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 categorization task, but one of the two target switches was illuminated beginning with skin indentation, continued after detection of skin indentation (variable delay period of 1.5–4.5 s between lights on and off), and turned off when the probe was lifted off from the skin. This visual cue instructed the animal which target switch was required to be pressed for reward.

Surgery: After the animals reached proficiency in the task (75–90 % of correct responses), they were implanted with a stainless steel chamber tilted 30° laterally to allow microelectrode penetrations for single neurones recording in the left putamen and, with a head holder for head fixation. Stainless steel Teflon-coated wires were also chronically implanted into the extensor digitorum communis, biceps and triceps brachii muscles of the right arm for EMG recording. The chamber and head holder were secured by screws and acrylic in the skull. All these procedures were carried out under aseptic conditions and pentobarbital sodium anaesthesia (30 mg kg^{-1}).

Electrophysiological recording: The activity of single neurone was recorded with glass-insulated, tungsten microelectrodes (exposed tips of 5–10 μm length), which were passed into the brain each day inside a rigid guide cannula of 0.6 mm outside diameter.⁸ Signals from neuronal activity were conventionally amplified, filtered, and monitored with oscilloscopes and heard with earphones. Neuronal discharges were selected by means of a differential amplitude discriminator (DAD). EMGs from the forearm and arm muscles were recorded through the chronically implanted electrodes of the moving arm in all recording sessions. EMG activity was filtered, rectified and converted into digital pulses by means of a DAD. Stimulus, behavioural control and data collection were carried out through a personal computer using standard computer

interfaces. The time between neural events, EMGs and between behavioural 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.

Analysis: Off-line inspection of data for each neurone was performed on the basis of raster plots in reference to each behavioural events: initial probe indentation of the skin (SP), detection of the indentation by closure of the key (KD), beginning and ending of the moving tactile stimuli (S), key release (KU), and end of the movement time (interruption of the target switches). Neuronal responses were classified according to each of these events and the statistical significance differences in impulse activity in two epochs [control (non-stimulus) period and the suspected change], were assessed with a sliding window procedure on the basis of the non-parametric one-tailed Wilcoxon matched-pairs signed rank test ($p < 0.001$). The non-parametric Kruskal–Wallis test was used to determine significant differences ($p < 0.05$) between the responses occurring during the stimuli, together with a test of multiple comparisons.²²

Histological reconstruction: Neuronal recording sites were marked with small electrolytic lesions by a passing negative current (10 μA for 20 s) through the microelectrode at a few positions in each of several tracks toward the end of the experiment. Positions of neurones were reconstructed from 50 μm coronal brain section stained with cresyl violet.

Results

General: During performance of the somesthetic task (Figs 1C, 2B), 907 neurones were recorded in the putamen contralateral to the responding arm; 443 of these responded in the task. We selected 226 neurones for further analysis on the basis that sufficient data were collected for dissecting the neuronal responses associated with any event of the task. Of these 226 neurones 57 responded in the period of skin indentation, 32 when the animal indicated detection of skin indentation, 30 during the delay period, 46 during the period of skin stimulation (sensory responses), 41 during the period of skin stimulation but continued during the reaction time period (sensory–motor responses), 17 during the reaction time (RT), 32 during the RT and movement time period (RT–MT), and 18 during the MT. These neurones which responded during the RT and MT were considered as ‘arm responses’. Sixty-three neurones were classified as ‘categorical’, since they showed differential responses for faster or slower speeds of the tactile stimuli. This last group of neurones was not separated from those that were classified as sensory, sensory–motor, or arm responses. The sum of these classes exceeds the total number of the reactive neurones because of the multiple relationships be-

FIG. 1. (A) Responses of a putamen neurone during the tactile categorization task in C. Vertical lines represent the beginning of indentation of the skin (SP = stimulus probe) and beginning of the moving stimuli (S = moving tactile stimuli). Larger vertical ticks represent detection of SP (KD = key down) and end of the moving tactile stimuli (KU = key up) to indicate categorization of the speed by projecting his free hand to one of two interrupt switches placed at reaching distance and at eye level. Neuronal impulses indicated as small vertical ticks. Each line represents 1 trial; the 10 trials per class (speed) were presented randomly. (B) The same putamen neurone studied with the same classes of stimuli as in A but delivered in the passive, non working state. (C) Averaged results during the tactile categorization task in A. ●, the percentage of trials in which the speed of the stimuli was judged higher; ○, the percentage response of the neurone calculated for the period comprising the beginning of the stimulus until the end of the reaction time. (D) Same putamen neurone was tested in the visual task, in which the animal was visually instructed which target interrupt switch had to be pressed for reward. Each trial began by illuminating one of two target switches beginning with indentation and ending by lifting off the probe from the skin. IL and IM indicate illumination of lateral or medial target interrupt switches, respectively. Long horizontal broken line below the rasters indicates illumination of the target switches. Stimulus parameters: 6 mm of traverse distance, 20 g of command force; the scanning was from distal to proximal on the distal pad of digit three of the left hand.

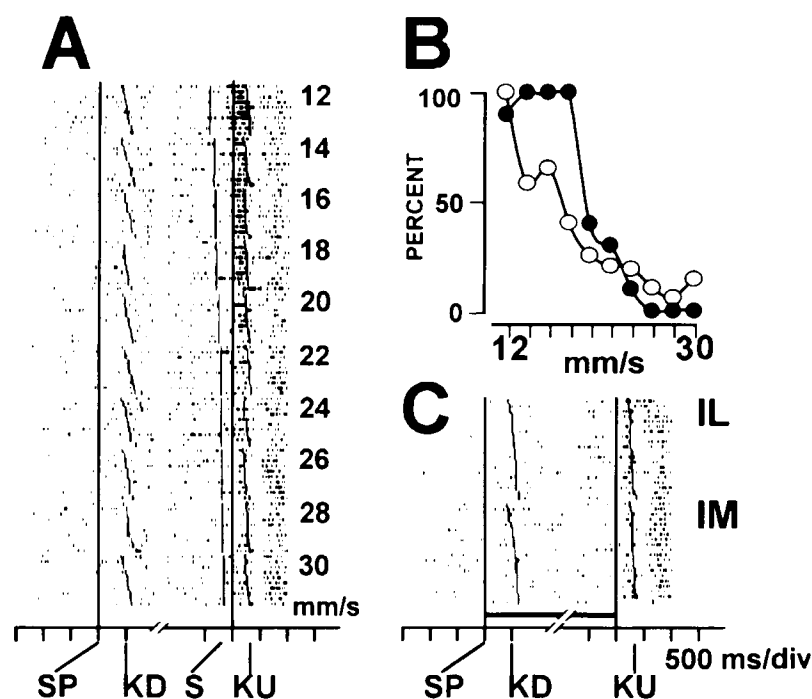
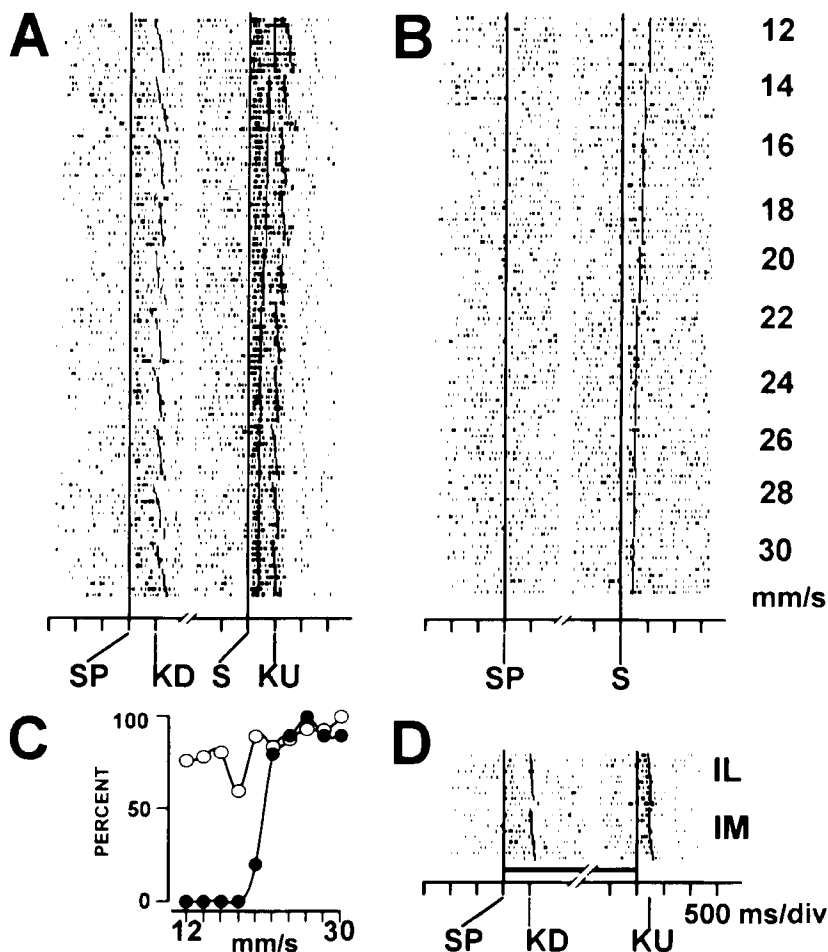


FIG. 2. (A) Differential responses of a putamen neurone during the tactile categorization task in B. Trials were aligned in reference to skin indentation and with the end of the period of skin stimulation (see Fig. 1 for description of abbreviations). (B) Averaged results during the tactile categorization task in A. ●, the percentage of trials in which the speed of the stimuli was judged lower; ○, the percentage response of the neurone calculated from the end of the stimulus until the end of the reaction time. (C) The same putamen neurone was tested in a visual task, in which the animal was visually instructed which target interrupt switch had to be pressed for reward. Stimulus parameters: 6 mm of traverse distance, 20 g of command force; the scanning was from distal to proximal on the distal pad of digit three of the left hand.

tween the non-categorical responses and other events of the task. In this paper, we describe those putamen neurones that responded during the period of skin stimulation, RT, MT, and also those which showed differential responses to different speeds of the tactile stimuli. All these classes of neurones were recorded in the arm region of the putamen (Fig. 3).

Sensory and sensory-motor responses: Forty-six neurones in the putamen ipsilateral to the stimulated hand responded during the period of skin stimulation (all stimulus speeds); 21 increased and 25 decreased their frequency of discharge with latencies (relative to onset of the moving probe) of 105.6 ± 33 ms and 73.1 ± 22 ms, respectively. Forty-one also responded during the period of skin stimulation but continued and ended with the end of the RT (Fig. 1A); 35 increased and six decreased their frequency rate with latencies of 111 ± 43 ms and 99.1 ± 38 ms, respectively. None of these two classes of neurones (three sensory and seven sensory-motor) discharged when the same set of stimuli were delivered passively (Fig. 1B). In this situation the stimuli were identical to those delivered during the categorization task, but the key was removed and the arm movements were restricted. In the visual control task, we tested six neurones that responded to the stimuli and 13 during the stimuli and the RT. Only one of the 6 that responded during the period of skin stimulation discharged when the lights were turned off. None of 13 neurones that responded during the period of skin stimulation and the RT discharged during the visual instruction period: five neurones did not even discharge during the reaction time. In only eight neu-

rones of this group was the RT component left intact (Fig. 1D). None of the responses occurring during the stimuli were correlated with earlier EMG activations of the muscles of the arm and forearm of the responding arm.

Arm responses: During classification of the tactile stimuli, 17 neurones increased their discharge rate during the RT, 32 during the RT-MT, and 18 during the MT. A number of these responding neurones were tested in the passive mode (three RT and four RT-MT) and in the visual control task (eight RT, 17 RT-MT, and three MT). None of them discharged in the passive mode condition. In the visual control task, most of these neurones discharged in a similar way as in the somesthetic categorization task, except for two of the eight RT neurones which became unresponsive.

Categorical responses: Sixty-three neurones showed differential responses during the tactile categorization task; 46 for low (Fig. 2A) and 17 for high speeds. These differential responses could be confined to the period of skin stimulation (16 neurones; all low speeds), during the stimuli and the RT (10 neurones; six low and four high speeds), during the RT (16 neurones; six low and 10 high speeds), during the RT-MT (nine neurones; eight low and one high speeds) or during the MT (12 neurones; 10 low and two high speeds). Some of these neurones, which showed differential responses were also tested in the passive mode (five neurones; two during the stimuli, two during the stimuli and the RT, and one during RT-MT), and in the visual control task (30 neurones; 10 that responded differentially during the period of skin stimulation, four during the stimuli and the RT, seven during the RT, four during RT-MT and five during the MT). None of the five differentially responsive neurones discharged when the moving tactile stimuli were delivered in the passive mode condition. Of the 30 differentially responsive neurones which were tested in the visual control task (Fig. 2C) only six neurones maintained the differential responses; four of the seven RT and two of the five MT. However, three of the four that responded during the stimuli and RT, and two of the five MT differential responses became responsive during the RT for both medial and lateral visual targets. One of the five neurones showing MT differential responses inverted its selectivity when the animal undertook the visual control task. None of these responses occurring during the categorization task were correlated with earlier EMG activations of muscles of the arm and forearm of the responding arm.

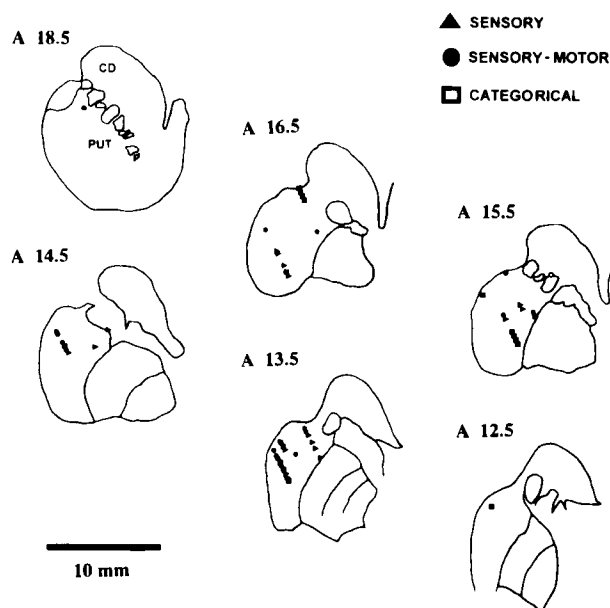


FIG. 3. Positions of putamen neurones with sensory (▲), sensory-motor (●), and differential responses during the categorization of the speeds (categorical, □). The responses plotted in these sections were recorded in one monkey. Similar positions for these three classes of responsive neurones were obtained in the left putamen of the second animal. Representative coronal sections of the left striatum are labelled in coronal stereotaxic planes.

Discussion

Categorical perception can be defined as the discrete perceptual responses derived from a range of continuum stimuli.²⁴ In this sensory task, the range of the speeds is the continuum stimuli and the arm move-

ments, the discrete responses. Thus, the sensory task employed in the present study contains all the requirements for the definition given above. With this approach, we addressed the question of whether the putamen is involved in categorical perception. Present findings suggest that the putamen plays a role in the categorical perception of somesthetic stimuli. For example, a large number of putamen neurones responded during the moving tactile stimuli, or during the stimuli and arm movements. A second class of putamen neurones also reflected differentially the categorization of the speeds of the tactile stimuli. It is therefore reasonable to suggest that these neuronal responses reflect different aspects of the somesthetic task.

The role of the putamen in motor behaviour is firmly established. However, three separate results suggest a role for this region of the striatum in the perception of somesthetic stimuli. First, somatic sensory areas of the parietal lobe send projections to the putamen.^{13,17,18} Second, previous neurophysiological studies have demonstrated that neurones in the putamen discharge to sensory cues when the animal responds to those cues by performing a movement.^{1-4,7,8,11} Third, two recent neurophysiological studies employing a sensory task to investigate the processing of somesthetic information in primary motor cortex²⁵ and SMA²⁰ have revealed that these two motor cortical areas may participate in higher order aspects of somesthetic perception.

The putamen contained neurones that responded to different aspects of the categorization task and only during the task. For example, none of the putamen neurones which responded to the somesthetic stimuli did so when the latter were delivered passively, and those putamen neurones which responded during the stimuli did not discharge in a visual control task. These findings suggest that the putamen may be involved in the sensory processing mechanisms of the present task.

We found in the putamen many neurones whose discharge reflects the categorization of the speed of the stimuli, for they discharge almost exclusively for lower or higher speeds during the stimuli, during the RT, or during the MT. Most of these neuronal responses did not reflect the intention of the animal to interrupt the medial or lateral target switches. Indeed, using the visual control task, we demonstrated that a large number of putamen neurones whose discharge reflected differentially the stimulus speeds did not respond when the animal interrupted the target switches after previous visual instruction. However, a small number of these

putamen neurones still showed differential responses during the visual control task; others became responsive for both target presses, or even inverted the differential responses. This last finding agrees with previous reports that there are neurones in the putamen that represent in their activity the intention to move the arm in a given direction.² Therefore, these results may suggest that the putamen is not only involved in the regulation of motor behaviour, but also in the sensory decision process in this somesthetic task.

Similar neuronal responses have been found in the SMA in this somesthetic learned task.²⁰ Anatomical studies have shown that the SMA sends massive bilateral projections to the putamen.^{15,16} This could suggest that these two anatomically related structures are parts of a distributed system which also involves parietal cortical structures for the processing of tactile stimuli in this somesthetic task.

Conclusion

The results obtained suggest that the primate putamen, in addition to its role in motor regulation, is also involved in higher order aspects of sensory-motor behaviour and in the sensory decision process in this learned somesthetic task.

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General Summary

Neurophysiological studies in monkeys suggest that a region of the basal ganglia called the putamen is involved in the preparation and execution of movements. The responses of most neurones in the putamen are similar to those recorded in the frontal motor areas of the cerebral cortex. Although these data imply a role for the putamen in different aspects of motor behaviour, somatic sensory areas of the parietal lobe are known also to project to this region. Here we recorded from neurones in the putamen of monkeys while they performed a behavioural task involving motor reactions (pressing switches) in response to a stimulus moved across the skin of the hand. Some cells responded only during the sensory stimulation; in others the response continued during the subsequent hand movement. This suggests that the putamen, in addition to its well known role in motor regulation, is also involved in higher-order aspects of sensory-motor behaviour and in the sensory decision process in a learned somesthetic task.