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Categorization of somaesthetic stimuli: sensorimotor performance and neuronal activity in primary somatic sensory cortex of awake monkeys

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We used psychometric techniques to study the sensorimotor performance of four monkeys trained to classify the speed of moving tactile stimuli. Animals performed the task by pressing one of two target switches to indicate whether the speed of probe movement across the glabrous skin of the hand was low or high. Psychometric curves indicated that animals classified the stimulus speeds irrespective of which finger was stimulated, traverse distance and direction. The mean values of the reaction (RT) and movement (MT) times during the correct categorization of low and high stimulus speeds were similar. However, a slight increase was detected in the mean values of the RT during the incorrect categorization but not in the MT. During the task, activity of single neurones ($n = 45$) was recorded in primary somatic sensory (SI) cortex. The results indicate that a class of neurones ($n = 12$) of SI cortex increased their impulse rates as a function of the stimulus speeds. However, the magnitude of their responses was similar during the correct and incorrect categorizations of stimuli. The same neurones also responded when the same set of stimuli used in the categorization task were delivered passively. Neurones of SI cortex responded with a latency of 25.8 ± 0.6 ms (± s.e.m.) relative to the beginning of the moving tactile stimuli during the categorization task. The same neurones ($n = 17$) also responded with a similar latency (24.6 ± 4.0 ms) when the stimuli were delivered passively. These results may suggest that, although this evoked neuronal activity may be important for the perception of the moving tactile stimuli, more central structures associated with SI cortex may determine the performance of this learned somaesthetic task.

Key words: Tactile categorization; Sensorimotor performance; Somatosensory cortex; Awake monkeys

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Introduction

The somatosensory cortex (SI) of subhuman primates seems an appropriate model for approaching the question of how the cerebral cortex represents tactile information. The hands of these animals and their peripheral and brain structures related to somatic sensitivity are similar to those of humans.[1,2] Similar sensory performance in somaesthetic tasks has also been observed in subhuman and human primates.[3] Recently, we have studied the representation of tactile stimuli in SI cortex[4] and the mechanisms by which these stimuli are processed by the motor centres to guide behaviour.[5]

A first objective of the research programme was to define quantitatively the neural representation of moving tactile signals in SI cortex.[4] A second objective was to design a sensory somaesthetic task in which the neuronal events in SI cortex can be correlated with the sensory performance. Animals categorized the stimulus speeds delivered to the glabrous skin of one finger of the restrained hand by pressing with the free hand one of two target switches. The sensory performance was evaluated with psychometric techniques and the motor responses by measuring the reaction (RT) and movement (MT) times during the categorization of the stimulus speeds. The results indicate that the sensorimotor performance can be measured in a reliable manner in the present task. We also recorded the responses of SI neurones with receptive fields on the finger tips during the categorization of the stimulus speeds. The results indicate that a class of neurones of SI cortex respond by increasing their impulse rates as a function of the stimulus speeds. However, the same class of neurones of SI cortex also responded when the same set of stimuli were delivered passively. These results may suggest that

the neuronal signals associated with the present task must be searched in those central somaesthetic areas anatomically linked to the SI cortex.

Materials and Methods

Somaesthetic task: Four monkeys (*Macaca mulatta*; 5.5 kg female and 4.5–5.5 kg males) were trained to perform a somaesthetic task in which they were required to categorize the speed of a probe (2 mm round tip) moving across the glabrous skin of one of the fingers of the left, restrained hand and indicate the speed by interrupting with the free hand one of two target switches (Fig. 1).

The left arm of the animal was secured in a half cast and maintained in a palm up position by gluing the back of the hand. The free hand operated an immovable key (elbow joint at about 90°) and 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 (6, 8 or 10 mm), direction and force (20 g) in which half of them were considered as low (12, 14, 16, 18 and 20 mm s^{-1}) and the rest as high (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.[6]

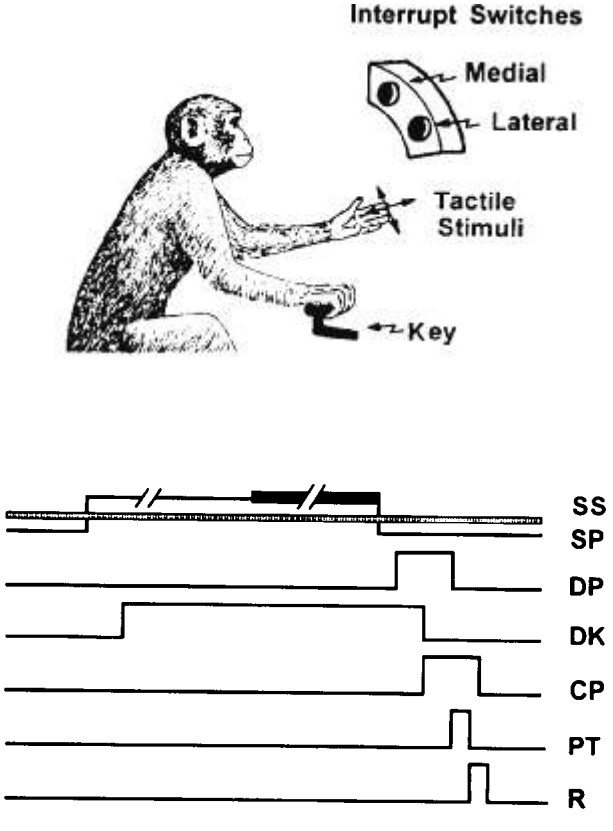

FIG. 1. Diagram of the monkey working in the categorization task; below, the schematic outlines of the task sequence. Bold broken line means variable stimulus speeds. Descriptions of the task sequences, stimulus-set, and sensory-motor performance execution are given in the text. SS, skin surface; SP, stimulus probe; DP, detect period; DK, detect key; CP, choice period; PT, project to target; R, reward.

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 which did not exceed 1 s (Fig. 1). He maintained this position through a variable delay period (1.5–4.5 s, beginning with detection of the indentation of the skin) until the probe moved at any of the 10 speeds. He indicated the detection of the end of the motion by removing his hand from the key within 600 ms, and whether the speed was low or high by projecting his free hand to one of the two switches within 1 s (medial switch was used to indicate low speeds and lateral one for high speeds). The animal was rewarded for correct categorization of the speed by a drop of water. The tactile stimuli were neither visible nor audible in any part of the task. The number of correct and incorrect 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 judgments of the speeds as > 20 mm s^{-1}.

Surgery: After animals reached proficiency in the task (75–90% of correct responses), two were implanted with a stainless steel chamber tilted 30° laterally to allow microelectrode penetrations for single neurone recording in the right postcentral gyrus, and with a head holder for head fixation. The centre of the chamber was fitted to a 10 mm hole made in the skull, exactly over the area of the hand representation. Stainless steel Teflon-coated wires were chronically implanted into the extensor digitorum communis (EDC), biceps (BIC) and triceps (TRI) brachii muscles of the right arm for EMG recordings; the wires were brought to a connector fixed in the skull. The chamber, head holder and the connector were secured by screws and acrylic in the skull. All these procedures were carried out under aseptic conditions and sodium pentobarbital anaesthesia (30 mg kg^{-1}).

Electrophysiological recording: The activity of single neurones was recorded extracellularly with glass-coated platinum-iridium electrodes, (2–3.5 MΩ), which were passed transdurally into the postcentral gyrus. Neuronal signals from the microelectrode were amplified, filtered and monitored with oscilloscopes and with earphones. Neuronal discharges were converted into digital pulses by means of a differential amplitude discriminator (DAD). A record was kept of the depth at which each neurone was isolated along the length of each penetration. Micro-lesions were made at the end of each penetration by passing

5–10 μA through the tip of the microelectrode for 10 s, to aid reconstruction of the penetration. 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 interfaces. The time between neuronal 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.

Data analysis: The number of correct and incorrect categorizations in a run was used to construct psychometric functions (plotted as the percentage of judgments of the speed as >20 mm s^{-1}). Logistic functions of the form $f(x) = 1/(1 + e^{-[B_0 + B_1 x]})$ were fitted to these data points. All logistic regressions were significant ($p < 0.0001$, see Fig. 2). We also measured the reaction time (RT) and movement time (MT) during the categorization of the stimulus speeds. The non-parametric Kruskal–Wallis test and a test of multiple comparisons[7] were used to determine significant differences ($p < 0.05$) between the RTs, and between the MTs occurring in response to the stimuli (all classes).

Off-line inspection of data for each neurone was performed on the basis of raster plots with reference to each behavioural event (Fig. 1): initial probe indentation of the skin (SP), detection of the indentation (KD), beginning and ending of the moving tactile stimuli (S ON–OFF), key release (KU, end of the RT), and end of the MT (interruption of the target switches). Neuronal responses were classified according to each of these events and the statistically significant differences in impulse activity in two epochs (control (non-stimulus period) of identical duration to the suspected changes produced by the stimulus), 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 and a test of multiple comparisons were used to determine significant differences ($p < 0.05$) between the neuronal responses occurring during the stimuli.[7] An analysis of the response latency of the neuronal discharges relative to the beginning of the moving stimuli was calculated and served to define the discharges associated with the stimulus period.[8]

Histological reconstruction: After the experiments, animals were anaesthetized with ketamine (6 mg kg^{-1}) and sodium pentobarbital (40 mg kg^{-1}, i.p.) and perfused through the carotids with PBS 0.1 M followed by 4% paraformadehyde in PB 0.1 M. The

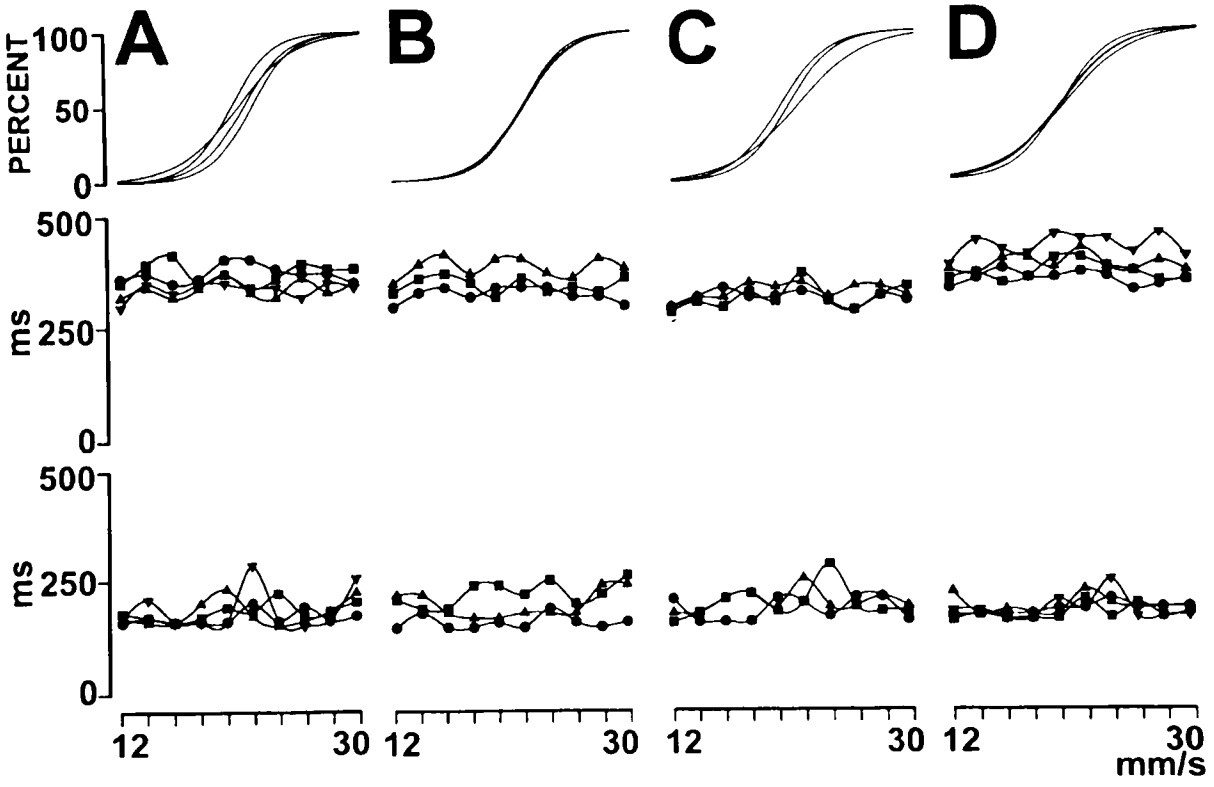

FIG. 2. Logistic functions (top), mean values of the RTs (middle) and MTs (bottom), calculated during the categorization of the stimulus speeds. Descriptions of A–D are given in the text.

brain was removed and suspended in paraformaldehyde. Later, a block of the right hemisphere containing the postcentral gyrus was sectioned at 50 μm and these sections were stained with cresyl violet. We used the tracks and the electrolytic lesions, together with the micrometer readings obtained during the experiments, to identify the neuronal recording sites in the postcentral gyrus.[9]

Results

Somaesthetic performance: Animals reached proficiency in the task in about 2 months after training began. The minimum training period required was 40 days for monkey M1, 50 days for monkeys M2 and M3, and 70 days for monkey M4. During this training period, animals were first required to detect the end one of two clearly different speeds (12 or 30 mm s^{-1}). Animals did so very well in a few weeks, since their score reached >95% correct responses. Similar behavioural reactions were produced by these two stimuli, as determined by the RTs (370.7 ± 10 and 360.5 ± 7 ms (mean ± s.e.m.) for low and high speeds, respectively). During this training period the stimuli were presented in the distal segment of digit 3, with a fixed traverse distance of 6 mm, direction (distal to proximal) and force (20 g). In the second part of the training period, animals were required to categorize the two speeds by projecting their free hand to one of the two interrupt target switches (medial for 12 mm s^{-1} and lateral for 30 mm s^{-1}). Animals learned this part of the task in about one week, reaching scores of >95% correct responses, with RTs of 383.0 ± 1.7 and 388.0 ± 1.9 ms, and MTs of 198.0 ± 2.6 and 193.0 ± 1.8 ms for low and high speeds, respectively. When animals reached this stage of the task, the complete set of speeds was delivered on digit 3, with the same parameters used during the training period.

Figure 2A (top) shows the psychometric curves of the four animals, represented in the form of logistic functions fitted to the data points (not shown). They are plotted as percentage of speeds judged as as >20 mm s^{-1}. The data were obtained from one run performed by each animal (10 trials per class). The middle section of Figure 2 shows the mean values of the RTs, and the bottom shows the MTs for the different speeds during the categorization task. It can be observed that animals performed the categorization of the stimulus speeds in a similar manner. No significant differences between the mean values of the RTs and MTs for low (RT: 352.5 ± 2.0 ms; MT: 175.1 ± 2.4 ms) or high (RT: 337.9 ± 2.1 ms; MT: 194.9 ± 3.6 ms) speeds were detected for each animal or between the different animals (Fig. 2A). Figure 2B shows that the performance of the categorization task, RTs and MTs were not affected when the stimuli were delivered for the first time in digit 2 or digit 4, compared with digit 3 (data are from monkey M4, and similar results were obtained in monkeys M1–M3). It is also remarkable that the categorization task was not affected if the traverse distance was modified (data are from monkey M4, and similar results were obtained in monkeys M1–M3). Figure 2C shows the logistic curves and the RTs and MTs when the set of the stimuli were delivered in digit 3, but with traverse distances of 6, 8 and 10 mm (data are from monkey M4, and similar results were obtained in monkeys M1–M3). Mean values of the RTs and the MTs were not affected. Finally, animals performed the categorization task irrespective of the direction of the stimulus speeds. Figure 2D shows the logistic curves when digit 3 was scanned in four different directions (distal to proximal and opposite, medial to lateral and opposite). Mean values of the RTs and the MTs were not affected by the directions of the scanning and remained similar to situations A–C of Figure 2.

A slight increase in the mean RTs was detected when the animal made incorrect categorizations of the stimulus speeds (342.3 ± 1.5 ms for correct and 366.5 ± 5.1 ms for incorrect categorizations) but this was not seen for the MTs (186.2 ± 2.4 ms for correct and 176.5 ± 4.8 ms for incorrect categorizations). The higher percentage of incorrect categorizations occurred with the intermediate speeds (18–22 mm s^{-1}).

Neuronal responses of SI cortex during the categorization task: We studied 45 neurones in area 1 of SI cortex during the categorization of the stimulus speeds. All these neurones possessed cutaneous receptive fields confined to one digit (distal segment of digit 2, 3 or 4 of the left, restrained hand). These neurones were recorded between the cortical surface and a depth of 2000 μm. They were also classified according to the adaptation to a light, sustained indentation of the skin in their receptive fields. Thirty-one neurones had quickly adapting responses (QA) and 14 slowly adapting (SA) properties. More posterior penetrations recorded neurones with cutaneous receptive fields located in more than two fingers, corresponding to area 2[10]. Histological reconstructions of the penetrations confirmed that the recorded neurones studied were located in area 1.[9]

Figure 3 shows the responses of a QA neurone during the categorization of the stimulus speeds. This neurone responded with a train of impulses to the contact of the stimulus probe with the skin and responded again during the scanning in the distal segment of digit 3, where the cutaneous receptive field was confined. The EDC-EMG of the responding arm was recorded simultaneously. Neuronal responses were not associated with the muscle activity (Fig. 3A,B), indicating that this neural activity was entirely dependent on the tactile stimuli. All 45 neurones

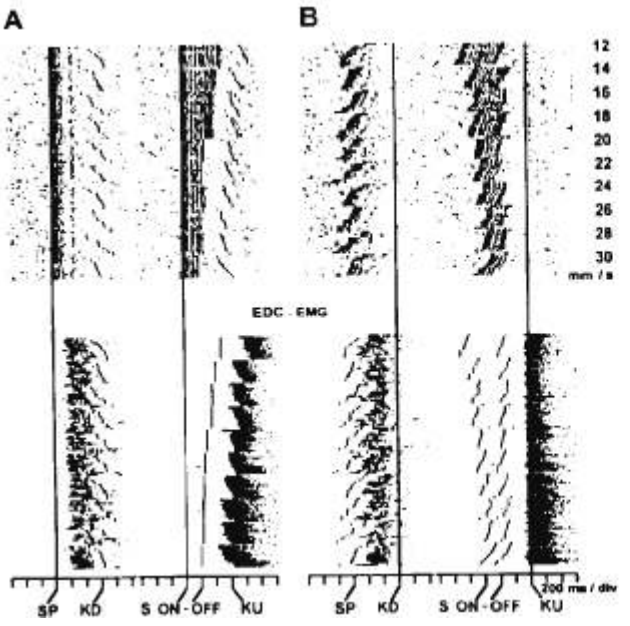

FIG. 3. Responses of a neurone of area 1 whose cutaneous receptive field was scanned with the set of stimulus speeds that the animal categorized. The receptive field was located in the distal segment of digit 3, and it was classified as a quickly adapting. (**A**) Vertical lines indicate beginning of indentation by the stimulus probe (SP) and beginning of the scanning (S-ON). Vertical lines after the beginning of the stimulus indicate the end of the scanning (OFF). Small vertical lines indicate detection of skin indentation by the stimulus probe (KD) and detection of the end of the moving stimuli (KU). These two events are shown in rank ordering (first trial in each class is the shorter RT). Neuronal activity (top) and below the EDC-EMG (extensor digitorum communis of the responding arm) are represented in the form of small vertical tics. Each line corresponds to one single trial. Stimuli were presented randomly. (**B**) the same neuronal and EMG activity but now aligned with respect to KD and KU. Stimulus parameters: traverse distance, 6 mm; direction, distal to proximal; constant force, 20 g, speeds 12–30 mm s^{-1}.

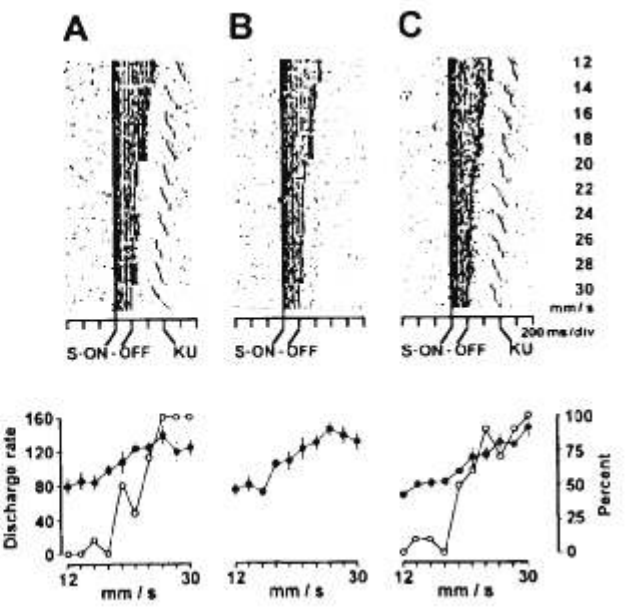

FIG. 4. Responses of a SI cortical neurone during the tactile categorization task (**A**,**C**) and when the stimuli were delivered passively (**B**), in the non-working situation. Large vertical lines indicate beginning of the stimuli (S-ON) and medium vertical lines indicate the end of each stimulus speed (OFF). Small vertical lines indicate detection of the end of the stimuli (KU, end of reaction time). Neuronal discharges represented as vertical tics. Bottom, A and C during tactile categorization (○, percentage of trials in which the animal judged that the speed was high; ●, mean frequency rates (± s.e.m.) of the neurone as a function of the stimulus speeds). B, discharge rates during the passive delivery of the stimuli (non-working situation). The same receptive field and stimulus parameters as described in Fig. 3.

showed statistically significant differences in their mean impulse rates during the moving tactile stimuli (Wilcoxon, $p < 0.01$), compared with the control (non-stimulus) period. However, the Kruskal–Wallis test ($p < 0.01$) showed that only 12 of the 45 neurones studied (10 QA and 2 SA, all with tonic responses during the scanning) had significant differences in the mean impulse rates associated with the stimulus speeds. Although the rest of the neurones responded to the stimuli (compared with the control period), no differences in the impulse rates were found between low and high stimulus speeds (21 QA and 12 SA).

Another striking property of neurones of area 1 was that all of those tested in the categorization task (Fig. 4A,C), responded similarly when the stimuli were delivered passively (Fig. 4B). In this condition, the same set of stimuli were delivered in the same receptive field of the recorded neurone, but the categorization was restricted, just by removing the key and the interrupt target switches. Thus, in this condition the animal remained alert, but was no longer using the stimuli to indicate categorization with the free hand. This was observed in the 9 neurones in which impulse rate varied as a function of the stimulus speed (during categorization: 54.8 ± 8.9 imp s^{-1}; during passive presentation of the stimuli: $50.1 + 9.0$ imp s^{-1}) and in the seven neurones that did not show variations in the discharge rate as a function of the stimuli (during categorization: 27.0 ± 0.9 imp s^{-1}; during passive presentation of the stimuli: 27.1 ± 1.1 imp s^{-1}). Similar neuronal responses were observed when the animal made correct or incorrect categorizations. This occurred in the 12 neurones which were sensitive (correct responses: 50.5 ± 7.4 imp s^{-1}; incorrect responses: 51.5 ± 8.0 imp s^{-1}) and for the 33 neurones which were insensitive (correct responses: 34.7 ± 3.7 imp s^{-1}; incorrect responses: 35.9 ± 4.0 imp s^{-1}) to the stimulus speeds.

The response latencies relative to the beginning of the moving stimuli were determined in the 45 neurones of area 1. These latencies ranged from 18 to 38 ms (25.8 ± 0.6 ms, calculated from the correct responses of all classes in 45 neurones). These latencies did not vary as a function of the stimulus speeds when the stimuli were delivered during the categorization (24.8 ± 4.0 ms, calculated in 17 neurones), or in the passive mode (24.6 ± 4.0 ms, calculated in the same 17 neurones). However, slight increases in the response latencies were observed when the animal made incorrect categorizations (28.8 ± 1.4 ms determined in 41 neurones, $p < 0.03$) of the stimulus speeds.

Discussion

Three major observations were made in the present study. First, the categorization of the moving tactile stimuli is irrespective of the stimulated skin surface of the hand, traverse distance and direction. Second, a class of neurones of SI cortex increased its impulse rates as a function of the stimulus speeds during the categorization task. However, these neuronal discharges also occurred when the same set of stimuli were delivered passively. Third, the response latencies of neurones of SI cortex relative to the beginning of the moving stimuli were similar between the different classes during the categorization and non-categorization tasks.

Animals categorized the stimulus speeds on the basis of a single stimulus. This was achieved since, during the training period, they learned to identify the lowest and the highest speed (12 and 30 mm s^{-1}). The set of stimulus speeds was indicated by pressing with the free hand one of two target switches. To perform this task, it is very likely that animals had to produce a 'mnemonic template' of the edges of the stimulus sets during the training period (the lowest and the highest speed). This mnemonic template must read and classify the evoked neuronal activity elicited by the stimulus to create a decision process. By contrast, in a sensory discrimination task, animals use two stimuli, separated by a fixed interval of time, in which the second stimuli is compared with the first one to create a decision process during sensory discrimination.[3] Therefore, this task is neither a simple sensory detection and nor a discrimination task. Instead, we propose that this represents a sensory categorization task.[11]

The results indicate that the animals performed sensory categorization on the basis of the stimulus speeds. It is interesting to see that the performance was not altered when the stimuli were presented with different traverse distances. Psychometric curves were almost identical. However, we cannot rule out the possibility that the animals made the categorization on the basis of the stimulus duration, since they categorized the stimulus speeds with a fixed traverse distance during a run. Psychophysical studies have shown that humans confound changes in stimulus speed with changes in the movement distance.[12]

Psychometric curves were similar when the stimuli were delivered for the first time on the fingers which had not been stimulated before, or when new different directions were introduced. This means that once the monkey knows the task he was able to generalize the categorization of the stimuli. However, we do not really know whether this generalization can only be made when the stimuli are presented in the same hand. In a different sensory somaesthetic task, the transfer of the task from one hand to another is made almost immediately.[13]

Behavioural motor reactions of the animals were quantified by measuring the RTs and the MTs during the execution of the tactile categorization task. The results indicated that the RTs and MTs were similar between the four performing animals. The mean values of the RTs and the MTs did not change substantially between the different classes of the speeds being categorized by the animals, although a slight increase was detected in the RTs, but not in the MTs, during the incorrect categorizations. Thus, the sensory performance is reflected in the RTs. Mountcastle and colleagues have measured the RTs in a sensory somaesthetic detection task and have indicated that it varies as a function of the stimulus amplitude.[13] However, these authors indicated that once humans and trained monkeys performed the task with stimuli above the threshold, the RT duration decreased and also became more regular. The stimuli used in the present task were well above the detection thresholds. This may suggest that the slight increase in the RT during the incorrect categorizations may be reflecting the difficulties of the animal in categorizing the stimulus speeds, but not in the detection of the stimuli.

An objective of the present study was to determine the neuronal activity of SI cortex as animals categorized the stimulus speeds. All neurones studied responded during the categorization task. However, only some responded as a function of the stimuli delivered in their receptive fields. These neurones from area 1 also discharged when the stimuli were delivered passively. This may indicate that, although this evoked neuronal activity may be important for the perception of the somaesthetic stimuli, more central structures associated with SI cortex may determine the performance of the categorization tactile task. A similar observation was made in a sensory somaesthetic discrimination task.[3]

It may appear obvious that neurones of SI cortex (among the cortical somatic sensory areas of the parietal lobe) are the first to respond to the somaesthetic stimuli; however, few studies have paid attention to it. In the present study we determined that neurones of area 1 responded with a latency of 25.8 ± 0.6 ms and, in preliminary experiments, we observed that neurones of area 2 respond with a latency of 58.7 ± 2.8 ms (26 neurones studied, unpublished results). Although we have not measured the response latency of those neurones of somaesthetic areas of the posterior parietal lobe, cortical processing of the somaesthetic stimuli probably begins in the SI cortex. We have observed that the response latency of neurones in the SI cortex are similar when the stimuli are categorized (correct responses) or during the passive delivery of the same set of stimuli. However, a slight increase in the response latency was observed in the same neurones studied in the categorization task

when the animals made incorrect categorizations of the stimulus speeds (28.8 ± 1.4 ms). We do not know whether this slight increase in the response latency has a functional meaning.

The SI cortex of the postcentral lobe is only one of several brain structures implicated in somaesthetic perception. Indeed, many authors have studied the sensitivity of neurones of the SI cortex to different parameters of the tactile stimuli, in behaving[3,14–16] and in naive monkeys.[4,17] These observations indicate that SI cortex represents in the evoked neuronal activity the physical properties of the somaesthetic stimuli, although it has been difficult to relate this neural activity with the perception of the stimuli. Interestingly, in monkeys trained in the somaesthetic categorization task, we have recorded neurones in the supplementary motor area and putamen that respond to the stimulus speeds, but only when the animals performs the categorization task.[5,18] The same observation was made by Mountcastle and colleagues in the primary motor cortex in a sensory somaesthetic discrimination task.[19] This suggests that there is a transformation of the somaesthetic information in those central structures anatomically connected to SI cortex.

Conclusion

The results obtained suggest that categorization of moving tactile stimuli is independent of the stimulated skin surface of the hand, traverse distance and direction. Neurones of the SI cortex respond to the moving tactile stimuli; however, they do not reflect in their activity the categorization process. It is suggested that this must be searched for in more central somaesthetic areas anatomically linked to SI cortex.

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