

RESEARCH NOTE

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Role of primary somatic sensory cortex in the categorization of tactile stimuli: effects of lesions

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Abstract We lesioned the right primary somatic sensory (SI) cortex in two monkeys trained to categorize the speed of moving tactile stimuli. Animals performed the task by pressing with the right hand one of two target switches to indicate whether the speed of a probe moving across the glabrous skin of the left hand was low or high. Sensory performance was evaluated with psychometric techniques and motor behavior was monitored by measuring the reaction (RT) and movement (MT) times before the experiment and throughout the 60 days after the ablation of SI cortex. After the lesion, there was a slight increase in the RTs but no change in the MTs, indicating that removal of SI cortex did not affect the animals' capacity to detect the stimuli. However, monkeys lost their ability to categorize the stimulus speeds. This effect was observed from the 1st day after the lesion until the end of the study. We conclude that somatosensory areas outside SI can by themselves process tactile information in a limited way and that the extraction of higher-order features that takes place during the categorization task requires the intervention of SI cortex.

Key words Lesions · Somatosensory cortex · Categorization task · Monkey

Introduction

Recently, we quantified the sensorimotor performance of monkeys working in a tactile categorization task (Romo et al. 1996). Animals were trained to press, with the right hand, one of two target switches to indicate whether the speed of a probe moving across the glabrous skin of the restrained left hand was low or high. Psychophysical measurements indicated that animals categorized the

stimulus speeds irrespective of the particular finger stimulated, the distance traversed by the probe, and the stimulus direction. Therefore, we found this paradigm well suited for investigating, in somesthetic and motor cortical areas, the neuronal processes associated with the animal's performance and with the categorization process. Using the tactile categorization task, we previously recorded the responses of neurons in primary somatic sensory (SI) cortex with receptive fields on the finger tips (Romo et al. 1996). We found a class of neurons whose discharge rates varied smoothly with stimulus speed. However, these neuronal responses were also present when the same stimuli were delivered passively and, furthermore, were not specifically linked to the speed categories used (i.e., these cells were tuned to stimulus speed, not to speed category). In view of these results, we suggested that the neuronal signals associated with the categorization process should be sought in those central somesthetic areas linked to SI cortex. However, as shown in this report, the removal of SI cortex contralaterally to the stimulated hand produces a severe deficit in the animal's ability to categorize tactile stimuli, but does not interfere with the detection of the same stimuli.

Materials and methods

Somesthetic task

Two monkeys (*Macaca mulatta*; 6- to 8-kg males) were trained to perform a somesthetic task in which they were required to categorize the speed of a probe (2-mm round tip) moving across the glabrous skin of one of the fingers of the restrained left hand. They indicated the speed category by pressing, with the right hand, one of two target switches. All animal procedures were carried out according to institutional protocols that meet or exceed NIH and Society for Neuroscience guidelines.

The left arm of the animal was secured in a half-cast and the hand maintained in a palm-up position. The right hand operated an immovable key and two target switches with centers located at 70 mm and 90 mm to the right of the midsagittal plane. They were placed at reaching distance, 250 mm away from the animal's shoulder, and at eye level. We used a set of ten speeds, from 12 to 30 mm/s, at which the probe could move. Half of them were con-

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sidered as low (12, 14, 16, 18, and 20 mm/s) and the rest as high (22, 24, 26, 28, and 30 mm/s). In all trials the probe scanned a fixed traverse distance (6 mm), in the same direction and with constant force (20 g). Stimuli were delivered by a computer-controlled tactile stimulator 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 he detected a step indentation of the skin of the restrained left hand. He indicated detection by placing his right hand on an immovable key in a period not exceeding 1 s. He maintained this position throughout a variable delay period (1.5–4.5 s), beginning with detection of the skin indentation and ending when the probe moved at any of the ten speeds. He indicated the detection of the end of the motion by removing his hand from the key within 600 ms (RT) and indicated whether the speed was low or high by projecting his free hand to one of the two switches within 1 s (MT). The medial switch was used for low speeds and the lateral one for high speeds. The animal was rewarded for correct categorization of the speed with 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 ten trials per class (speeds) presented randomly, was used to construct psychometric functions. These psychometric functions were plotted as the percentage of judgments in which the speed was classified as high (higher than 20 mm/s), as a function of speed. Logistic functions of the form $f(x)=1/[1+e^{(B_0+B_1x)}]$ were fitted to the resulting data points. All logistic regressions were significant ($P<0.001$).

Surgery

After 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 neuronal recording in the right postcentral gyrus and with a head holder for head fixation. The center of the chamber was fitted to a hole made in the skull, exactly over the hand representation in the postcentral gyrus. The chamber and the head holder were secured with screws and acrylic to the skull. All these procedures were carried out under aseptic conditions and sodium pentobarbital anesthesia (30 mg/kg).

Electrophysiological identification of the hand area in the postcentral gyrus

We recorded the activity of single neurons with glass-coated platinum-iridium electrodes (2–3.5 M Ω), which were passed transdurally into the postcentral gyrus. A record was kept of the depth at which each neuron was isolated along the length of each penetration. We identified the hand region in areas 3b, 1, and 2, according

to the somesthetic properties of these neurons (Kass et al. 1979; Powell and Mountcastle 1959; Ruiz et al. 1995). Based on this electrophysiological study, we subsequently ablated the hand representation in the postcentral gyrus.

Lesion of primary somatic sensory cortex

Under ketamine anesthesia (5 mg/kg), the dura was opened and subpial tissue was aspirated to remove the hand area. The lesion was made under the microscope, using the landmarks obtained during the electrophysiological identification of the hand area in the postcentral gyrus. Afterwards, the dura was closed in layers, and the animal was returned to his home cage for recovery. Because of the short duration of the ketamine anesthesia, animals recovered very quickly. We studied the sensorimotor performance of the two animals for 60 consecutive days following this lesion.

Histological reconstruction

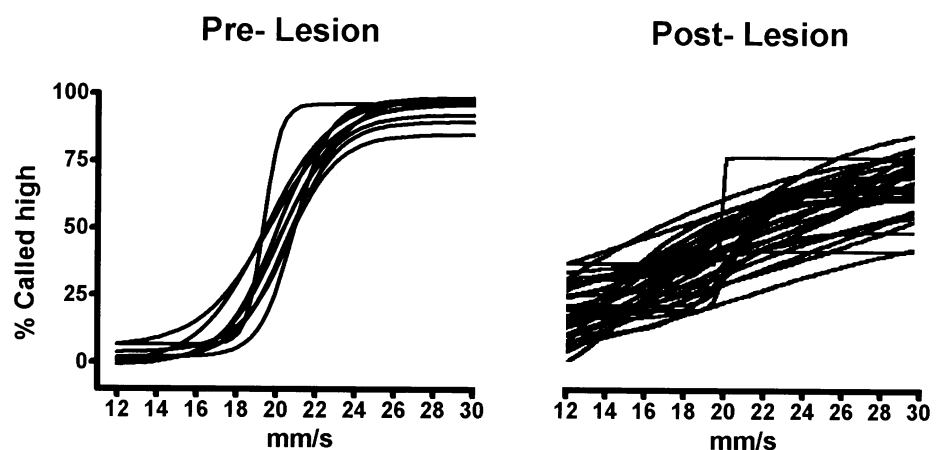
After the experiments, animals were anesthetized with ketamine (6 mg/kg) and sodium pentobarbital (40 mg/kg) and perfused through the carotids with PBS 0.1 M followed by 4% paraformaldehyde in PB 0.1 M. The brain was removed and suspended in paraformaldehyde. Later, a block of the right hemisphere containing the postcentral gyrus was sectioned at 50 μ m and the sections were stained with cresyl violet. We used these sections to reconstruct the lesions placed in the right postcentral gyri of the two animals.

Results

Somesthetic performance in normal animals

Figure 1 (left) shows 11 psychometric curves from monkey M1, obtained during 11 consecutive days before the ablation of the hand area in SI cortex. These are logistic functions fitted to the data points (not shown). They are plotted as the percentage of trials in which the speed was judged as higher than 20 mm/s, as a function of speed. Each curve represents data from five runs (100 trials per run; 10 trials per class) performed each day by this animal. From the profiles of the psychometric curves, it can be appreciated that the animal performed the categorization of stimulus speeds in a similar manner from day to day. The second animal (M2) performed similarly. The

Fig. 1 Psychometric curves for the categorization of tactile stimulus speeds. The curves on the *left* were measured before (11 consecutive days) the unilateral lesion of primary somatic sensory cortex. The curves on the *right* were measured after (31 consecutive days) the lesion. After ablation of SI cortex, performance in categorization degrades significantly. Data are from monkey M1; similar results were obtained in monkey M2



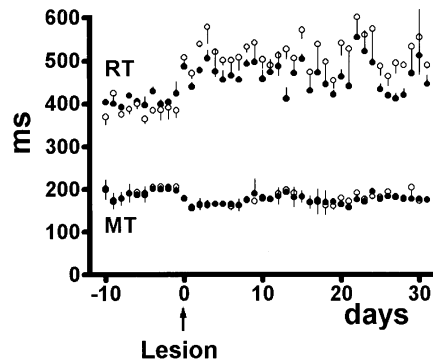


Fig. 2 Reaction (*RT*) and movement (*MT*) times for low and high tactile stimulus speeds during the categorization task, before (11 consecutive days) and after the lesion (31 consecutive days) of primary somatic sensory cortex. *Filled circles* indicate the *RTs* and *MTs* for low stimulus speeds and *open circles* for high stimulus speeds. Data are mean \pm SD values for monkey M1; similar results were obtained in monkey M2

mean values of the *RTs* and *MTs* were not significantly different for low (*RT*, 418.8 \pm 30.7 ms; *MT*, 193.8 \pm 17.5 ms) and high (*RT*, 386.8 \pm 26.8 ms; *MT*, 191.0 \pm 15.3 ms) speeds, or across animals. Figure 2 shows that these quantities did not vary noticeably from day to day either.

Effects of lesioning SI cortex on the somesthetic categorization task

The lesion in the right hemisphere of monkey M1 included areas 3b, 1, and 2 of the postcentral gyrus (Fig. 3); a similar lesion was placed in monkey M2. This lesion also affected the arm and face areas. We also lesioned accidentally the arm area of primary motor (*MI*) cortex. This lesion does not compromise the selectivity of the effects produced by the removal of SI, neither for the categorization of moving tactile stimuli nor for the motor performance in the same task. Figure 1 (right) shows the effects of SI cortex removal on the somesthetic performance of monkey M1. Thirty-one psychometric functions from 31 consecutive days after the lesion are shown. The profiles of the psychometric curves changed considerably, indicating that speed categorization was done almost by chance. The effects observed in monkey M1 were similar to those produced by an identical lesion of SI cortex in monkey M2. Slight increments in the mean values of the *RTs* (low, 466.5 \pm 39.2 ms; high, 517.9 \pm 44.5 ms) were detected following the lesion, but no change in the *MTs* was observed (low, 176.7 \pm 17.0 ms; high, 175.1 \pm 15.3 ms). Figure 2 shows the daily *RT* and *MT* values throughout the experiment. The fact that animals could perform the task with comparable *RT* and *MT* values before and after the lesion indicates that they were able to detect the somesthetic trigger stimuli, skin indentation, and probe movement. However, after the lesion they could not categorize the speeds correctly.

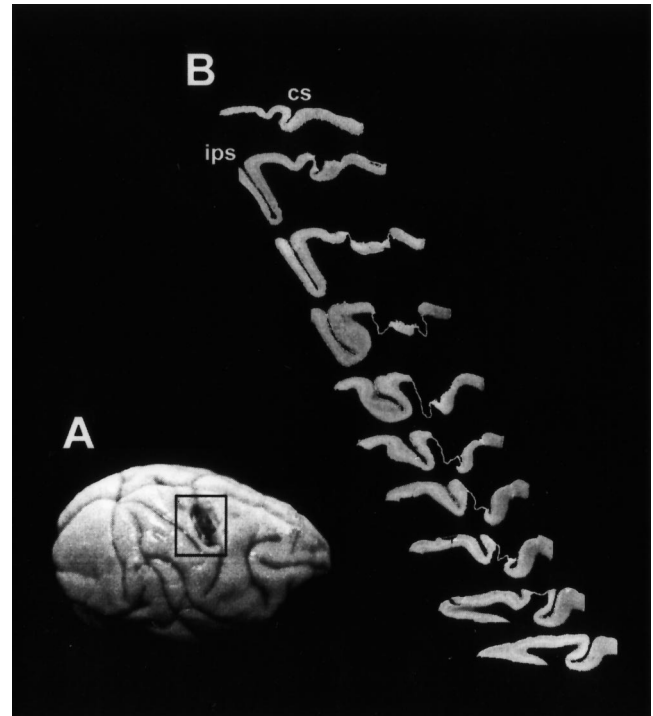


Fig. 3A, B Histological reconstruction of the lesion made in the right hemisphere of monkey M1 (**A**). **B** This lesion included areas 3b, 1, and 2 in the hand-arm and face regions. The arm region of primary motor cortex was also removed. We show one section every 0.8 mm from medial (*top*) to lateral (*bottom*) (*CS* central sulcus, *ips* intraparietal sulcus)

Discussion

We determined the capacity of two monkeys to categorize the speed of moving tactile stimuli following a lesion of SI cortex. Its removal prevented the monkeys from categorizing correctly. This effect was permanent, since animals never recuperated this capacity, despite intensive training following the lesion. In contrast, the animals' ability to detect the stimuli was unaffected, as revealed by the measurements of the *RTs* and *MTs*.

The role of SI cortex in somatic sensitivity is firmly established. Human patients with lesions in parietal cortex, which includes SI cortex, have permanently elevated detection thresholds in the contralateral hand (Roland 1987). Studies in monkeys indicate that extensive lesions of the parietal lobe (SI, SII, and area 5) and frontal motor areas (*MI*, lateral premotor cortex, and supplementary motor area) affect the capacity of monkeys to discriminate somesthetic stimuli (LaMotte and Mountcastle 1979). Animals never recuperated this ability; however, they preserved the capacity to detect the stimuli, although the detection threshold was elevated. The results obtained in the present study demonstrated that a lesion confined to SI cortex (areas 3b, 1, and 2) produced a permanent loss in the capacity of monkeys to categorize the speed of moving tactile stimuli. In general, our findings are comparable with those obtained by LaMotte and Mountcastle (1979) in a different somesthetic task.

These authors interpreted their results in terms of a disorder in somesthesia. This interpretation is consistent with the present results, which can be explained assuming that the lesion destroys the neural machinery that actually carries out the categorization. However, another possibility is that the speeds are correctly categorized and that the later association between the speed categories and the locations of the target switches are disrupted. Although we favor the first alternative, given that the lesion was made in an early cortical structure, it is unclear how these moving tactile stimuli are transformed into a visuomotor command signal for target location in the present task. Thus, the second alternative cannot be ruled out.

Animals detected the stimuli very efficiently after removal of SI cortex, as indicated by the behavioral motor reactions triggered by the stimuli. This suggests that other cortical areas carry out this function. Indeed, the somesthetic areas of the posterior parietal lobe were spared from the lesion, and it is well known that they receive thalamic inputs (Burton 1986). Thus, this ascending excitatory input bypassing SI cortex and reaching the posterior parietal lobe could be efficiently transferred to the frontal motor areas (Jones 1986; Jones et al. 1978; Jones and Powell 1969) and from them to the spinal cord for the execution of the behavioral motor reaction (Galea and Darian-Smith 1994). The results indicate that, in order to analyze complex features of the somesthetic signals, these need to be processed by SI cortex. This region is necessary for the somesthetic areas of the posterior parietal lobe to be fully functional. This result is consistent with other studies showing that these areas depend critically on SI cortex (Pearson and Powell 1985; Pons et al. 1987).

Previously, we studied the neuronal responses of SI cortex in the same categorization task described here (Romo et al. 1996). We found that the neuronal discharges of SI cortex vary smoothly with the speed of moving stimuli and do not correlate with the categories these belong to. In addition, the responses are indistinguishable whether the animal performs the task or whether the stimuli are delivered passively, without requiring a behavioral response. The fact that the neural responses in SI cortex are independent of the task raises the question of its functional role in somesthetic perception. We proposed that SI provides the initial substrate for the cortical processing of moving tactile stimuli leading to their categorization (Romo et al. 1996; Ruiz et al. 1995). The present results support this hypothesis. Thus, according to these neurophysiological and lesion studies, a more elaborated processing of the somesthetic information, which leads to somesthetic perception, must occur in those somesthetic and motor areas linked to SI cortex. Interestingly, neuronal activity reflecting the categorization or discrimination of somesthetic stimuli has been recorded in the supplementary motor area (Romo et al. 1993b) and in MI cortex (Mountcastle et al. 1992): some neurons in these areas are specifically tuned to the speed categories used in the task (Romo et al. 1997). This suggests that the perceptual process involves both somesthetic and motor areas. Experiments are in progress to

determine the roles of the somesthetic areas between SI cortex and motor areas of the frontal lobe in this learned somesthetic task.

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