Neuronal Encoding of Texture Changes in the Primary and the Secondary Somatosensory Cortical Areas of Monkeys During Passive Texture Discrimination

WAN JIANG, FRANÇOIS TREMBLAY, AND C. ELAINE CHAPMAN
Centre de Recherche en Sciences Neurologiques, Département de Physiologie and École de Réadaptation, Faculté de Médecine, Université de Montréal, Montreal, Quebec; and École des Sciences de la Réadaptation, Université d’Ottawa, Ottawa, Ontario, Canada

INTRODUCTION

Several parietal cortical areas, including the primary and the secondary somatosensory cortical areas (SI and SII, respectively), are known to play important roles in the ability to appreciate surface texture with the use of touch. Texture discrimination in the monkey is seriously impaired after lesions of areas 3b, 1, and SII (Carlson 1981; Murray and Mishkin 1984; Randolph and Semmes 1974; Ridley and Ettinger 1976). Texture discrimination thresholds are also elevated after area 2 lesions (Randolph and Semmes 1974).

In agreement with the results of lesion studies, single-unit recordings have shown that neurons in both SI, including areas 3b, 1, and 2, and SII of monkeys signal differences in texture explored with the use of active touch. Neuronal discharge in both SI and SII varies as a function of the explored texture, signaling differences either between smooth and rough surfaces (raised Braille dots) (Ageranioti-Bélanger and Chapman 1992; Chapman and Ageranioti-Bélanger 1991) or between varying degrees of roughness provided by periodic gratings with spatial periods (SPs) ranging from 0.75 to 3.15 mm (Darian-Smith et al. 1982; Sinclair and Burton 1991, 1993). In the studies of Sinclair and Burton, texture-related neurons in both SI and SII showed graded changes in mean discharge frequency in response to the periodic gratings, suggesting that an intensive code, based on mean firing rate, might underlie the central representation of texture in both areas.

We report here a novel difference in the texture sensitivity of SI and SII neurons in monkeys trained to discriminate the presence or absence of a change in surface roughness, produced by incrementing the SP of rectangular arrays of raised dots over one dimension (range: 2–5 mm). SI neurons showed a graded change in discharge when SP was increased; in contrast, SII neurons showed a nongraded change in discharge, i.e., their discharge signaled the presence of a change in texture but not its magnitude. Preliminary results have been published in abstract form (Chapman et al. 1995; Jiang and Chapman 1994).

METHODS

Two adult monkeys (Macaca mulatta) (monkey F, 8.7 kg; monkey H, 6.0 kg) were trained to perform a passive texture discrimination task. The animal preparation and the behavioral task have been described elsewhere (Tremblay et al. 1996). Briefly, the monkey was seated in a primate chair with the behavioral apparatus mounted in front of the animal, at waist height, and firmly clamped to the chair. The monkey was trained to discriminate changes in the texture of nylon polymer surfaces mounted on a drum (tactile stimulator) that was in turn rotated, under computer control, underneath the digit tips of the monkey (Fig. 1B). The animal was conditioned to rest one hand on the surface of the apparatus, placing the third and fourth digit tips on the textured surface that formed the floor of a small aperture over the drum (1.8 × 1.8 cm) (Fig. 1C).

The surfaces were fabricated from photographically reduced computer graphics phototetched onto a flexible letterpress plate with the use of an ultraviolet polymerization technique. Four different textured surfaces (dimensions 20 × 100 mm) were employed (Fig. 1D). One half of each surface (50 mm) had a standard texture consisting of a rectangular array of raised dots (0.8 mm diam, 1 mm high) with a center-to-center distance of 2 mm between the
rows and columns. For one surface (Fig. 1D, top), the standard (S) surface, the second half of the surface was the same as the first half (2 mm SP throughout, surface physically continuous). For the other three surfaces [modified (M) surfaces], the SP was increased over the second half to 3, 4, or 5 mm between adjacent rows (M₁, M₂, and M₃, respectively), i.e., in the direction of scanning. During data acquisition, the order of presentation of the surfaces was pseudorandom, with 50% being the S surface (no change in texture) and the other 50% being the M surfaces (change in texture).

The tactile stimulator consisted of a drum (circumference 40 cm) mounted on a drive shaft coupled to a DC motor (PMI Type U9M4F) through a 100:1 reduction gear (adapted from a stimulator described by Johnson and Phillips 1988). The surfaces were attached to the drum with double-sided adhesive tape. The position of the drum was monitored by means of a light-emitting diode (LED) and optical sensor mounted on either side of a disk (5.4 cm diam) incorporated into the drive shaft. The LED and sensor were aligned so that a series of 497 narrow slits around the circumference of the disk rotated between the pair. The precision of the measurement was such that one pulse was generated every 0.72° of rotation of the drive shaft. The absolute position of the drive shaft was recognized through a second LED–optical sensor pair mounted to detect a single reference point. A universal joint was incorporated into the drive shaft, permitting a maximal vertical displacement of 5 mm. The vertical force exerted by the fingers on the drum was monitored via a pair of strain gauges mounted beneath a rigid restraining arm that eliminated movement in the horizontal plane (see Fig. 1 in Tremblay et al. 1996). Vertical oscillations were diminished by means of an oil-filled damper mounted between the restraining arm and the floor of the steel case.

The drum was activated by the laboratory minicomputer (PDP 11-73) that delivered a constant voltage to the DC motor. The direction of rotation of the drum was away from the animal (see → in Fig. 1, C and D). For all recordings, a constant voltage (3.5 or 4.0 V) was applied initially to the motor for a standard duration (1,500 or 1,150 ms, respectively). Both displaced ~8.2
cm of surface underneath the monkey’s digit tips, yielding average tangential velocities of 53 or 67 mm/s, respectively. Although not reported here, two additional speeds were also frequently employed (84 and 105 mm/s; see Fig. 1A).

During each intertrial interval (3–5 s) the drum was rotated until the absolute reference point was regained. It was then rotated to the initial position of another surface (Fig. 1, B and C). The animal indicated its willingness to initiate a new trial by positioning its digit tips over the surface forming the floor of the aperture. The finger position was visually verified by the experimenter and manually adjusted if necessary before the next trial was initiated. After a 300-ms delay (Fig. 1A), a light was illuminated (3 × 3 array of LEDs located at eye level, 35 cm in front of the animal); 200 ms later, the drum began to rotate. The monkey was conditioned to remain immobile during the period of the drum rotation. After the drum stopped, the animal was trained to indicate whether a change in texture was encountered by pushing (“no change”) or pulling (“‘change”) a lever with the contralateral hand. The response lever was mechanically disabled until 1,550 ms after the motor was engaged. This delay was chosen so that even with the slowest speed, the surface presentation was usually finished before the response could occur. During the intertrial interval, the lever was repositioned to the neutral, locked position. Correct trials were rewarded with a drop of dilute juice or water.

Extracellular recordings of single neurons were made from either SI or SII in the hemisphere contralateral to the stimulated hand with the use of glass-coated tungsten microelectrodes. Cells were classified as responding to cutaneous stimuli (touch and/or light pressure) or to deep stimuli (deep pressure over the fingers and/or joint manipulation), and these stimuli were used to define the location of their receptive field (RF). Cells that were unresponsive to peripheral stimulation were classified as “no-RF.” For most of the SI neurons, RF testing included the ipsilateral side of the body. All neurons recorded in SII were also tested to determine whether their discharge varied with reaching movements of either arm and/or manipulation of small objects (food morsels). The rate of adaptation to manually applied stimuli was evaluated for cells with a clear peripheral RF. Cells were classified as rapidly adapting (RA) if their discharge was transiently modified by static stimulation; slowly adapting (SA) units responded throughout 1–2 s of static stimulation.

For each cell, a minimum of 30 trials was recorded during the performance of the passive texture discrimination task (15 trials for the S surface, 5 trials for each of the 3 M surfaces). Each trial lasted 3 s (Fig. 1A) and the following data were acquired: neural interspike intervals (1-ms resolution); force (digitization rate 200 Hz); and the times of the onset of the light, the beginning, the midpoint and the end of the drum rotation, the lever response, and the reward (if lever response was correct). For each scanning speed tested, an average of ~45–120 trials was collected in a block. An average of 40 min was required to complete all testing.

Unitary discharge was examined with the use of dot rasters and peri-event histograms aligned on the different events in the trial (see Fig. 2). For all units, the mean discharge rate in each trial was measured over three standard epochs: at rest (spontaneous discharge, epoch 1, 1st 300 ms of the trial); during the presentation of the first half of the textured surface, epoch 2; and during the presentation of the second half of the textured surface, epoch 3 (see Fig. 2). Cells were classified as modulated if the mean discharge rate during either epoch 2 or epoch 3, was significantly different from the spontaneous discharge rate, epoch 1 (2-tailed paired t-test, P < 0.01). Cells were classified as texture-related if the discharge in epoch 3 showed a significant change across all four types of surfaces (S and M surfaces) with the use of a one-way analysis of variance (ANOVA, P < 0.01). The texture-related cells were further categorized as graded if the discharge during epoch 3 showed a significant change across M1, M2, and M3 (1-way ANOVA, P < 0.05) or nongraded if the ANOVA showed no significant change (P > 0.05) in discharge across the three M surfaces. In interpreting the results of ANOVAs, the Bonferroni correction was applied to the results of the F tests (level of significance/number of tests). The corrected levels of significance were P < 0.005 (texture-related) and P < 0.025 (graded), respectively.

For monkey F, electrolytic lesions were made at the completion of the recording period for later reconstruction of the electrode trials. The surface of the brain was photographed and later sectioned. Electrode tracks were reconstructed from 30 μm (1 of 3) parasagittal sections stained with cresyl violet. SI and the subdivisions of areas 3a, 3b, 1, and 2 were distinguished according to the criteria described by Powell and Mountcastle (1959) and Jones et al. (1978). For SII, we used the cytoarchitectural criteria described in Jones and Burton (1976) and Burton and Jones (1976). In monkey F, 151 neurons were recorded in SI: 67 in area 3b, 43 in area 1, and 41 in area 2; 94 neurons recorded in the upper bank of the lateral sulcus were assigned to SII. The majority of the SII units were located in the lateral-posterior subregion of SII, whereas a few were located slightly more anteriorly in the medial region of SII. The second monkey (monkey H) is still under experimentation. The location of the central sulcus was determined electrophysiologically: 42 neurons located within a region 3 mm posterior to the central sulcus were tentatively assigned to SI.

RESULTS

The data base consisted of a total of 193 neurons recorded from SI of three hemispheres in two monkeys (both hemispheres in monkey F and the left hemisphere in monkey H) and 94 neurons from SII of one monkey (the right hemisphere of monkey F). The discharge of 153 of 193 (79%) SI neurons and 66 of 94 (70%) SII neurons was significantly modulated during the presentation of the surfaces in the discrimination task. Texture-related changes in discharge were observed in 51 SI and 19 SII neurons. All of the SI neurons and 18 of 19 SII texture-related neurons had a cutaneous RF that included the digit tips in contact with the surfaces [59 RA (41 in SI and 18 in SII), 9 SA, and 1 Pacinian-like]. For the SII neurons, 17 of 19 had a unilateral RF on the contralateral hand, whereas the remaining 2 had a bilaterally symmetric RF on both hands. The RF of one other SII texture-related neuron was deep.

As described in the METHODS, texture-related cells were classified as graded or nongraded, depending on whether or not the discharge pattern changed with SP across the three M surfaces. Figure 2A shows a typical graded neuron recorded from SI. This cell showed an initial transient increase in discharge associated with the start of drum rotation and maintained its discharge rate slightly higher than its spontaneous level throughout the presentation of the S surface. This cell increased its discharge rate as the modified halves of the surfaces were presented (epoch 3) and the increase was proportional to the SP (see the bar plot in Fig. 2A, right). A significant difference in discharge during epoch 3 was obtained for this cell both when all four surfaces were included in the ANOVA [F(3,33) = 20.79, P < 0.0005] and when only the three M surfaces were retained in the model [F(2,21) = 9.00, P < 0.002]. A regression analysis indicated that there was a significant positive linear relationship between the mean discharge rate and SP (r = 0.826, P < 0.0005, df = 33) but not force (r = 0.299, P > 0.1, df = 33).
TEXTURE ENCODING IN SI AND SII

Figure 2. Examples of primary somatosensory cortex (SI) graded (A) and secondary somatosensory cortex (SII) nongraded (B) neuronal discharge patterns to the surface presentation (both from the same hemisphere of monkey F). Rasters and histograms (binwidth 20 ms) of cell discharge are aligned on the onset of drum rotation ( []). Average vertical force is also shown (middle). Trials are sorted according to the surface presented and rearranged in increasing order of response time (irregular line running through each raster). Mean discharge frequency was calculated during 3 epochs (see M in B), and the values during epoch 3 are plotted at right (mean ± SE). Open circles: discharge frequency (mean ± SE) during the first 300 ms (epoch 1). For each unit the cutaneous receptive field (RF) is shown; areas of higher sensitivity to light tactile stimuli are darkened. Both units were rapidly adapting (RA) (contralateral RF only). Scanning speed 53 mm/s.

Figure 2B shows a typical example of a nongraded neuron recorded in SII. Similar to the cell in Fig. 2A, this cell showed a transient increase in discharge at the beginning of the surface presentation (and also the end in this case). When the digits were in contact with the modified second half of the surfaces, there was a clear sustained increase in discharge (compare the rasters and histograms of the M and S surfaces). The bar plot shows the mean discharge rate during epoch 3 as a function of SP. The ANOVA showed that discharge rate was significantly changed during epoch 3 when all four surfaces were included in the model \[ F(3,69) = 8.11, P < 0.0005 \]. This difference disappeared, however, when the same analysis was applied to the three M surfaces \[ F(2,42) = 0.01, P = 0.993 \]. No significant relationship was found between discharge and force during epoch 3 in this cell \( r = 0.185, P = 0.128, df = 69 \). Thus the discharge varied in a “one-step” fashion, signaling the presence of a change in SP but not its magnitude.

In general, most of the texture-related neurons in SI were classified as graded (44 of 51, 86%); a smaller proportion of graded neurons was encountered in SII (7 of 19, 37%). All graded neurons showed a significant linear relationship between the mean discharge rate measured during epoch 3 and SP (regression analysis, \( P < 0.01 \)). Most of the graded responses (42 in SI, 6 in SII) were positive, i.e., discharge increased with an increase in SP, but a few cells (2 in SI, 1 in SII) had negative graded responses, i.e., discharge decreased with an increase in SP. In contrast, nongraded responses to changes in texture were demonstrated by the majority of texture-related neurons in SII (63%, 12 of 19); only a small fraction of SI neurons were nongraded (14%, 7 of 51). Most of the nongraded responses were positive (7 in SI, 10 in SII), although in two SII units, negative responses were observed. Overall, the distribution of graded and nongraded neurons in SI and SII was significantly different \( \chi^2 = 15.696, df = 1, P < 0.0005 \).

Figure 3 summarizes the mean discharge rate during epoch 3 of all texture-related neurons in SI (Fig. 3A) and SII (Fig. 3B) that were tested with a scanning speed of 53 mm/s and that showed an increase in discharge in response to the increase in SP. This included 29 of 51 cells in SI (25 graded, 4 nongraded) and 16 of 19 in SII (5 graded, 11 nongraded) [excluded cells were 22 SI neurons (19 graded, 3 nongraded) and 3 SII units (1 graded, 2 nongraded)]. Inspection of Fig. 3, A (SI) and B (SII), shows that the pattern of discharge in relation to the changes in texture is strikingly different in the two structures. Despite considerable variability in the discharge rate of each cell and its actual relation to SP, the response of the SI sample displayed a clear tendency to show a graded increase in mean discharge rate with an increase in SP [ANOVA across 4 surfaces: \( F(3,116) = 4.43, P < 0.006 \); ANOVA across 3 M surfaces: \( F(2,87) = 2.64, P < 0.06 \)]. In contrast, the SII sample showed a single step increase in discharge for the M surfaces [ANOVA across 4
FIG. 3. Histograms show discharge frequency (mean ± SE) during epoch 3 (see Fig. 2 legend) for 29 texture-related neurons in SI (A) and 16 texture-related neurons in SII (B) as a function of spatial period (SP). Open circles: spontaneous discharge frequency (mean ± SE), epoch 1.

Our results demonstrate that there exist two classes of texture-related neurons in SI and SII: graded neurons modified their discharge rate in proportion to changes in SP, whereas nongraded neurons varied their discharge rate as long as there was a change in SP between the first and the second half of the surfaces but provided no information about the magnitude of the change. Graded and nongraded neurons were, moreover, differentially distributed, so that graded neurons were found mainly in SI, and nongraded neurons in SII. The observation that the graded texture-related neurons showed significant linear relationships between their mean discharge rate and SP over the tested range of 2–5 mm agrees and extends the results reported by Sinclair and Burton (1991, 1993), who tested neuronal responses in SI and SII with an SP range of 0.75–3.15 mm (periodic gratings with a constant ridge width of 0.25 mm and groove widths of 0.5–2.9 mm). We also confirm the observations by Sinclair and Burton that a smaller number of texture-sensitive neurons (2 of 51 in SI, 3 of 19 in SII) was negatively related to the change in SP: the discharge rate of these neurons decreased with an increase in SP.

In contrast to Sinclair and Burton (1993), however, we report here that the majority of SI and SII texture-related neurons were nongraded, i.e., the neurons signaled the difference in texture of the M surfaces, but their mean discharge rate did not reflect the physical characteristics of the scanned surfaces. This finding was unexpected, and suggested to us that such a response pattern might correspond to a higher-order representation of surface texture specifically related to the behavioral demands of our task, no change versus change. Such a suggestion would be consistent with the results of lesion studies in macaque monkeys that have indicated that information flow in the parietal lobe proceeds serially through SI to SII (Pons et al. 1992).

Interpretation of our results is, however, potentially confounded by one factor. Connor et al. (1990) reported that the mean discharge frequency of the primary mechanoreceptive afferents that innervate the glabrous skin of monkeys increases up to SPs of 3–4 mm and thereafter declines as the SP of raised dots (dot diameters ranging from 0.5–1.2 mm) is increased further in both dimensions in a square tetragonal array. Our tested SPs thus spanned the rising limb (2 mm) and the peak of their stimulus–response curves (3–5 mm), and so one explanation for the nongraded cells was obviously that the mean discharge frequency of the primary afferents did not vary over the range of 3–5 mm. We do not believe that this contributed significantly to our results, because SI neurons (and some SII units), in the same monkey, were graded across the entire range of SPs tested. The difference between our results and those of Connor et al. (1990) can likely be explained by the fact that we changed SP in only one dimension, across rows, whereas Connor et al. changed it across two dimensions, rows and columns.

Several alternate explanations for our results were also considered. First, the nongraded cells might have been specifically tuned to specify finer increments in SP than used here, i.e., their responses might have been graded from 2 to 3 mm, reaching a plateau at 3 mm. Such a suggestion would be consistent with the results of Sinclair and Burton (1993), because their surfaces did not extend much beyond SPs of 3 mm (see above). In this regard, it is of interest that when speed was incremented, the nongraded response pattern was preserved (Jiang and Chapman, unpublished observations).

The importance of this observation lies in the fact that an increase in the scanning speed increases the temporal frequency of stimulation (temporal frequency = speed/SP) (Darian-Smith and Oke 1980). Temporal frequency is also increased when SP is decreased. Because, at least with our sample to date, nongraded neurons retain their response pattern at higher speeds (range tested: 53–105 mm/s), it would appear unlikely that this mechanism can explain our results. Further experiments are, however, warranted, particularly with the use of a wider range of SPs to demonstrate the ability of our results to be generalized.

Second, we considered the related possibility that the nongraded response might be explained by saturation. Inspection of Fig. 3, however, shows that the mean spontaneous rate of SII neurons (16 ± 3 imp/s, mean ± SE; n = 16) was
actually significantly lower ($t = 2.887, df = 43, P < 0.01$) than that of the SI neurons ($31 \pm 3$ imp/s, $n = 29$). Moreover, the nongraded SII neurons, when sensitive to changes in scanning speed, significantly increased their discharge rate when tested at higher speeds and all of them retained the nongraded pattern (above), making it unlikely that saturation contributed significantly to the results.

Third, one obvious difference between this study and that of Sinclair and Burton (1993) is the mode of touch (passive and active, respectively). Preliminary analyses lead us to believe that this did not contribute to the difference in results, because nongraded patterns were also observed in the majority of SII neurons tested with the use of active touch in the same monkey (monkey F). A more likely explanation is that the difference can be explained by differences in the experimental paradigms. In the study by Sinclair and Burton (1993), surfaces containing different textures were separated physically by raised bars and the monkeys did not have to indicate a decision until the same surface had been repetitively scanned four times. In our task, the surfaces contained no physical markers that would aid in the comparison. Moreover, the task required the animal to make a discrimination decision after a single presentation of the surface. Perhaps more importantly, the nature of the discrimination was different in the two tasks. In Sinclair and Burton’s task, the monkeys were required to discriminate the smoother of a pair of textured surfaces, and a change in surface texture was presented in every trial. This contrasts with our study, in which the animals were required to discriminate the presence or absence of a change in texture, and texture changes were only present in about one half of the trials. In fact, the suggestion that neuronal discharge in SII is not strictly related to the SP, or physical characteristics, of the textured surface is actually supported by the data presented by Sinclair and Burton (1993). Inspection of their Figs. 2 and 4 indicates that there was no simple relation between discharge rate and SP because the response to the same SP varied depending on whether it was scanned first or second. It thus seems likely that the nongraded SII texture responses may reflect the behavioral demands of our task. Because the key point of our task was to detect the presence or absence of a change in texture, information about the physical details of the surfaces may have been redundant and was therefore “gated” out in SII. Such a suggestion is consistent with previous studies that have clearly shown that the sensory responsiveness of cortical neurons can be either enhanced or diminished according to the importance of the sensory information to the ongoing behavioral task (Chapman 1994 Chapman and Ageranoti-Belanger 1991; Hsiao et al. 1993; Jiang et al. 1991; Poranen and Hyvarinen 1982).

In conclusion, we confirm that the analysis of surface texture is distributed across multiple fields in SI and also SII. The nongraded texture responses described in SII may reflect a form of feature extraction, signaling the presence of a change in texture but not its magnitude. Such neuronal discharge properties contrast with the graded response properties encountered in SI, and suggest that texture information is sequentially processed, first in SI and then in SII. This notion is consistent both with the results of lesion studies (above), and also with Mishkin’s proposal (1979) that SII might serve a role in somesthesis similar to that of the infero-temporal cortex in vision, being specialized for recognizing global, rather than specific, features. Further support for this suggestion comes from the observation by Caselli (1991, 1993) that unilateral damage to the parietotemporal cortices in humans, including SII, results in tactile agnosia (impaired tactile object recognition) in the absence of more basic deficits in somatosensory perception.

We thank the following for excellent technical assistance: R. Albert, the late R. Bouchoux, M. Bourdeau, D. Cyr, G. Filosi, C. Gauthier, and C. Valiquette.

This research was supported by grants from the Medical Research Council of Canada and the Université de Montréal. W. Jiang is supported by the Université de Montréal; F. Tremblay was supported by the University of Ottawa and the Université de Montréal; and C. E. Chapman was a chercheur-boursier of the Fonds de la Recherche en Santé du Québec.

Address for reprint requests: C. E. Chapman, Centre de Recherche en Sciences Neurologiques, Faculté de Médecine, Université de Montréal, P.O. Box 6128, Station: Centre Ville, Montreal, Quebec H3C 3J7, Canada.

Received 17 September 1996; accepted in final form 14 November 1996.

REFERENCES

AGERANIOTI-BELANGER, S. A. AND CHAPMAN, C. E. Discharge properties of neurones in the hand area of primary somatosensory cortex in monkeys in relation to the performance of an active tactile discrimination task. II. Area 2 as compared to areas 3b and 1. Exp. Brain Res. 91: 207–228, 1992.


CARLSON, M. Characteristics of sensory deficits following lesions of Brodman’s areas 1 and 2 in the postcentral gyrus of Macaca mulatta. Brain Res. 204: 424–430, 1981.


JOHNSON, K. O. AND PHILLIPS, J. R. A rotating drum for scanning embossed