

Research report

Representation of orientation in the somatosensory system

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Received in revised form 23 April 2002; accepted 1 May 2002

Abstract

In this paper we discuss how orientation is represented and transformed in the somatosensory system. Information about stimulus orientation plays an important role in sensory processing. In touch it provides critical information about how stimuli are positioned on the hand, which is important for grasping and lifting objects. It also provides important information about tactile shape. Psychophysical studies show that humans have a high capacity to discriminate the orientation of shapes and gratings indented into the finger pad. Further, these studies demonstrate that orientation discrimination is a reliable and stable method for assessing tactile spatial acuity. Neurophysiological studies suggest that orientation information is processed by the slowly adapting type 1 (SA1) afferent system. While orientation is poorly represented in the responses of individual afferent fibers, it is well represented in the population response properties of peripheral SA1 afferents and in the responses of central neurons in the primary (S1) and secondary (S2) somatosensory cortex. In S2, neurons with orientation selective and orientation non-selective responses tend to have large receptive fields that span multiple pads on multiple digits. Neurons in S2 that are orientation selective have similar tuning functions on different finger pads. These neurons may provide position-invariant responses or may be responsible for integrating features across hands, which is important for haptic object recognition of large shapes from the hand. Neurophysiological studies in trained animals show that the responses of about 85% of the neurons in S2 are affected by the animals focus of attention and that attention to the orientation of a bar modifies both the mean firing rate (i.e. gain) of neurons encoding orientation information and the degree of synchronous firing between pairs of neurons. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Somatosensory; Orientation tuning; S1 cortex; S2 cortex; Attention; Tactile

1. Introduction

Although it is well established that orientation information plays an important role in visual form processing [21], its role in tactile processing is not understood. In vision, neurons are tuned to simple local features, such as oriented bars, at the earliest levels of the processing pathways and to complex shapes, such as faces and hands, at the highest levels [8]. At intermediate processing stages such as area V4, neurons are selective to oriented shapes that are intermediate in complexity such as curves and angles pointing in particular directions [31]. There have been few studies that have investigated how orientation is represented in the somatosensory system. However, there is strong evidence to suggest that two-dimensional form may be

processed in similar ways in the two sensory systems [1,17].

In touch, cutaneous form processing begins with activity evoked in the peripheral slowly adapting type 1 (SA1) afferent fibers [24]. These afferents have small receptive fields, innervate the skin of the finger pad densely, and convey to the central nervous system a high-quality spatial neural image of stimuli in contact with the finger pad [19,32]. This peripheral neural image flows centrally via neurons in the dorsal column nuclei and ventroposterior nuclei of the thalamus to activate neurons in area 3b of primary (S1) cortex, which in turn activates neurons in secondary (S2) cortex. Both 3b and S2 cortex have been shown in ablation studies in monkeys to be important cortical areas for processing tactile spatial form [30,35].

In this paper, we first discuss psychophysical studies of orientation discrimination in humans. Then we review peripheral and central neurophysiological studies of orientation processing in the somatosensory system.

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In particular, we describe the results of recent experiments performed on peripheral afferents in anesthetized monkeys and on neurons in S1 and S2 cortex in awake behaving monkeys using scanned and statically indented oriented bar stimuli. We show that while orientation information is poorly represented in the responses of individual afferent fibers, it is well represented in the responses of individual neurons in both S1 and S2 cortex. We also present evidence that neurons in S2 cortex have large receptive fields that encompass multiple fingers, many neurons in S2 have similar orientation tuning curves across different finger pads on the same hand, the responses of orientation selective neurons are dramatically affected by the animals focus of attention, and selective attention has significant effects on the degree of synchronous firing between pairs of neurons in animals performing an orientation discrimination task. These findings suggest that orientation selectivity is an emergent property of central neurons and that orientation tuned neurons play an important role in the representation of cutaneous form information and, possibly three-dimensional shape information from the hand. The changes that are observed in the degree of synchronous firing between neurons may be a neural correlate of selective attention.

2. Psychophysics of orientation discrimination

In one of the earliest studies using oriented gratings, Johnson and Phillips [25] demonstrated that humans have a high capacity for discriminating horizontal and vertical gratings placed on the distal finger pads. In that study, they hypothesized that discrimination must be based on spatial rather than intensive cues since the intensive cues are identical when the gratings are placed in either orientation on the skin. They found that subjects could not discriminate between the orientations of gratings until the spacing between the gratings (groove widths) exceeded 0.5 mm. In a similar study they showed that the threshold (50% probability of discriminating a gap from no gap) gap size was 0.84 mm. These thresholds are nearly identical to the thresholds that are found in subjects performing two-point limen and letter discrimination tasks (for a review see [27]), which are also tasks that depend primarily on spatial cues.

Since those studies, the grating orientation discrimination task has become a standard method for assessing spatial acuity in the somatosensory system (e.g. [5,26]). Studies using this task have shown that (1) the threshold spatial acuity is slightly greater on the lip and tongue than on the fingertip (0.51 and 0.58 mm, respectively) [39,44]. (2) Acuity does not differ significantly between matched locations on the left and right hands [39,45]. (3) There is a small but significant decline in acuity as one

progresses from the index finger to the ring finger [45]. (4) Sensory deficits in patients recovering from nerve injury are closely related to their ability to perform grating orientation tasks [43]. (5) Patients with dyslexia are impaired significantly in their ability to discriminate grating orientation [16]. (6) Spatial acuity declines with age [48]. (7) Women tend to have better acuity than men [48]. Also (8) there may be close links between the visual and tactile mechanisms used to discriminate grating orientation [49].

The ability of subjects to discriminate the orientation of stimuli may be biased depending on the orientation of the grating relative to the finger. Essock et al. [13] tested the ability of subjects to discriminate between smooth surfaces and gratings placed at three different orientations on the finger. They found that the sensitivity for detecting gratings was highest for gratings oriented proximal-distally along the finger, lowest for gratings oriented medial-laterally and intermediate for oblique gratings. This effect was robust and was observed on fingers of both hands and increased as the intensity of the stimuli were increased. They concluded that there is an anisotropy in orientation discrimination in the somatosensory system which they surmised is based on anisotropies in the distribution of orientation selective neurons.

In a similar study, Craig [4] found that subjects exhibited no anisotropy when performing a grating orientation discrimination task. Not only were the thresholds nearly identical (0.8 mm for proximal–distal vs. 0.85 for the medial–lateral orientation), but subjects also showed no differences in proximal–distal and medial–lateral sensitivity functions (i.e. sensitivity to detect a smooth surface from a grating with gaps that are near threshold). Differences between the two studies could be due to differences in the contact forces that were used or to stimulus edge effects since Essock used flat gratings and Craig used gratings that were machined into curved domes.

In another study, Craig and Kisner [6] examined the stimulus factors that affect spatial acuity when measured using oriented gratings. They showed that performance improved as both the groove width increased and as the linear extent of the grooves increased on the finger. The increase in performance with increase in the linear extent of the bars was not simply due to the groove being longer since performance decreased when subjects were tested with multiple grooves that had the same orientation but did not form a single continuous groove.

3. Peripheral representation of orientation

There is strong evidence suggesting that orientation discrimination is based on the population response of

the SA1 afferents. Of the four kinds of peripheral afferents that innervate the skin, only these afferents have sufficient spatial acuity and innervation density to account for human psychophysical performance in the spatial acuity tasks (for a review see [27]). The receptive fields of SA1 afferents are approximately circular in shape with diameters of about 2 mm. Individual SA1 afferents show little or no orientation selectivity to bar stimuli. This is illustrated in Fig. 1, which shows the responses of four peripheral SA1 afferents to scanned oriented bars. In these experiments, ten oriented embossed bars (0, 30, 45, 60, 75, 90, 105, 120, 135, 150, 180 degrees) were mounted on a drum that repeatedly scanned the patterns across the neuron's receptive fields. The orientation of the drum relative to the finger was changed systematically and the experiment was repeated until the drum scanned across the finger in eight different directions (separated by 45°). In Fig. 1 the *X* axes represents the orientation of the bar independent of the scan direction and the *Y* axes represents the mean peak impulse rates evoked by the oriented bar. In all cases, the rates evoked were independent of the orientations of the bars.

In contrast to individual peripheral afferents, populations of SA1 afferents convey significant orientation information. Two separate studies using curved shapes have shown that the population responses of SA1 afferents encode both the orientation and shape of objects in contact with the skin [12,28]. In the first of

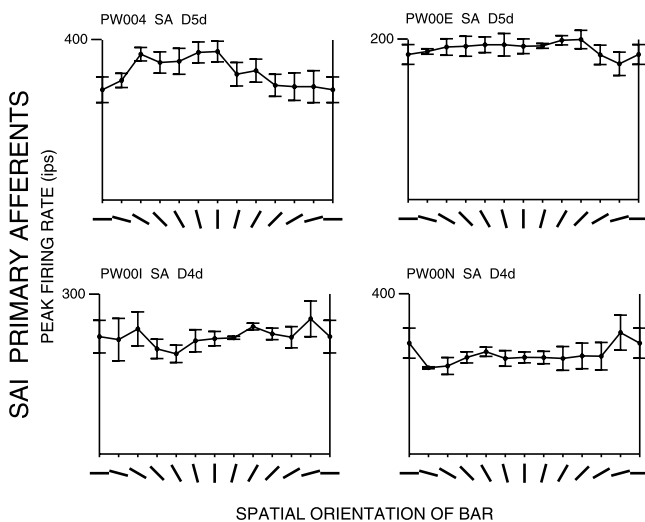


Fig. 1. Peak firing rates of four peripheral SA1 afferents to oriented bars repeatedly scanned at eight different directions across the center of the receptive field. The ten oriented bars (0, 30, 45, 60, 75, 90, 105, 120, 135, 150, 180 degrees) were embossed onto a plastic drum that was lowered onto the neurons receptive field and rotated across the finger at 20 mm/s. After about a dozen scans the drum was raised and rotated to a different orientation with respect to the finger and lowered onto the skin. This procedure was repeated for eight different scanning directions (45° separations). The plot shows the mean peak-firing rate (\pm S.E.M.) evoked by the oriented bars (15° separations) independent of scanning velocity.

these studies, Khalsa et al. [28] recorded the responses of peripheral SA1 and rapidly adapting (RA) afferents in monkeys to curved oblong shapes with a radius of 5 mm along the major axis and a radius of 1–5 mm along the minor axis. These stimuli were repeatedly indented and stepped across the receptive fields of peripheral afferents at four different orientations and the results were plotted as two-dimensional spatial event plots. They found that both the shape and orientations of the objects are faithfully encoded in the population responses of the SA1 but not the RA afferents. They also found that the SA1 population response was mildly biased toward stimuli placed proximal-distally along the finger.

Dodson et al. [12] studied the neural coding of orientation using cylinders placed on the finger pads of humans and monkeys. In their psychophysical studies they found that humans can discriminate orientation differences of 5.4° for cylinders with a curvature of 521 m⁻¹ and that this difference limen decreased as curvature decreased (DL = 4.2° for a curvature of 172 m⁻¹). In their neurophysiological studies they found that the shape and orientation of the cylinders were encoded most effectively in the responses of the SA1 afferents with a change in the orientation of the cylinder resulting in a corresponding change in the orientation of the population response. Their data also suggests that human performance in orientation discrimination may be degraded for stimuli oriented in the medial–lateral orientation.

4. Representation of orientation in S1 cortex

There have been surprisingly few studies on the representation of orientation in S1 cortex. Earlier studies indicate that neurons with orientation tuned responses are not common in area 3b [22,34,44], however, recent studies suggest otherwise [10,18]. In the earlier studies, Pubols and Leroy [34] studied the responses of neurons in S1 cortex of the raccoon using 'hand-held' probes and found that only about 20% of the neurons (21/110) had preferred responses to bars placed at a particular orientation on the animal's forepaw. Hyvarinen and Poranen [22] studied orientation tuning in monkeys trained to perform a vibratory detection task. In that study they found that 25% (9/36) of the neurons in S1 showed orientation tuned responses. Warren et al. [46] found that only 3% (4/121) of the neurons showed orientation tuned responses to hand-held gratings rolled back and forth across the receptive field.

Recent studies using controlled stimuli suggest that orientation tuned responses are common in area 3b of S1 cortex [10,18]. In a series of studies, DiCarlo et al. studied the responses of neurons in area 3b to random-

dot patterns scanned in multiple directions and velocities across the receptive fields [9–11]. Briefly, they showed that neurons in 3b have a variety of receptive field structures (Fig. 2) that are virtually unaffected by scanning velocity. Further, they showed that a receptive field model that contained a central excitatory region flanked by one or more inhibitory regions and a temporally delayed region of inhibition that overlaps the excitatory region accurately explained the neural responses. Asymmetries in the relative positions and balance between the excitatory and inhibitory subregions within the receptive field structures of these neurons suggest strongly that a majority of the neurons in 3b should show orientation tuned responses. For example, a thin bar placed vertically over the center of the receptive field of neurons like the one shown in Fig. 2A would evoke a large response while a horizontal bar

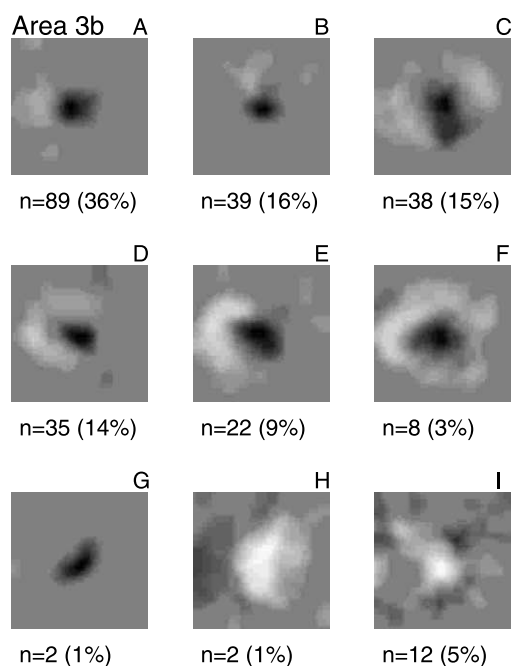


Fig. 2. Receptive fields from the distal finger pads in area 3b of the alert monkey. Each panel illustrates a typical example of a receptive field type, the total number of receptive fields of that type, and the percentage of neurons with that type ($n = 247$). The gray scale represents the grid of excitation and inhibition ($10 \times 10 \text{ mm}^2$) that best described the neuron's response to a random-dot stimulus pattern scanned across the receptive field. Dark regions represent excitatory regions; lighter regions represent inhibitory regions. Gray represents the regions where stimuli had no effect on the response rate. (A) An excitatory region flanked by a single inhibitory region located on the trailing (distal) side of the excitatory region. (B) A region of inhibition located on one of the three non-trailing sides of the excitatory region. (C) Two regions of inhibition on opposite sides of the excitatory region. (D) Inhibition on three sides of the excitatory region. (E) Inhibition on two contiguous sides of the excitatory region. (F) A complete inhibitory surround. (G) An excitatory region only. (H) Receptive field dominated by inhibition. (I) Receptive fields not easily assigned to one of the preceding categories. From DiCarlo et al. [11]; reprinted with permission.

placed over the field would evoke a much weaker response due to the asymmetrical inhibitory surround located to the left of the excitatory center. DiCarlo and Johnson [10] confirmed this hypothesis in a study in which they measured the orientation tuning preferences and receptive field structures of neurons in area 3b. They found that neurons in 3b exhibit a wide range of orientation preferences to scanned bars and that the responses are consistent with the orientation selectivity predicted by a receptive field model that contained an excitatory center flanked by one or more inhibitory regions [10]. Furthermore, they showed that the orientation sensitivity in S1 is greater for neurons in the supergranular and infragranular layers than in layer IV, which suggests that orientation selectivity is not based on the orientation tuning properties of peripheral or ascending neurons and must be an emergent property of central neurons.

Hsiao et al. [18] recorded the responses of 66 neurons in S1 cortex to statically indented oriented bars. In those studies, the responses of neurons in areas 3b and 1 with receptive fields located on the distal finger pads were recorded while a bar was repeatedly indented into the center of the finger pad at one of eight orientations. They found that about 75% (50/66) of the neurons showed significant orientation selectivity. Examples of two orientation selective neurons from area 3b of S1 cortex are shown in Fig. 3. These neurons were highly selective to bars oriented -45 and $+45^\circ$ relative to the mediolateral axis across the finger pad. There were several findings in this study: (1) Most of the tuned neurons showed sustained responses to the bar stimuli suggesting that these neurons received their inputs from peripheral SA1 afferent fibers. (2) While the population of neurons showed tuned preferences for bars indented at all eight orientations, there was a mild bias in the number of neurons that showed tuning to bars placed proximal-distally along the finger pad. (3) The sharpness of tuning varied greatly between neurons. And (4) Also a large percentage of the neurons in area 3b were highly orientation selective with more than 60% of the neurons exhibiting firing rates at the preferred orientation that were more than double the rates evoked at the non-preferred orientation. These results and those shown by DiCarlo and Johnson [10] demonstrate that orientation information from single finger pads is well represented in the response properties of neurons in area 3b of S1 cortex. Further studies need to be done to determine if these orientation selective neurons are organized into functional columns as they are in primary visual cortex.

5. Representation of orientation in S2 cortex

How orientation is represented in S2 cortex is poorly understood. However, evidence suggests that SII plays

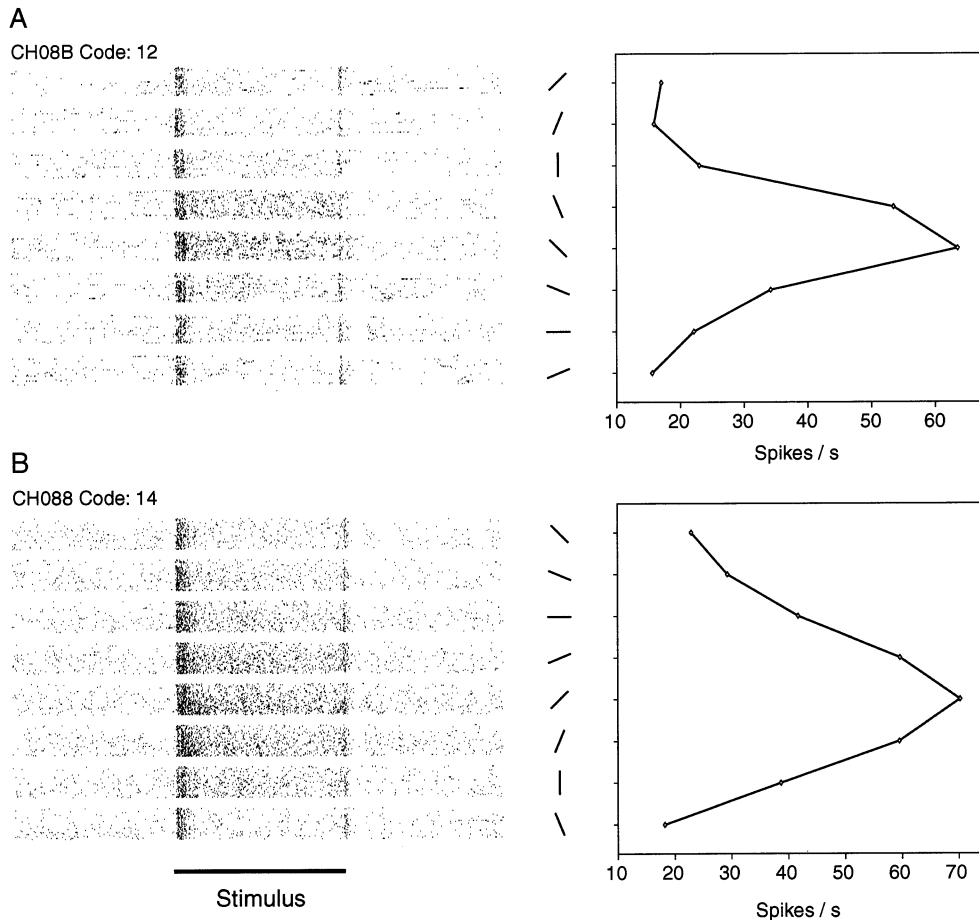


Fig. 3. Responses of two neurons in S1 cortex of monkeys that were awake and behaving to statically indented bars. The left panel shows raster plots of the response sorted according to the orientation of the bar. The bar was indented into the skin for 500 ms with a contact force of 10 g. The panel to the right shows the mean firing rates evoked by the bar. (A) Example of a neuron with a sharp tuning curve. (B) Example of a neuron with a broader tuning curve.

an important role in processing tactile spatial form. Not only does S2 receive a large feed forward projection from S1, but studies where ablations are made in S2 show that trained animals without S2 cortex are unable to perform a wide variety of tactile tasks [30,36,37]—like those produced when area 3b is ablated. Specifically, Murray and Mishkin [30] found that animals with S2 ablated were unable to perform texture discrimination tasks (hard vs. soft and rough vs. smooth), form discrimination tasks (square vs. diamond) and orientation discrimination tasks (horizontal vs. vertical). In addition, neurons in S2 tend to have large receptive fields that often span several digits on the same hand (receptive fields $< 10 \text{ cm}^2$, [38]) and often respond to stimulation of both hands [2,7,38,40,47].

Fitzgerald et al. [15] studied the responses of neurons in S2 to oriented bars presented to finger pads on the restrained hands of awake and behaving monkeys performing a visual discrimination task that was unrelated to the tactile stimuli. For each trial, the bar was centered above either the proximal, middle or distal

finger pads of digits 2–5, rotated to one of eight orientations (separated by 22.5°) and driven into the skin for 500 ms. This was repeated until each orientation and pad was stimulated eight times.

Eighty-two percent (952/1155) of the neurons in S2 were driven by the bar stimuli and about 30% of these neurons showed orientation selective responses. Fig. 4A and B show histograms of the number of finger pads driven by the bar stimuli, which is a measure of the neurons receptive field size. The results are separated into those neurons that showed orientation tuned responses on one or more finger pads (4b) and those that were driven but did not show tuning on any pad (4a). Fig. 4A illustrates that neurons in S2 have a wide variety of receptive field sizes. Approximately 20% of the neurons had single finger pad receptive fields and the rest had receptive fields that included multiple pads on multiple fingers. There is a systematic decrease in the number of neurons with large receptive fields on the fingers. Neurons that had receptive fields that spanned 11 or more pads, most likely had receptive fields that

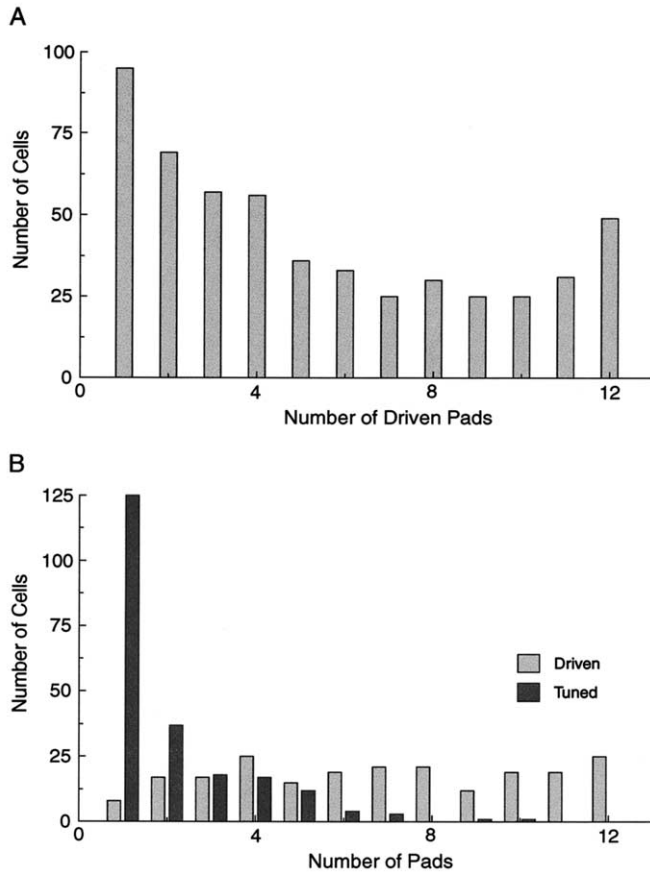


Fig. 4. Histograms of the receptive field sizes of neurons in S2 cortex that show orientation selective and non-selective responses. (A) Receptive field sizes for neurons that did not show orientation selective responses on any of the distal pads but had firing rates that were significantly different (elevated or suppressed) relative to the spontaneous rate of the neuron. (B) Receptive field sizes for neurons that showed orientation tuned responses. The black bars represent only those pads that were orientation selective. The gray bars represent the receptive field sizes for neurons that were driven by the stimulus and showed orientation selective responses on one or more finger pads.

include more proximal parts of the hand. If you exclude responses shown in Fig. 4, the mean receptive field size for neurons in S2 cortex is about 3–4 pads which means that S2 is concerned primarily with processing information from, multiple rather than single, fingers.

Results are shown in Fig. 4B for neurons that showed orientation selectivity on one or more finger pads. In this figure, the black bars represent the finger pads that showed orientation tuning and the gray bars represent the number of finger pads from those tuned neurons that were driven but showed untuned responses. This figure shows that many neurons in S2 have receptive fields with orientation selective responses on multiple finger pads. Furthermore, the receptive fields for many neurons are not homogenous with the responses from some pads showing tuned responses and others showing untuned responses. There are potentially many explanations for why tuning was not observed on all of the pads.

One possibility is simply that the neurons are differentially sensitive to bars on the different pads and that the responses are too weak on some pads to show significant tuning on these pads. Another explanation is that the differences may be due to selective attention mechanisms. In these experiments, since the neural responses were recorded while the animals were awake and not attending to the tactile stimuli, it is highly likely that many of these untuned responses would show tuning if the animal was required to attend to the orientations of bars on its fingers (e.g. see Fig. 6).

As in S1 cortex, neurons in S2 showed tuning preferences for all eight orientations and neurons exhibited a wide variety of tuning preferences. Some neurons showed sharply tuned responses (Fig. 6) while others showed only mild tuning. Similar to what is seen in S1, about 70% of the neurons with orientation selective responses in S2 had firing rates at the preferred orientation that were at least double the rates evoked by the bar at the non-preferred orientation.

A common feature of neurons that showed tuning on multiple finger pads is that the orientation selectivity for most of these neurons was highly similar across finger pads. This is illustrated in Fig. 5 for two neurons that had tuned responses on 3 and 5 pads. The neuron shown in Fig. 5A had tuned responses on 5 pads; the distal pads of digits 2, 3, 4 and 5 and the middle pad of digit 4. The right part of this figure combines the orientation preferences across the fingers and illustrates the close similarity in tuning preferences across the 5 pads. Fig. 5B shows the response for a neuron that showed tuning on three different finger pads. This neuron had a receptive field that included the distal pads of digits 2 and 3 and the middle pad of digit 3. This neuron also showed orientation preferences that were highly similar across finger pads.

There are two ways of interpreting these results. One possibility is that these responses may be indicative of a mechanism whereby neurons in S2 show position-invariant responses to oriented bar stimuli placed on the hand. Position-invariant responses are commonly found in higher visual areas [29]. Another possibility is that these responses may be indicative of a mechanism that is involved in haptic shape processing, which depends on integrating cutaneous and proprioceptive information across fingers. For example, the edge of a table is perceived differently when touched by multiple fingers held parallel to each other than if the same edge is touched simultaneously with the fingers crossed.

6. Effects of selective attention

Previous studies have shown that the neuronal responses in SII, and to a lesser extent in SI, are affected by the attentional state of the animal [3,20,23,33,41].

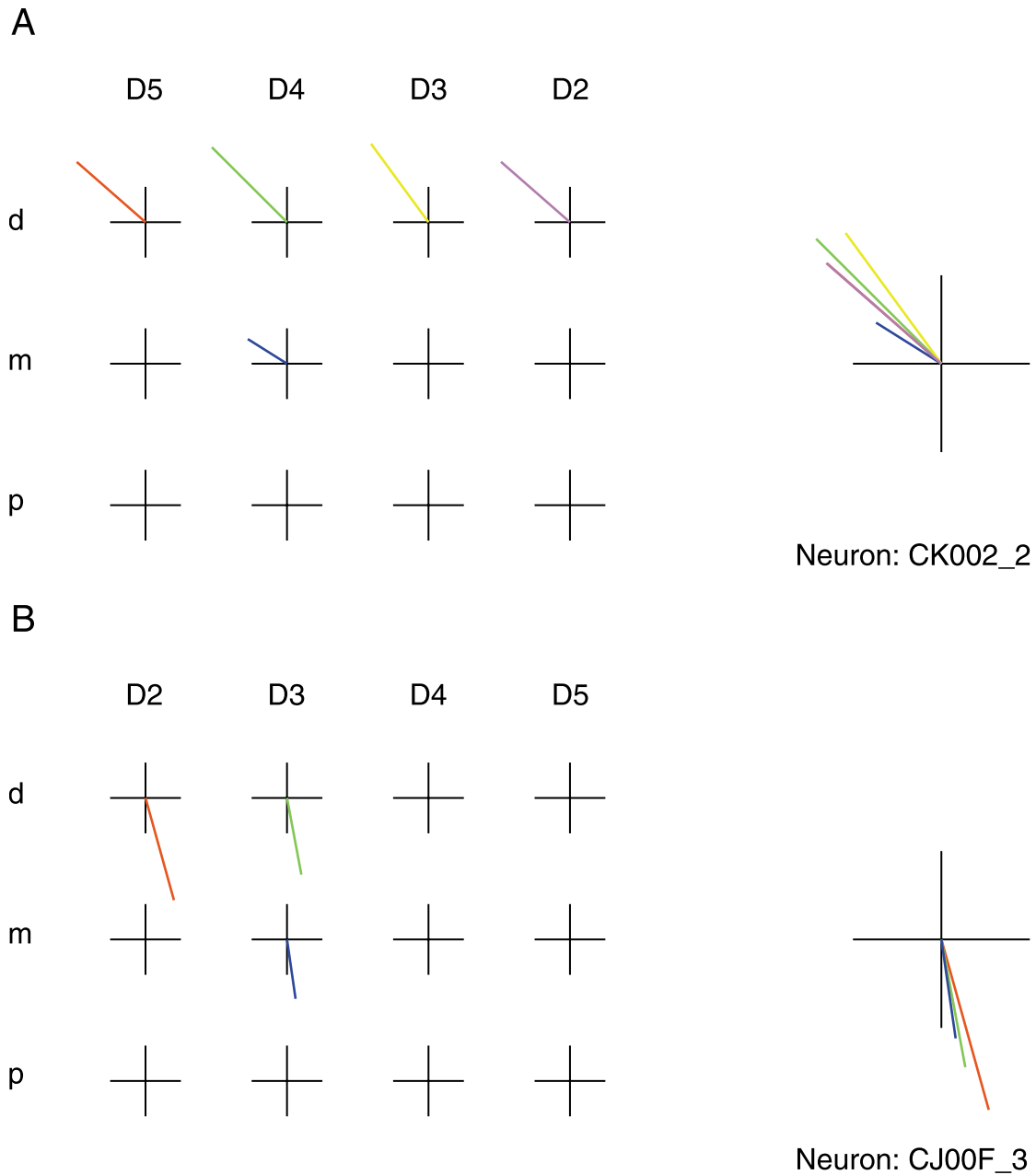


Fig. 5. Similar orientation tuning across finger pads in S2 cortex. (A) Example of a neuron that showed orientation selective responses on 5 finger pads—the distal pads of digits 2, 3, 4 and 5 and middle pad of digit 4. Left panel shows the tuning vector for each finger pad that showed significantly tuned responses. The angle of the vector represents the preferred orientation of the bar and the length of the vector represents the strength of the response at the tuned orientation. The right panel shows the tuning vectors from the different pads plotted on the same graph. The plot shows clearly that the orientation tuning preferences were highly similar across pads. (B) Example of a neuron that showed orientation selective responses that were similar across three finger pads—the distal pads of digits 2 and 3 and the middle pad of digit 3.

These studies also suggest that attention modulates the firing rate of neurons in highly specific ways [20].

Recently, Fitzgerald et al. [14] investigated the effects of selective attention on the responses of neurons in S2 cortex in animals trained to perform an orientation discrimination task. Animals were trained to perform behavioral tasks that required them to either ignore the tactile stimulus or to selectively attend to the orientation of bars presented to the distal finger pads of the

restrained hand. In the tactile task, a bar was indented into the skin of the distal finger pad in one of eight randomly chosen orientations for 500 ms, removed from the skin for 1000 ms and then indented back into the skin at either the same orientation or at the orientation orthogonal to the first stimulus for an additional 500 ms. After receiving both stimuli, the animal was required to pull a switch with its foot if the orientations of the two bars were the same or to push the switch if the

orientations were different. In the visual task, the animal was presented with a white square on a video monitor and was required to push the switch when the square dimmed while the hand was presented with the same tactile stimuli that was presented during the tactile task. During the recording sessions, the animal's focus of attention was switched back and forth between the two tasks.

Of the 212 neurons that were studied, 82% (59/72) of the neurons that showed orientation selectivity and 74% (104/140) of the neurons that did not show orientation selectivity were affected by the animal's focus of attention. Of those neurons that showed attention modulated responses, about half showed increased firing rates (55%) when the animal performed the tactile task, and the rest showed decreased rates. The effects of attention on orientation tuning were often quite dramatic (Fig. 6). The left side of the figure shows raster plots of the responses sorted according to the stimulus orientation and the animal's behavioral state. During the presentation of the first stimulus (denoted by S1) when the animal was performing the tactile task, there is an enhanced response to bars oriented -45° to the long axis of the finger. The responses evoked by the stimulus when the animal performed the visual task were much weaker. The enhanced attention effects are also observed during the delay period between the two stimuli and during the initial presentation of the second stimulus. The response to the bar is suppressed midway through the presentation of the second stimulus. The figure to the right demonstrates the dramatic effects that attention has on the mean firing rates and, in particular, on the orientation tuning curves.

These results demonstrate that selective attention has large effects on the responses of neurons in S2 cortex.

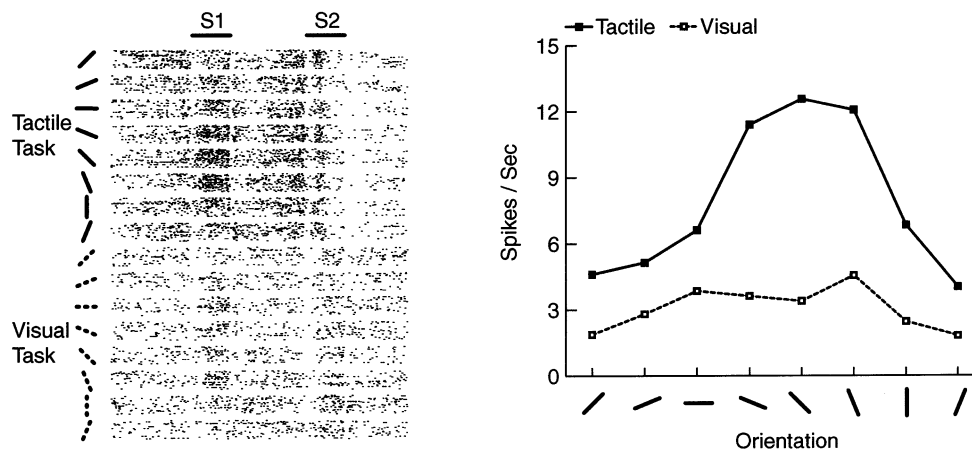


Fig. 6. Effects of attention on orientation tuned neurons in S2 cortex. Left panel shows raster plots of the responses evoked by bars at eight orientations (separated by 22.5°) while the animal performed a tactile orientation match to sample task (left-top eight raster plots—solid oriented lines) or a visual light dimming detection task (left-bottom eight raster plots—dashed oriented lines). The bar was indented into the skin for 500 ms (S1) at the orientation shown on the left, raised for 1000 ms and indented back into the skin at either the same orientation or at the orthogonal orientation (S2). The rasters are sorted according to the orientation of the first bar. The right panel shows the mean impulse firing rates evoked by the oriented bar during the presentation of the first stimulus while the animal performed the tactile (solid line) and visual (dashed line) tasks.

Not only are stimulus responses altered but the responses during the delay period are affected when the skin is not being stimulated. During the presentation of the first stimulus, switching attention to the bar can change a weakly tuned response into a strongly tuned response (Fig. 6). The effects of attention are not simply changes in gain, which can be seen by inspecting the responses evoked during the delay period when no stimulus was in contact with the skin. Interestingly, the responses during this period show tuning curves that are slightly broader than the tuning observed during the presentation of the first stimulus. One possibility is that the activity during the delay period is related in some way to the memory of the orientation of the first stimulus.

Attention affects more than just the firing rates of neurons. Recent recordings from neurons in S2 that employed multiple electrode arrays have shown that the degree of synchronous firing between neuron pairs was significantly modified when the animal performed the tactile task. Steinmetz et al. [42] investigated the synchrony of neuronal discharge in 648 pairs of responses from 436 neurons S2 cortex in three animals trained to switch their attention between a visual task and three different tactile discrimination tasks. One task was to perform the same-different orientation discrimination task described earlier. They found that in animals performing all three tasks that most neuron pairs in S2 cortex fire synchronously and, for all three animals, the degree of synchrony changed when the animals performed the tactile tasks. On average, synchrony changed in about 17% of the neuron pairs with synchrony increasing in 80% and decreasing in 20% of the pairs. Fig. 7 shows the responses of one pair of neurons in the animal trained to perform the orientation discrimination

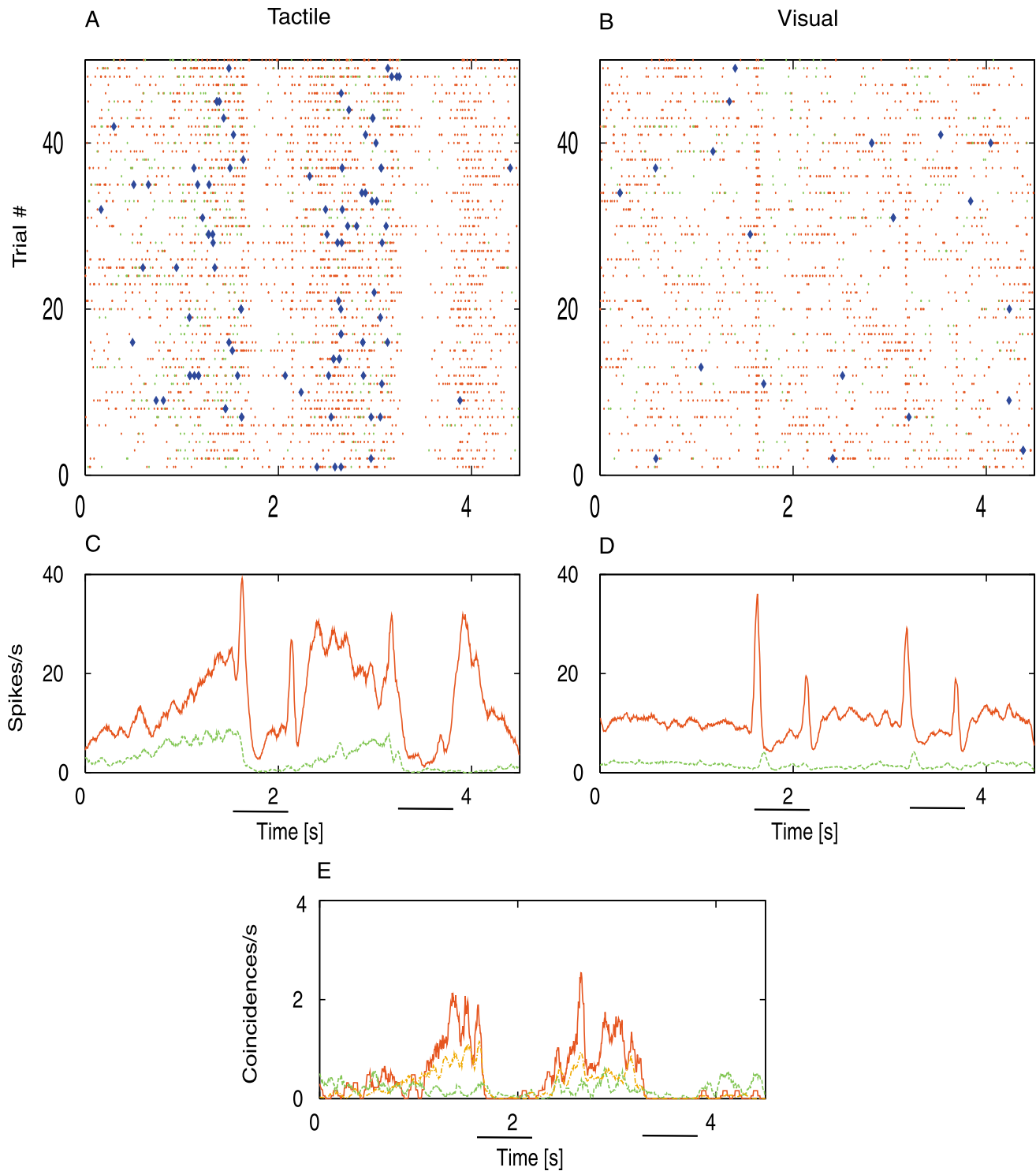


Fig. 7. Illustration of the effects of attention on synchronous firing between neurons in S2 cortex. The response rasters are triggered at the onsets of 50 tactile stimulus periods while the monkey performs the bar orientation discrimination task (A) and the visual dim detection task (B). Each row in the raster represents one stimulus period corresponding to the presentation of the first bar (500 ms) followed by a 1-s delay period and the presentation of the second oriented bar (500 ms) which was at the same orientation as the first bar or at the orthogonal orientation. Red and green dots represent the action potentials of the two neurons. Peristimulus time histograms are shown below each raster plot with corresponding colors (C and D). Synchronous events, defined as spikes from each neuron within 2.5 ms of each other, are represented as blue diamonds. The number of synchronous events is much higher when attention is directed towards the tactile stimuli. This change in synchrony is also apparent in plots of rates of synchronous events shown in (E): red curve—tactile task, green curve—visual task, orange curve—coincidences expected by chance.

task. The top two panels show stimulus raster plots of the responses of the two neurons that were recorded simultaneously while the animal performed the tactile (a) and visual tasks (b). During the visual task, both neurons showed a burst of activity when the bar contacted and left the skin (especially the neuron shown in red). The pattern of activity evoked by the bars while the animal performed the tactile orientation discrimination task is very different. Both neurons showed a 'buildup' of activity just before the stimuli came in contact with the skin, which is indicative of an anticipatory response to the stimulus. In addition, there was an increase in the degree of synchronous firing during this anticipatory period, which is indicated by the blue triangles (also see Fig. 7C). The increase in synchronous firing between the two neurons cannot be explained by either the stimulus-driven events or by the changes in attention-induced modulation of the firing rate (compare red and orange plots in Fig. 7E) and must be due to another mechanism. Our working hypothesis is that selective attention somehow alters the temporal structure of spike trains by increasing (or decreasing) the probability of firing between populations of neurons. Increasing the synchrony between neurons has two effects. One effect is to cause local populations of neurons to become more salient; they act like members of a chorus singing together. In this case, the synchronized responses accentuate the message from the neurons that fire synchronously. The other effect of increasing synchronous firing is that the combined synaptic effects provide larger excitatory post-synaptic potentials on downstream target neurons. Consequently, the information conveyed by these neurons is more likely to be propagated by downstream target neuron(s) that receive inputs from the synchronously firing cells. A working hypothesis is that modifying the degree of synchronous firing is the neural correlate of selective attention.

7. Conclusions

While there have been relatively few studies on how orientation is represented in the somatosensory system, there is strong evidence to suggest that, like in the visual system, orientation plays an important role in processing form. Psychophysical studies show that our capacity to recognize orientation is determined by spatial processing among the SA1 afferent fibers. While individual SA1 afferents show little or no orientation tuning, populations of these afferent fibers convey a robust representation of the orientation of objects in contact with the skin. In the central nervous system, neurons in S1 cortex have a variety of receptive field structures that extract information about spatial features of stimuli. One feature that is well represented in

those neurons is stimulus orientation. Although the receptive field structures of neurons in S2 cortex are not understood, evidence suggests that information is combined from the different finger pads in systematic ways, which results in neurons that are sensitive to tactile features that span several fingers. Future studies are needed to determine whether orientation columns exist in primary somatosensory cortex and to determine the role that orientation information plays in tactile processing.

Acknowledgements

The research reported here was supported by NIH grants NS34086 and NS38034. We would like to thank Takashi Yoshioka for his helpful comments and suggestions concerning this manuscript.

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