Effects of a Cross-Modal Manipulation of Attention on Somatosensory Cortical Neuronal Responses to Tactile Stimuli in the Monkey

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Meftah, El-Mehdi, Jafar Shenasa, and C. Elaine Chapman. Effects of a cross-modal manipulation of attention on somatosensory cortical neuronal responses to tactile stimuli in the monkey. J Neurophysiol 88: 3133–3149, 2002; 10.1152/jn.00121.2002. The role of attention in modulating tactile sensitivity in primary (SI) and secondary somatosensory cortex (SII) was addressed using a cross-modal manipulation of attention, somatosensory versus visual. Two adult monkeys (Macaca mulatta) were trained to perform two tasks: tactile discrimination of a change in the texture of a surface presented to digits 3 and 4 and visual discrimination of a change in the intensity of a light. In each trial, standard texture (2 mm spatial period, SP) and visual stimuli were presented. These were followed by an increase in SP and/or luminance. Each trial was preceded by an instruction cue (colored light) that directed the animal to attend and respond to the change in one modality while ignoring any change in the other modality. The two tasks were interleaved during the recording, on a trial-by-trial basis. Extracellular recordings were made from 178 neurons (SI, 102; SII, 76), all with a cutaneous receptive field on the stimulated digit tips. Discharge was quantified in both tasks during the instruction, the standard-stimuli, and the texture-change periods. The results showed that selective attention to tactile stimuli had qualitatively and quantitatively greater and earlier effects in SII than SI. Twenty-four of 102 SI cells showed a significant change in discharge with the direction of attention. For almost all cells (20/24), discharge was enhanced when attention was directed toward the tactile stimuli; the effects were most frequent in the analysis interval that encompassed the change in SP (16/24). A significantly higher proportion of SII cells were attention-sensitive (47/76). The effects were concentrated in the texture-change period (39/47) but also included earlier periods in the trial (instruction period, n = 15; standard-stimuli period, n = 32). Attention-related modulation that spanned all three intervals (n = 11) likely reflected baseline changes in discharge. For the texture-sensitive cells (43 in SI, 37 in SII), the mean change in discharge frequency (post texture change – pre-texture change) in each task was significantly increased in SII but not SI with selective attention. The results are consistent with a two-stage modulation of parietal cortical discharge, an initial stage (SI) in which there is some enhancement of sensory responses to the salient feature, the texture change, and a second stage (SII) in which baseline changes occur, along with further feature selection. These controls may be independently exerted on SI and SII, or they may reflect top-down controls from SII to SI.

INTRODUCTION

Selective or voluntary attention is an example of a higher-level, adaptable control mechanism, whereby one can choose to respond to a particular event or stimulus while ignoring any concurrent competing stimuli. Stimulus selection can be based on any number of attributes, including its spatial location, physical characteristics, modality, and behavioral significance. For the somatosensory system, psychophysical experiments have shown that attention can modify the perception of tactile stimuli. Direction of attention to a particular spatial location (spatial attention) enhances performance on more complex tactile discrimination tasks but not simple detection tasks (Posner et al. 1978; Sathian and Burton 1991; Whang et al. 1991). In contrast, cross-modal manipulations of attention (direction of attention to a specific modality, e.g., tactile vs. visual) enhance performance of both simple tactile detection tasks as well as more complex tactile discrimination tasks (Boullier 1977; Posner et al. 1978; Post and Chapman 1991; Zompa and Chapman 1995). In particular, we have shown that cue condition (valid, neutral, or invalid) in a cross-modal manipulation of attention (tactile vs. visual) significantly modifies the ability of human subjects to discriminate a change in the texture of surfaces scanned under the immobile digit tip (Zompa and Chapman 1995). Subjects are faster and more accurate when attention is directed toward the change in texture as compared with when it is misdirected toward the visual modality. The same cross-modal paradigm also results in speeded-up detections of weak vibrotactile stimuli (Post and Chapman 1991).

Although we have a wealth of information regarding the effects of selective attention on the central processing of visual stimuli (reviewed in Colby 1991; Desimone and Duncan 1995; Kanwisher and Wojciulik 2000), there is relatively little known about the neuronal mechanisms that underlie the effects of attention on tactile perception. Attentional influences are thought to underlie observations that the behavioral significance of a cutaneous stimulus modifies parietal cortical neuronal responses, producing a relative enhancement in response to relevant (rewarded) stimuli as compared with irrelevant (unrewarded) stimuli (Chapman et al. 1984; Hyvärinen et al. 1980; Nelson 1988; Poranen and Hyvärinen 1982; Salinas et al. 2000). Although attentional influences may well have been responsible for the modified discharge with behavioral relevance, it remains that none of these earlier studies explicitly controlled attention. Furthermore, other factors may have con-
A  TACTILE DISCRIMINATION TASK

Hold 0.5 s  Instruction 2 s  Stimulation 3 s

Green light

Yellow light  $V_0$

Tactile stimulus

SP = 2 mm  SP = 4.7 mm

Standard stimuli on  Texture change  Response and reward

Tactile stimuli

SP = 2 mm  SP = 3.7 mm  SP = 4.7 mm

B  VISUAL DISCRIMINATION TASK

Hold 0.5 s  Instruction 2 s  Stimulation 3 s

Lever

Instruction cue

Red light  $V_0$

Visual stimulus

Yellow light  $V_3$

SP = 2 mm

Standard stimuli on  Visual change  Response and reward

Tactile stimuli

SP = 2 mm  SP = 4.7 mm

Visual stimulus

C  INSTRUCTION CUES  MODALITY

Green 'G'  Directed: Tactile

Red 'R'  Directed: Visual

D

<table>
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<th>SP (mm)</th>
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<td>2</td>
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$T_0$

$T_1$

$T_{2,1}$

$T_{2,2}$

140 mm

E

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tributed to the results, including motivation, arousal, reward expectancy, and intention to move.

It is only recently that the results of several controlled studies of selective attention on parietal cortical neural responses to tactile stimuli have been published. These studies showed that attention modifies the responses of neurons in primary (SI) and secondary (SII) somatosensory cortex to cutaneous stimuli (Burton and Sinclair 2000; Burton et al. 1997; Hsiao et al. 1993; Steinmetz et al. 2000). There was general agreement that attentional effects are more pronounced in SII than in SI, but the sign and timing of the effects within each trial were very different in these studies. Hsiao and collaborators reported relative enhancement of cell discharge when attention was directed to the tactile stimulus. The effects were nongeneric in that responses to both target and nontarget tactile stimuli were enhanced with attention. In contrast, Burton and colleagues found that response suppression predominated, an effect that was largely limited to one portion of the trial—specifically the period that preceded the interval in which the stimulus to be detected might occur. A number of factors likely contributed to the differences in the results, including differences in the experimental paradigms, the sensorimotor abilities of the animals, and criteria for choosing cells for inclusion in the studies.

The present study was undertaken to examine the role of selective attention in modulating tactile sensitivity in SI and SII cortex using a modified version of the cross-modal paradigm, validated in psychophysical experiments in humans (above), omitting the divided attention condition (neutral cue) because performance was not significantly different from that in the valid and invalid trials. Three specific questions were addressed. First, what is the sign of attentional modulation of neuronal responsiveness in SI and SII cortex? Because tactile detection and discrimination are improved with a cross-modal manipulation of attention, we expected that attention would enhance tactile responsiveness in a population of cells in SI and SII cortex. Second, what is the pattern of attentional modulation across the various events that occur during the exploration of a textured surface containing a change in spatial period (SP)? In other words, are the attentional effects restricted to the interval containing the change in SP or is discharge modulated throughout the sequential scanning of the standard and modified portions of the surface? To explain our observation that texture discrimination is improved with attention (Zompa and Chapman 1995), we hypothesized that attention would specifically enhance cortical responsiveness during the period in which the change in SP was presented. Finally, is there any selectivity in the attentional effects? Specifically, are texture-sensitive cells (i.e., those whose discharge frequency varies with SP) more likely to be modulated by attention than non-tactile-sensitive cells?

Preliminary reports of the results have been presented (Mef-tah and Chapman 1997, 2001).

METHODS

Experiments were performed in two adult monkeys (Macaca mu-latta; G, 8.5 kg, and I, 9.2 kg). The paradigm was adapted from that developed by Zompa and Chapman (1995). The monkeys performed two tasks (Fig. 1A and B): tactile discrimination of a change in the texture of a surface presented to the distal phalanges of digits 3 and 4 (D3/4) and visual discrimination of a change in the intensity of a light. The monkey initiated the trial by depressing the response lever with the nonstimulated hand. After a hold period of 0.5 s, an instruction light appeared that directed the animal to attend and respond to the change in one modality while ignoring any change in the intensity of the other modality (Fig. 1C); green light, tactile; red light, visual. Two seconds later, the standard texture and visual stimuli were presented; these were followed by a change in stimulus intensity in one or both modalities. When both modalities changed, the two changes did not occur at the same time. Animals were rewarded with a drop of juice for detecting the change in intensity of the signaled modality by releasing the response lever. The two tasks were interleaved during the recording, so that the animal had to direct its attention to the appropriate modality on a trial-by-trial basis.

Tactile stimulation and discrimination task

The surfaces consisted of truncated, cylindrical raised dots (1 mm height and 0.6 mm diam) in a rectangular array (see Jiang et al. 1997). As shown in Fig. 1D, dot spacing was constant within the rows: 2 mm spatial period (SP, center to center distance between dots). Dot spacing between the rows, corresponding to the direction that the surfaces were scanned under the fingers pads (Fig. 1E), was 2, 3.7, or 4.7 mm. The entire strip (20 × 400 mm) was attached to the circumference of a cylindrical drum (Fig. 1E). The strip was divided into four segments (140 mm long) corresponding to the four surfaces presented in these experiments. The standard stimulus, T0, had a constant longitudinal SP of 2 mm, as in previous studies from this laboratory (Jiang et al. 1997). The modified surfaces, T1 and T2, also had a longitudinal SP of 2 mm over the first part of the surface presented to the monkey (Fig. 1D). SP increased to either 3.7 (T1) or 4.7 mm (T2) over the second part of the surface, i.e., within the range used by us previously (see the preceding text). For the modified surfaces, the length of standard texture that preceded the modified texture was either 50 (T2,1) or 85 mm (T1 and T2,3). Because scanning speed was the same in all trials (mean: 50 mm/s, range: 47–52 mm/s), the time of the change in surface texture varied according to the segment presented (~1 s, T2,1; ~1.7 s, T1, and T2,3).

The tactile stimulator was described in Tremblay et al. (1996). Briefly, it consisted of a cylindrical drum of 400 mm circumference mounted on a drive shaft and rotated by means of a DC motor through a 100:1 reduction gear. The position of the drum and its angular displacement was monitored using a photoelectric system [light-emitting diodes (LEDs) and optical sensors; precision 0.72°]. The surface was accessible for palpation by the digital pads of D3/4 through a rectangular aperture (18 × 22 mm; see Fig. 1E). The direction of the scan was proximal to distal relative to the digits (see

FIG. 1. Time course of events for the tactile (A) and visual (B) discrimination tasks. Schematic representations of the stimuli are shown below. C: during the experiment, the animal was seated in front of a panel containing green and red lights that served as the instruction cues, and the visual stimulus (a yellow light). D: tactile stimuli used in the experiments. Four segments (left) were identified on the continuous band (right) that was mounted around the circumference of the tactile stimulator. The standard surface (T0) had a spatial period (SP) of 2 mm within and between the rows of raised dots. For the modified surfaces (T1, and T2), SP between the rows was initially 2 mm but then increased to 3.7 or 4.7 mm. E: hand posture. Digits 3 and 4 of the stimulated hand contacted the texture through a small window over the top of the tactile stimulator. The opposite hand rested on the response lever; the latter was released when the animal perceived a change in the signaled modality. RT, reaction time; SP, spatial period.
arrow, Fig. 1E). To monitor the vertical contact force applied during a trial, a universal joint was incorporated in the drive shaft, permitting some movement (~5 mm) in the vertical plane. A pair of strain gauges was mounted beneath the rigid restraining arm that prevented displacement of the drum in the horizontal plane. The force signal was linear over a range of 0.04–3.92 N with a resolution of 0.01 N. The stimulator was mounted in front of the animal, firmly clamped to the primate chair at waist height.

The sequence of events in a sample tactile trial is shown in Fig. 1A. Prior to each trial, the drum was repositioned. During this 4- to 6-s interval, there were no instruction lights, and the drum rotation speed was faster than that used in the trial. Once the initial part of the chosen surface formed the floor of the aperture, a brief tone indicated that the next trial could be initiated by depressing the response lever. As pointed out in the preceding text, the subsequent hold period (0.5 s) was followed by the instruction light (2 s) and finally the stimulation period (~3 s, corresponding to the time required to present the 140 mm of surface). The monkey had to release the response lever during a precise time window, 200–700 ms, after the texture change entered the aperture to be rewarded. The maximum time limit was longer than for the light change (400 ms, see following text) to compensate for the fact that it took 360 ms for the texture change to traverse the aperture (18 mm at 50 mm/s).

**Visual stimulation and discrimination task**

As illustrated in Fig. 1C, a panel containing the instruction and stimulation lights was placed directly in front of the monkey head at eye level (~35 cm distance). The standard visual stimulus, V_0, (3 × 3 array of yellow LEDs, 10.6 cd/m²) was clearly visible under the recording conditions (ambient light, 2.4 cd/m²). Three incremental increases in light intensity were employed (16.5 cd/m², V_1; 33.3 cd/m², V_2; 50.2 cd/m², V_3; Fig. 1B). The increase in light intensity occurred with equal probability at any one of three delays after the onset of the standard stimulus (0.9, 1.3, or 1.7 s). The shortest and longest delays corresponded to the approximate time that the texture change occurred. The time window for a rewarded lever release was set at 100–400 ms after the increment in luminance.

**Experimental design**

During the experiment, the tactile and visual trials were interleaved (order quasi-random). 50% of the trials contained a change in only one modality. In these trials, the standard visual stimulus (V_0) was presented during the tactile task (Fig. 1A), while the standard texture (T_0) was presented during the visual task (Fig. 1B). In the other 50% of the trials, both modalities changed. In the latter trials, the changes were never at the same time, and the two changes occurred at delays for which the two reaction time (RT) windows did not overlap. This design ensured that the animal’s attention was focused on the signaled modality. For example, in the visual task, the light change was sometimes preceded by a change in texture (segment T_2, plus the longest delay light change). In this case (see Fig. 2), the monkey had to ignore the change in surface texture and respond only after the change in light intensity. Responses to the unsignalled modality were not rewarded, and the response was classified as an error. Thus neural activity elicited by the texture change was recorded as the animal attended and discriminated the change in texture as well as when it ignored the texture change and discriminated the change in light intensity. All factors were counterbalanced to the extent possible (task, texture, light intensity, and delay). Complete testing of each cell required ~120 trials: 60 tactile and 60 visual trials (order quasi-random). Each of the three modified textures was presented an equal number of times (~30 trials/modified surface). When both modalities changed, only the shortest and longest visual delays were used. The shortest light delay was always paired with the longer latency change in texture (T_1 and T_2); the longest light delay was paired with the shorter latency change in texture (T_2,1).

**Training**

Animal training took ~6–12 mo. The monkeys were initially trained to perform the visual discrimination task, releasing the response lever (raising the heel of the hand from the lever) after the change was perceived. They were then conditioned to place the contralateral distal phalanges of D3/4 on the tactile surface that formed the floor of the aperture and to remain immobile throughout the entire stimulation period of ~3 s, i.e., as the visual and tactile stimuli were presented. Subsequently, they were trained to discriminate a change in surface texture. The two tasks were then interleaved, and finally, we added trials in which both modalities changed so that the monkey learned to ignore the unsignalled modality in favor of the signaled one. Training continued until the animal performed the tasks with a low and stable error rate (<10%). Note that both monkeys left their digits in contact with the surface throughout the recording sessions, even while the drum was repositioned during the intertrial interval (4–6 s).
Surgical procedures

After training was complete, a chronic recording chamber was implanted under aseptic conditions over the cortex contralateral to the stimulated hand (right hemisphere, monkey G; left hemisphere, monkey I) giving access to the hand representation in both SI and SII. The surgical procedures used for the implantation of the recording chamber have been described (Chapman and Ageranoti-Belanger 1991; Tremblay et al. 1996). Briefly, the monkey was first sedated with ketamine (15 mg/kg im) and then intubated for intratracheal administration of isoflurane (2%). The dosage of isoflurane was adjusted as required during surgery to maintain a deep level of anesthesia. Physiological parameters (temperature, heart rate, and respiration rate) were monitored throughout the surgery. Antibiotics (enrofloxacin: 5 mg/kg) were administered prior to surgery, and for 3 days postoperatively. Postoperative analgesia was provided for a minimum of 72 h (buprenorphine: 0.01 mg/kg). Animal care and housing conformed with published guidelines ["Principles of Laboratory Animal Care" published by the National Institutes of Health (publication no. 86-23, revised 1985) and “Guide to the Care and Use of Experimental Animals” published by the Canadian Council on Animal Care, revised 1993]; the experimental protocol was approved by the institutional ethics committee.

Data acquisition and analysis

During the recording sessions, the monkey was seated in a primate chair with the head immobilized to allow single-unit recordings. The extracellular activity of single neurons in SI and SII cortex was recorded with glass-coated tungsten microelectrodes (0.4–1 MΩ). During the recordings, we searched for cells that were modulated by the presentation of the textures and that had a cutaneous receptive field (RF) on the stimulated digits (D3/4 contralateral to the recordings). For each electrode penetration, a written record was kept of the depth at which each cell was recorded along with the depths that the first sign of activity appeared and the transition between active and silent zones. For each cell, we determined whether it had a peripheral RF using a variety of manually applied stimuli and passive movements. If a RF was found, the cell was then classified as either cutaneous (sensitive to touch) or deep (sensitive to joint manipulation or tap over muscle bellies). Cutaneous RFs were mapped using handheld probes and the adaptation rate to manually applied stimuli was determined. Units whose discharge rate was modified for 1–2 s of static stimulation were classified as slowly adapting (SA); those whose discharge was only transiently modified by static stimulation were classified as rapidly adapting (RA). Laterality was systematically tested for most SII cells (contralateral, ipsilateral, or bilateral).

The task and the data acquisition were under computer control. Data collection procedures have been described previously (Ageranoti-Belanger and Chapman 1992; Chapman and Ageranoti-Belanger 1991, Tremblay et al. 1996). For each trial, the following data were collected: neural spike intervals (1-ms resolution), vertical contact force (digitization rate, 200 Hz), the cue condition, and specific timing data (times of different events in the trial including the time of the change in the texture and/or light and the time of the response). Trial duration was 4.5 s in the initial recordings; this was increased to 6.5 s in later recordings to record discharge during the entire instruction period along with the preceding hold period. For each trial, we carefully monitored the position of the digits on the stimulated hand, rejecting trials in which the monkey did not maintain contact with the surface throughout the trial. We also inspected the vertical contact force records at the time of acquisition: trials in which contact force varied by more than ±0.2 N prior to the time of the lever response were rejected.

Patterns of discharge were examined using rasters and peri-event histograms aligned on different events in the trials. Cell discharge frequency was initially analyzed by determining whether there was a significant change in discharge during the presentation of the stimuli. For this, cell discharge in each trial was measured at rest (period 5 in Fig. 2: final 500 ms of the trial) and compared with the discharge measured during the presentation of the stimuli (period 4: stimulus on to stimulus off). For this and all other analyses, only trials in which the animal received a reward were included, i.e., only trials in which attention was correctly directed toward the signaled modality. Modulated cells showed a significant change between the discharge at rest and their discharge during the time that the surfaces were scanned under the digit tips (2-tailed paired t-tests). For cells that showed multiple changes in discharge during the stimulation period (increase and decrease), the global measure during the stimulation period was replaced with individual measures that encompassed the period in which discharge was modulated. Most frequently, we employed a window restricted to the first 700 ms of standard stimulus presentation (period 2 in Fig. 2).

Cells were classified as attention-sensitive if there was a significant difference in discharge between the tactile and visual tasks (independent t-tests, $P \leq 0.01$) and this independent of any variations in vertical contact force on the stimulated side. Differences in mean rate had to be $\geq 2.0$ imp/s to be considered as physiologically significant. The analyses focused on three time intervals (Fig. 2): instruction period (final 500 ms of the instruction period); standard-stimuli period (initial 700 ms of presentation of the standard stimuli, $V_1$ and $T_1$); and texture-change period (initial 400 ms following the texture change). For the latter period, the analyses were restricted to data collected with surface $T_{2 \rightarrow 1}$ (early change in texture), and the interval corresponded to the RT period in the tactile task, i.e., prior to the release of the lever. These trials were identical in terms of motivation, arousal, and intention to respond, but differed in two regards: the direction of attention but also preparation to respond (tactile) versus withhold response (visual). As there were fewer trials available for comparison (30 vs. 120), the level of significance was modified ($P \leq 0.05$). Additional analyses are described in RESULTS.

For each cell, the intensity of the attentional modulation in each time interval was quantified by calculating an attentional modulation index, $\text{AMI}$ (e.g., Luck et al. 1997; Motter 1994): $\text{AMI} = (\text{texture attended} - \text{Texture ignored}/(\text{texture attended} + \text{texture ignored})$. Positive values indicated that discharge rates were higher during the tactile task as compared with the visual task, and vice versa for the negative values. It should be noted that this is a nonlinear scale: a twofold increase in discharge in the attended condition, gives an AMI of 0.33; a fivefold increase gives a value of 0.67. The percent change between the attended and ignored tactile responses was calculated as: 100*(texture attended – texture ignored)/texture ignored). For this report, texture-sensitivity was assessed for the early modified texture, $T_{2 \rightarrow 1}$, because in this case the texture change preceded the motor response in both tasks. We measured discharge frequency during two periods in each trial: the 200-ms interval immediately before the texture change (standard surface, 2 mm SP) and the texture-change period (preceding text and Fig. 2). Paired t-tests (pre- vs. post-change, $P \leq 0.05$) were used to classify cells as texture sensitive. Positive results were verified by repeating the test on the data obtained with both modified textures ($T_1$ and $T_2$). Three cells failed to maintain their classification with this second test, and so were classified as non-texture sensitive.

Finally, the $\chi^2$ test of independence was used for comparisons of frequencies. For most statistical tests, the level of significance was set at $P \leq 0.01$.

Histological methods

Near the end of the experiment, the monkey was sedated with ketamine (15 mg/kg) to perform electrolytic lesions in selected electrode tracks to delimit the region of the recording tracks. After the final session, the monkey was killed with an overdose of pentobarbital and perfused through the heart with formol-saline solution. The brain
was then exposed, photographed, and later sectioned. Electrode tracks were reconstructed from 50-μm parasagittal sections stained with cresyl violet. In SI, areas 3a, 3b, 1, and 2 were distinguished according to the criteria of Powell and Mountcastle (1959), and Jones et al. (1978). In SII, the cytoarchitectonic criteria described by Jones and Burton (1976) were used.

RESULTS

Task performance

During the data acquisition period, both monkeys performed at a very high level: average performance in the discrimination tasks was 93–96% in monkeys G and I, respectively. In both cases, errors were approximately equally distributed across the trials in which both modalities changed as compared with trials in which only one modality changed (monkey G, 7.7 vs. 6.5%; monkey I, 4.3 vs. 3.5%).

In a complementary series of psychophysical experiments, we determined the discrimination threshold for an increment in the spacing of the raised dots by systematically varying the difference presented for each monkey (Fig. 3A). Behavioral testing was carried out under the same conditions as the recording sessions (tactile and visual tasks interleaved, etc). Inspection of the psychophysical curves shows that discrimination performance was almost identical in the two animals. Discrimination threshold, defined as the difference that was correctly identified on 75% of the trials, was 0.54 mm in monkey G (i.e., 2.54 vs. 2.0 mm) and 0.49 mm in monkey I. The differences presented during the cell recordings, 1.7 and 2.7 mm, were clearly suprathreshold for both monkeys, corresponding to ~3.3–5.2 times discrimination threshold. The corresponding Weber fraction (difference/standard) was ~25%, consistent with Sinclair and Burton’s (1991a) estimate in monkeys.

In one monkey (G), we also determined the discrimination threshold for an increment in light intensity (Fig. 3B). Discrimination threshold was 5.2 cd/m². The increments presented in the experiments corresponded to 2.4, 6.2, and 11.5 times threshold. The two lower intensities were within the same range as the increments in SP presented in the tactile task and so consistent with the interpretation that the tasks were of similar difficulty. Note that we used relatively large changes so that the rate of reward, and motivation, remained high throughout the recording sessions.

Database

We report here the results of single-unit recordings made from 102 cells in SI and 76 cells in SII in two monkeys that met our inclusion criteria (see METHODS). 1) Cells had a cutaneous RF that included the distal phalanges of D3/4 on the hand contralateral to the recordings, i.e., the stimulated digits. 2) All cells were modulated during one or more of the periods defined during each trial (periods 2, 3, or 4, Fig. 2) as compared with the discharge at rest (period 5). The majority of cells were recorded in monkey G (67 in SI, 59 in SII), and these data are used for most of the illustrations. Recordings in a second monkey (histology not yet available) confirmed the results obtained in the first monkey in all respects (35 cells in SI, 17 cells in SII).

The histology for monkey G is shown in Fig. 4. Of 67 cells recorded in SI cortex, 29 were assigned to area 3b, 9 to area 3b/1, 12 to area 1, and 17 to area 2. The recordings in SII included cells that had a cutaneous RF restricted to the contralateral hand (38/76) and cells with a bilaterally, symmetric cutaneous RF (38/76). The adaptation rate of cells to punctate, manually applied stimuli was determined for most cells (174/178). In both regions, approximately one-half of the sample showed an RA response to maintained stimuli (SI, 48/100; SII, 35/73); the remaining cells showed evidence of an SA response to sustained light touch. In SI, the RF was restricted to a single digit in 30/102 cells while in SII almost all of the RFs spanned multiple digits (74/76). Finally, 85/102 SI cells were sensitive to light touch; the remaining cells required more intense stimulation for activation and/or moving stimuli. The majority of the SII sample were likewise sensitive to light touch (69/76); only 7/76 required moderate touch for activation.

Effects of attention on discharge during the instruction and standard-stimuli periods

Figure 5 shows examples of the patterns of discharge in three SI neurons during the instruction and the standard-stimuli periods in the tactile and visual tasks. The trials are sorted
according to the instruction given (tactile or visual task), but during acquisition the different trial types were randomly interleaved. None of these cells showed an effect of attention.

In these examples, stimulus onset was followed by a phasic increase in discharge. The discharge thereafter remained elevated during the period in which the two standard stimuli (2 mm SP texture and baseline light intensity) were presented to the animal, although the degree of modulation varied. The discharge of the cell shown in Fig. 5B, middle, stayed high throughout the interval, while the cell in Fig. 5C showed a relatively large drop in discharge after the phasic burst. Inspection of the data indicates that attention itself had little or no effect on cell discharge in these three examples. Whether the animal was discriminating a change in texture (top) or a change in light intensity (middle), the pattern of discharge was very similar during both the Instruction period and the standard-stimuli period. Likewise, response magnitude was not different, as can be seen by inspection of the superimposed histograms below. Independent t-tests (tactile vs. visual) confirmed that mean discharge frequency was not significantly modulated by attention in any of the three examples. An absence of any attentional effect in both periods was a common finding in SI (89% of the SI cells, 91/102).

In contrast, attentional effects at the start of the trial were more frequent in SII (Table 1). Examples of the most typical pattern encountered are shown in Fig. 6. Both cells showed a short-latency increase in discharge following the onset of the standard stimuli. Although the pattern of discharge was similar in the two tasks, tactile and visual, the magnitude of the response to the presentation of the standard stimuli was significantly higher when attention was directed toward surface texture as compared with when attention was directed toward the light. Inspection of the superimposed histograms shows that the enhanced discharge during the tactile task was restricted to the second interval (standard stimuli) and that the effect persisted throughout this period.

The attentional modulation in the tactile task could not be explained by differences in contact force between the stimulated digits (D3/4) and the textured surface: the averaged force traces from the trials performed in each task (---) are indistinguishable when superimposed (see force traces that accompany

FIG. 4. Surface reconstruction (top left) of the entry points of the recording tracks made in monkey G along with 3 parasagittal sections at different lateralities. Large dots show the tracks from which the cells in the current database were recorded; small dots show tracks that did not contribute data to this report. Low-intensity intracortical microstimulation elicited movement in tracks that traversed the anterior bank of the central sulcus (section A-A’). CS, central sulcus; IPS, intraparietal sulcus; LS, lateral sulcus; PCS, postcentral sulcus.
the superimposed histograms). The difference could also not be attributed to changes in contact force with the opposite hand, which was resting on the response lever (see Fig. 6B). In 40% of the recording sessions, we monitored contact force on the response lever and found no changes, in either monkey, during these two analysis intervals as a function of the task (tactile vs. visual). Moreover, identical results were obtained in cells with a RF restricted to the contralateral hand (compare Fig. 6, right and left).

Overall, close to one-half of the SII neurons (46%, 35/76) showed a significant difference in discharge during one or both of the first two intervals (instruction, standard stimuli).

**Effects of attention on discharge during the texture-change period**

In SI, the majority of cells (84%, 86/102) were not attention-sensitive during the texture-change period (Table 1). An example is shown in Fig. 7A. This cell showed an increase in discharge following the presentation of the texture change, but

![Fig. 5](image)

**TABLE 1. Distribution of attention-related modulation in SI and SII**

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<tr>
<th>Attention Sensitivity</th>
<th>n</th>
<th>Instruction period n (%)</th>
<th>Standard Stimuli Period n (%)</th>
<th>Texture-Change Period n (%)</th>
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<td>8 (8)</td>
<td>16 (16)</td>
<td>10.48, ( P = 0.005 )</td>
<td></td>
</tr>
<tr>
<td>SII 76</td>
<td>15 (20)</td>
<td>32 (42)</td>
<td>39 (51)</td>
<td>17.06, ( P = 0.0002 )</td>
<td></td>
</tr>
<tr>
<td>( \chi^2 ) test</td>
<td>( \chi^2 = 13.5, P &lt; 0.0005 )</td>
<td>( \chi^2 = 29.34, P &lt; 0.0005 )</td>
<td>( \chi^2 = 25.89, P &lt; 0.0005 )</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Values are numbers of cells with percentages in parentheses. SI and SII, primary and secondary somatosensory cortices. * Independent t-tests (\( P < 0.01 \)) were used to determine if attention modulated cell discharge frequency (tactile vs. visual tasks, surface \( T_{2,1} \)).
the magnitude of the increase was not significantly different for the tactile and visual tasks, i.e., the texture-related response did not vary with the direction of attention. The discharge of the remaining 16% (16/102) of SI cells was significantly modulated by attention (12 enhanced, 4 suppressed in the tactile task), and an example is shown in Fig. 7B. As in the preceding example, there was an increase in discharge specifically related to the presentation of the texture change during the tactile task (top). During the visual task, the texture-related increase was still present but diminished. Inspection of the force traces indicates that the difference in discharge could not be attributed to variations in contact force on the stimulated side (see superimposed traces). This cell was typical in that attentional modulation was observed in the texture-change period, but discharge in the earlier instruction and standard-stimuli periods was identical for the tactile and visual tasks. Similar results were obtained in 13 of 16 SI cells that were attention sensitive in this period. Only 3/16 were attention sensitive during both the standard-stimuli and texture-change periods.

Neurons in SII were significantly more likely than those in SI to be attention-sensitive during the texture-change period (Table 1). The discharge of 51% of the SII cells (39/76) was modulated by attention during this analysis interval (31 enhanced and 8 suppressed in the tactile task). Examples of the response patterns encountered are shown in Figs. 8 and 9. Figure 8, A and B, shows examples of cells with, respectively, bilateral and contralateral RFs. Both cells showed an increase in discharge related to the presentation of the texture change. In one case (Fig. 8A), the texture-related discharge disappeared when attention was directed away from the texture. In the other case (Fig. 8B), response magnitude was scaled down when the animal performed the visual task and ignored the texture change, but some evidence of a weak response to texture can still be seen, particularly in the superimposed histograms. As in the preceding examples illustrated, contact force was identical during the analysis interval and so did not contribute to the results. In both examples, discharge rates in the earlier analysis periods were not modulated by attention, as found in 12/39 SII cells modulated by attention during the texture-change period. For the cell shown in Fig. 8B, however, it is clear that the attentional effect was well developed 110 ms before the texture change was encountered, i.e., during the interval between the end of the standard-stimuli period (1st 700 ms of stimulation) and the beginning of the texture-change period. Note that this period was not included in our fixed-analysis windows (Fig. 2).

To get a better picture of the time course of effects that were “restricted” to the texture-change period (13 SI and 12 SII cells), we compared the discharge in the tactile and visual trials at the time when the early change in texture might have occurred but did not (t = 1 s after the onset of the standard stimuli; late change in intensity). All factors were identical (standard texture and visual stimuli) except for the direction of attention. The majority of cells (10/13, SI; 8/12 SII) showed no difference in discharge, i.e., the task-related effect was restricted to a modification of the response during the texture-
change period (e.g., cells shown in Figs. 7B and 8A). Seven cells showed evidence of modified discharge in the tactile versus visual trials when the change might have, but did not, occur including the cell illustrated in Fig. 8B. This was most likely explained by attention because the modulation was similar to that seen in the texture-change period, and, as described in the following text, the attentional effect was independent of motor planning.

The remaining 27 attention-sensitive SII cells in this period also showed attention-related modulation in one or both of the preceding analysis intervals. Sixteen cells were modulated in one of the earlier intervals, usually the standard-stimuli period (14/16), and an example is shown in Fig. 9D. Eleven neurons were modulated in all three periods analyzed (Fig. 9, A–C); no such cells were found in SI. When attentional effects were observed in multiple periods, the magnitude of the effects were frequently not the same across all periods. For example, the cell shown in Fig. 9C showed a small increase in discharge during the instruction period in the tactile task (tactile, ■; visual, □), followed by greatly enhanced responses during the subsequent standard-stimuli and texture-change periods. The sign of the attentional effect was usually the same in multiple periods (Fig. 9, A–C) but not always. The cell shown in Fig. 9D showed less discharge during the standard-stimuli period in the tactile task as compared with the visual task and higher discharge rates during the subsequent texture-change period. Indeed, this texture-sensitive cell only signaled the change in texture during the tactile task. The preceding suppression of discharge, in this case, served to enhance the response to the texture change.

**Contribution of movement preparation to task-related differences**

In this study, motor behavior was not an issue for the two initial analysis periods—instruction and standard stimuli—
because these periods preceded the change in stimulus intensity and the subsequent motor response. Apart from the direction of attention, the tactile and visual trials were identical (stimuli, motivation, intention to respond, and reward expectancy). Thus for fully two-thirds of the data set, attention-modulated sensory evoked discharge was clearly dissociated from the motor response.

In contrast, during the texture-change period, the animal prepared a motor response with the ipsilateral, unstimulated arm in the tactile trials but not during the visual trials used for comparison. Instead the monkey ignored the early texture change and waited for the later increase in the intensity of the light. Thus there was a possibility that movement preparation during what was essentially the RT period in the tactile task was responsible for the “attentional” effect. This was especially an issue for cells in which the attentional effects occurred in the texture-change period (16 in SI, 39 in SII). We therefore replotted the data from each cell classified as attention-related in this critical interval, aligning the data on the onset of the motor response, comparing data from the RT period in the tactile task (texture-change period) with that recorded in the visual task (essentially the visual-change period) in trials in which the light change was preceded by the early change in texture (surface T2). The data shown in Figs. 7B and 8 (bottom) are typical in that discharge in the tactile task was enhanced relative to that in the visual task even though all factors apart from attention were now matched, including preparation to move and SP. We quantified this observation using independent t-tests: mean discharge rates in the RT interval across the two tasks (independent t-tests) were significantly different for 12/16 and 38/39 attention-sensitive cells in SI and SII, respectively (including 6/7 cells showing early anticipatory discharge). This finding is consistent with our suggestion that the modified discharge in the texture-change period was mainly explained by the direction of attention. Most of the nonsignificant results were explained by a well-developed texture response in the visual trials (3 SI cells); in one other case (also SI), sensory-evoked discharge was seen in tactile trials when the animal failed to respond and absent when the response was made precociously in visual trials, making it unlikely that motor preparation contributed to the nonsignificant results. Thus for only one SII cell were we unable to

FIG. 8. A and B: SII unit activity during the texture-change period. Both cells showed an increase in discharge after the texture change entered the window (A, bilateral RF; B, contralateral RF). Attention significantly modulated the response in both cases (tactile > visual). For the cell shown in A, texture sensitivity was abolished during the visual task. For that shown in B, texture sensitivity was preserved during the visual task, but the degree of modulation was significantly reduced. In both cases, the difference was preserved when discharge during the RT period in the tactile and visual tasks was compared (below). Plotted as in Fig. 7B. N.B. The period to the left of the vertical line corresponds to the pre texture change interval; this was not included in the analyses (Fig. 2). Number of trials, 8–13/task.
confirm that the attention effect was independent of movement preparation.

Population analyses

SII cells were significantly more likely to be modulated by attention than were SI cells (47/76 vs. 24/102, $\chi^2 = 26.66, P < 0.0005$). In both regions, there was a nonuniform distribution of attentional effects across the trial, so that attentional effects were most frequent in the texture-change period (Table 1). For SII, the laterality of the RF did not contribute to the results (contralateral, 22/38; bilateral, 25/38, $\chi^2 = 0.5, P = 0.48$). Finally, for SI, there was some indication that the location of the cell contributed to the attentional effects: fewer cells in area 3b (4/29) were modulated by attention than in areas 1 and 2 (8/29), but the difference was not significant ($\chi^2 = 1.68, P = 0.19$).

Figure 10 summarizes the distribution of the attention modulation index [AMI = (texture attended − texture ignored)/(texture attended + texture ignored)] calculated for the population of SI ($n = 102$) and SII ($n = 76$) cells in each analysis period. In SI, the distribution was centered around 0 for all three periods, and a repeated-measures ANOVA indicated that AMI did not vary across the three intervals ($P = 0.76$). In contrast, AMI changed significantly across the three periods in SII ($P < 0.0005$). In the first two analysis periods, the distribution was again centered around 0. A shift toward positive values is evident in the texture-change period, and post hoc contrast analyses indicated that AMI in period 3 was significantly higher than in either of the two earlier periods ($P < 0.0005$). Paired comparisons across SI and SII indicated that the AMI was higher in SII only for the texture-change period (see Fig. 10). Responses to the attended tactile stimulus in the latter period (attention-sensitive cells only) were increased an average 84% in SI and 132% in SII ($t$-test, $P = 0.26$). Inspection of Fig. 10 also shows the sign of the significant modulations (●). In SI, responses to the attended tactile stimulus were generally greater with directed attention (positive AMI, 20/24). In SII, the majority of attention-sensitive cells also showed enhanced responses to the attended tactile stimulus (33/47).

As described in METHODS, cells were classified as texture sensitive if there was a significant change in discharge from the pre-change period as compared with the texture-change period. Forty-three of 102 SI cells and 37/76 SII cells were classified as texture sensitive. Examples were shown in Figs. 7, 8, and 9, C and D. The proportions of texture-sensitive cells (SI, 42%; SII, 49%) are similar to those found in previous studies (Jiang et al. 1997; Sinclair and Burton 1991b, 1993).
sensitive (SI: 11/43; SII: 26/37) and non-texture-sensitive cells (SI, 13/59; SII, 21/39). Six of 11 SI cells and 15 of 26 SII cells only signaled the texture change when the tactile input was attended. In other words, the response to the texture change was gated out during the visual task [examples shown in Figs. 8A and 9D (SII)]. In non-texture-sensitive SI cells, responses to attended tactile stimuli were enhanced (11/13). In contrast, attentional modulation of discharge in non texture-sensitive SII cells was more specific and targeted. For example all of the SII cells showing decreased discharge during the tactile task in the texture-change period were non-texture sensitive (n/H11005/8), suggesting an active suppression of responses that did not contribute to task performance (e.g., Fig. 9, A and B). More- over, of four SII texture-sensitive cells that showed decreased discharge in the Standard-stimuli period, this actually served to enhance the response to the subsequent change in surface texture in all cases (Fig. 9D).

Finally, we calculated the mean change (Δ) discharge frequency elicited by the texture change in each task (post-change — pre-change) for the texture-sensitive cells. For the SII sample, paired comparisons showed that the mean Δ discharge frequency was significantly greater during the tactile task as compared with the visual task (respectively, 16 ± 2 and 4 ± 2 imp/s, P < 0.0005). A modest difference was observed in the SI sample (15 ± 2 and 12 ± 2 imp/s, P = 0.057). These results reflected the differential distribution of attentional modulation in SI and SII. Interestingly, the Δ discharge frequency during the visual task was significantly lower in the SII population than SI (P = 0.004), suggesting that there might be an active suppression of tactile responsiveness in SII during the visual task.

**DISCUSSION**

The present results showed that selective attention results in a relative enhancement of tactile responses in both SI and SII parietal cortex. In both regions, the attentional effects were most frequent in the period that contained the salient texture change. Such observations provide a neuronal basis for the enhanced tactile detection and discrimination with directed attention (see INTRODUCTION). The results also showed that the attentional influences in SII were more frequent, earlier, larger, and more complex than those found in SI, frequently spanning multiple periods of the trial, yet showing considerable specificity. Thus inputs that did not contribute to performance of the texture discrimination task (e.g., discharge of non texture-sensitive cells) were actively suppressed in SII.

**Methodological considerations**

The experimental paradigm used in this study contained the elements essential for any study of attention. Thus competing stimuli were presented in all trials with both modalities (cued and uncued) changing on 50% of the trials. When the unsignalled modality was the first to change, the animals had to withhold their response until the signaled modality changed.
The psychophysical results showed that the animals performed the tasks with a high success rate, and there was no difference in performance across trials in which both modalities changed as compared with those in which only one modality changed. These results suggest that the animals used the instruction cues to direct their attention to the signaled modality. This conclusion is supported from the results of the separate psychophysical testing (Fig. 3). When the texture difference was reduced to 0.3 mm, performance declined to ~35% for both monkeys. This was explained by the fact that in ~25% of trials, the monkeys missed the change in SP and either did not release the lever or only released it after the drum rotation stopped. In other words, the animals performed the task as instructed, attending the expected but undetected change in texture. In this study, we restricted data analyses to rewarded trials—i.e., trials in which we were certain, on a post hoc basis, that attention was directed to the signaled modality. Another important element in these experiments was that tactile and visual trials were randomly interleaved so that the animals had to focus their attention on a given modality on a trial-by-trial basis. This undoubtedly made the task demanding—requiring cognitive control of attention on each trial. Moreover, this design ensured that any changes in, for example, motivation or arousal (Morrow and Casey 1992) during the course of the recordings were equally reflected in the data from each task.

We restricted our analyses to three time periods that captured the major events in the trial, encompassing the periods in which the instruction cue, the standard stimuli, and finally the texture change were presented. This approach gave an accurate reflection of the attentional influences observed in SI and SII. It did not, on the other hand, establish the time at which attentional influences restricted to the texture-change period developed. In these cases (13 SI and 12 SII cells), the time of onset of the attentional influence remains undetermined. Exceptionally, such effects were clearly developed prior to the time that the texture change was presented (Fig. 8B), likely reflecting anticipation of the attended change in surface roughness. Consistent with this, the same cell also showed anticipatory modulation when the early change in texture might, but did not, occur. More frequently, the attentional effects were more or less coincident with the texture change (Figs. 7B and 8A).

Finally, and as detailed in results, we were able to disassociate the effects of attention from preparation of the motor response for all but one cell (54/55 cells sensitive to attention in the texture-change period). This was an important consideration because there is evidence that SI responsiveness is modulated by motor intention (e.g., Nelson 1988) and that cells in both SI and SII can show profoundly altered responses to tactile stimuli after the discrimination (motor) response in attention paradigms (Burton and Sinclair 2000; Burton et al. 1997; Hsiao et al. 1993). The general absence of any effect attributable to movement on the ipsilateral side is consistent with the results of previous psychophysical experiments showing that contralateral hand and arm movements have no effect on the detection of tactile stimuli applied to the opposite arm (Chapman 1994; Chapman et al. 1987; Williams et al. 1998). This suggestion is likewise supported by our observation of similar results when the analysis of the texture-change period was extended to all trials (SI, 17 vs. 16% attention-sensitive; SII, 58 vs. 51%) (Meftah and Chapman, unpublished observations), including data from trials in which the texture-change interval followed as well as preceded the motor response. The small decline in the proportion of attention-sensitive cells when the analyses were restricted to a subset of the data mainly reflects the loss of power in the analyses.

Effects of attention on SI discharge

The proportion of attention-sensitive SI cells found here, 24%, is similar to Hyvärinen et al.’s (1980) report that behavioral significance modulated the discharge of 16% of SI neurons, supporting the notion that attentional influences contributed to their results. Our estimate is, however, substantially lower than the 50% value reported by Hsiao et al. (1993) and Burton and Sinclair (2000). Differences in experimental design, task difficulty (Spitzer and Richmond 1991), and the stimuli employed likely contributed to the difference.

Certainly there is an intriguing difference in the sign of the attentional effects reported by Burton and Sinclair (2000) as compared with that reported here. Our results are consistent with Hsiao et al.’s observation that SI attentional effects are practically always positive. We found that 83% of attention-sensitive SI cells showed enhanced discharge rates when attention was directed toward the tactile task. In contrast, Burton and Sinclair found that a majority of attention-sensitive SI cells, ~70%, showed evidence of response suppression when attention was directed to the contralateral hand, as compared with when attention was directed elsewhere (ipsilateral hand or an auditory stimulus). Relative enhancement of sensory responsiveness with selective attention has frequently been reported in the visual system (e.g., Luck et al. 1997; Moran and Desimone 1985; Reynolds et al. 1999; Spitzer and Richmond 1991; Spitzer et al. 1988), but there have also been a few reports of relative suppression with visual attention. In this regard, Motter (1993) used a large number of visual distractors in his paradigm and found that cueing was equally likely to suppress or facilitate visual responses in V1, V2, and V4. The inclusion of multiple competing stimuli in the study by Burton and Sinclair may well have contributed to their finding of response suppression with selective attention. In addition, the tactile cue that preceded the baseline stimulus, and indicated the modality or spatial locus to attend, may itself have generated the initial suppression of responses to the baseline tactile stimulus (Simões et al. 2001). Such a mechanism has also been observed in the visual system, and implicated in visual memory formation (reviewed in Desimone 1996).

Finally, and in agreement with previous studies (Burton and Sinclair 2000; Hsiao et al. 1993), there was no significant difference in the distribution of attentional effects within SI. Nevertheless, it is interesting that Hyvärinen et al. (1980; see also Iriki et al. 1996) noted a trend for more frequent attentional effects in caudal SI (rostral, 8%, vs. caudal, 19%), as also seen here (area 3b, 14%, vs. areas 1/2, 28%). Confirmation of this observation requires a larger sample size, given the low proportion of attention-sensitive cells in SI.

Effects of attention on SII discharge

The higher proportion of attention-sensitive cells in SII (62%) than SI (24%) could not be explained by differences in strategy because SI and SII were sampled in the same mon-
In a similar vein, the larger RFs that characterized SII also did not contribute to the results because no difference was observed between cells with a bilateral or contralateral RF. Although interpretation of the results of cells with a bilateral RF was potentially confounded by the fact that the animal’s discrimination response was made with the ipsilateral hand, we controlled for this by recording the contact force on the response lever in 75 of 178 cells. In the large majority of trials, there was no evidence of anticipation of the eventual lever response. When anticipation was evident, the trials were excluded from the analysis. Thus input from the ipsilateral responding arm likely did not contribute to the higher proportion of attention-sensitive cells in SII.

We found that 70% of attention-sensitive SII cells showed enhanced discharge when attention was directed to the tactile task. This estimate is very close to the value reported by Hsiao et al. (1993), 75% enhanced, but different from Burton et al.’s (1997) finding that tactile responsiveness in SII was mainly decreased with attention. As mentioned in the preceding text, differences in the experimental paradigm likely contributed to the opposite results in SII as well as SI.

We extend these results to show that the attentional effects frequently spanned two or even all three of the analyzed periods (60% of the attention-related SII sample), including the instruction period in which the task had been static and not dynamic (digits resting on the 2 mm standard texture that formed the floor of the aperture). There was considerable specificity in the attention-related modulation with 83% of the cells showing attention-related changes in discharge during the most critical epoch of the trial, the texture-change period. This observation was quantified with the AMI, which varied across the three analysis periods (instruction, standard stimuli, texture change) and showed an overall positive bias in the latter period, indicating enhanced discharge during the time that the modified texture was scanned under the digit tips of the monkey. There was a net enhancement of discharge of 132% during this period when considering only the attention-sensitive cells.

Although equal numbers of texture- and non-texture-sensitive cells were modulated by attention, as also found in SI, the effects were more specific in SII. Suppression of cell discharge, when it occurred (26% of attention-sensitive cells), was mainly found in non-texture-sensitive cells. This pattern of modulation effectively gated out input to SII cells that likely did not contribute to the performance of the texture discrimination task. On the other hand, four texture-sensitive cells also showed suppressed discharge in the immediately preceding interval, standard stimuli; but in these cases, the subsequent texture-related signal was amplified. Thus the net effect of attention in SII was to enhance discharge during the texture-change period so that the change in discharge frequency (post-texture change − pre-texture change) was significantly greater in SII during the tactile task as compared with the visual task.

Comparison of the effects of attention on SI and SII discharge

The present results indicate that there are large differences between SI and SII in the influence of attention on neural responsiveness to tactile stimuli. Relatively simple and focused attentional effects were found in SI in contrast to the earlier (instruction and standard-stimuli periods) larger and more complex patterns observed in SII. A parallel can be drawn between these observations and the hierarchy that has been described in the visual system, whereby attention modulates neural responses to visual stimuli at an early stage in processing, V1 (Motter 1993), but the effects are more prominent in later stages of processing, V4 and inferotemporal cortex (e.g., Luck et al. 1997; Reynolds et al. 1999; see also reviews by Desimone and Duncan 1995; Kanwisher and Wojciulik 2000). In agreement with Burton and Sinclair (2000), we interpret our results as being consistent with attentional influences modulating neural responses to tactile stimuli at an early stage in the somatosensory processing pathway, SI, and the effects being more prominent in later stages, SII.

In both parietal cortical regions, the attentional influences appeared to be designed so as to enhance the ability of cells to signal the salient texture change. But it was only in SII that the population signal carried by the texture-sensitive cells clearly reflected this enhancement. Given that the behavioral task was critically dependent on sensory inputs during this period, the results provide support for the Burton et al. (1997) suggestion that attention increases the gain of behaviorally relevant tactile inputs (see following text).

Functional implications of the results

Within the visual system, there is evidence that attentional influences can act in several ways. Attention can modulate the gain of neural responses to visual stimuli either directly or via controls over the access of afferent input to the cells (reviewed in Desimone and Duncan 1995). It can also modulate baseline firing rates (Luck et al. 1997), increasing the discharge rate independent of the stimulus, what Kanwisher and Wojciulik (2000) referred to, respectively, as multiplicative and additive mechanisms. The present results clearly show that stimulus-evoked activity was enhanced in both SI and SII. While the enhanced discharge during the texture-change period may represent an increase in gain, we were surprised that this was concentrated mainly in one period of the trial in SI despite the fact that tactile stimulation was presented throughout the standard-stimuli and texture-change periods. One explanation might be that the salient feature—the texture change—was enhanced rather than a general increase in responsiveness to the scanned texture. Such a suggestion is consistent with studies of visual attention that have shown, for example, that features such as color or movement are selectively enhanced with attention (Motter 1994; Treue and Martinez Trujillo 1999).

Changes in baseline discharge might have been responsible for the attention-related changes that spanned all three analysis periods. These effects were only seen in SII, suggesting that this mechanism was only operative at the SII level. This would be consistent with a two-stage modulation of parietal cortical discharge, an initial stage (SI) in which there is a selective enhancement of the salient feature, the change in surface texture, and a subsequent stage (SII) in which baseline changes are added. This view is, however, probably overly simplistic because additional feature selection also occurred in SII, as evidenced by the attention-related suppression of discharge in non texture-related cells. These controls may be independently exerted on SI and SII. An alternate explanation is that the effects seen in SI reflect top-down controls from SII (see also Burton et al. 1999) because the pattern of attentional modula-
tion in SI can be described as a subset of that seen in SII. Taken together, the results are consistent with Desimone and Duncan’s (1995) suggestion that attention is an emergent property of slow, competitive interactions working in parallel.

The present results do not provide a clear answer to the question of whether attention enhances responses to attended tactile stimuli or conversely suppresses responses to unattended stimuli. Although the population analyses indicated that the net effect was enhancement in SII, this could be accomplished by selective suppression of unnecessary tactile input. The absence of a response to the texture change that was seen in both SI and SII when attention was directed toward the visual modality (respectively, 14 and 41% of the texture-sensitive cells) is not conclusive because the change may have represented either selective enhancement during the tactile task or suppression during the visual task. The same argument applies to the relative enhancement of responses to the change in SP (tactile > visual) seen in a further 12 (SI) and 30% (SII) of the texture-sensitive cells. In fact, the only clear indication of the sign of the attention-related modulation comes from a consideration of the non texture-related SII cells. In these cases, there appeared to be an active decrease in neural responsiveness to the tactile stimulus (Fig. 9, A and B). Posner et al. (1980) argued that both mechanisms are important because the results of psychophysical experiments have shown that selective attention confers both significant benefits (valid cues) and significant costs (invalid cues). Thus we suggest that both mechanisms, enhancement and suppression, contributed to the present results.

Site of action of attentional influences

Evidence from functional imaging and evoked potential studies in humans suggests that attentional influences are exerted at the cortical level (Burton et al. 1999; Desmedt and Tomberg 1989; Mima et al. 1998). While it seems most likely that the attentional influences seen here are also exerted at the cortical level, it would be premature to rule out a potential contribution of subcortical attentional effects. It is known, for example, that arousal modulates tactile responsiveness in ventrobasal (VB) thalamus (Morrow and Casey 1992), but changes in arousal did not contribute to the present results because the monkeys were alert and engaged in performing the task throughout each recording session. On the other hand, most evidence suggests that attentional influences per se do not appear to modulate neuronal responsiveness to tactile stimuli in VB thalamus, the major relay of lemniscal input to SI (Poranen and Hyvärinen, 1982; Tremblay et al. 1993; cf. Morrow and Casey 2000). Similar studies have not, however, been directed at the ventroposterior inferior thalamic nucleus, the major source of thalamic input to SII (Friedman and Murray 1986). This could be a potential source of the attentional influences because it appears to receive extralemniscal inputs, and Tremblay et al. (1993) proposed that extralemniscal pathways may be involved in modulation of tactile perception by attention.

Their earlier studies in the nociceptive system showed attention-related modulation of sensory responsiveness to noxious stimuli in the parafascicularis, but not in VB, thalamus (Bushnell and Duncan 1989; Bushnell et al. 1993). Further study is needed to address the importance of subcortical structures to the attentional modulation of tactile inputs.

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ATTENTION AND TACTILE RESPONSIVENESS IN SI AND SII


