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Spatial pattern representation and transformation in monkey somatosensory cortex

(neurophysiology/tactile sense/form perception)

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ABSTRACT **Embossed letters, used previously in pattern recognition experiments in humans, were used to study the spatial patterns of neural activity evoked in peripheral fibers and cortical neurons in areas 3b and 1 of the primary somatosensory cortex of alert rhesus (*Macaca mulatta*) monkeys. The object was to investigate the representation and transformation of spatial information during the early stages of peripheral and cortical neural processing. Our method consisted of sweeping each letter of the alphabet across the skin repeatedly and constructing a two-dimensional plot (called a spatial event plot) of the action potentials evoked in afferent fibers and cortical neurons. By using this method, slowly and rapidly adapting primary afferents were shown to transmit isomorphic neural images of the letters. Although the slowly adapting images were more spatially acute, both populations conveyed images of sufficient quality to account for human psychophysical performance. In the cortical areas studied, the slowly adapting neurons of area 3b stood out for the acuity, complexity, and variety of their responses. Some of the spatial event plots for these neurons were isomorphic and at least as acute as those obtained from any primary afferent. Others were highly structured but nonisomorphic. The quality and variety of responses in area 3b slowly adapting neurons suggest that they play an important role in the processing of information underlying tactual pattern recognition. The rapidly adapting neurons of area 3b and all types of neurons in area 1 yield much less structured and differentiated responses.**

A significant problem in the study of sensory systems and their neural mechanisms concerns the representation and transformation of spatial form within the central nervous system. Our working hypothesis, which provides a strategy for investigating this question, is that one function of sensory systems is to transform the primary representation of a stimulus from the form dictated by the peripheral sensory mechanisms to the form required by the higher processes leading to memory and perception. In the case of the visual and somatosensory systems, the primary representation of spatial form (e.g., a letter of the alphabet) would be an isomorphic (1) mosaic of neural activity in a population of primary sensory neurons. The final representation, according to this hypothesis, would be the one that is compared with previously stored representations for the purposes of perception and recognition. Although this final representation may be isomorphic, the evidence suggests that this is unlikely. Most of the alternatives that have been suggested, such as feature-based representation, spatial frequency decomposition, and holographic representation (2–5), involve processes in which the activity of single neurons in the final representation is affected by a large number (if not all) of the neurons in the primary representation. If such massive convergence is required to form the final representation, whatever it might be, the connectivity of sensory systems suggests that this convergence is achieved in stages. The functional correlate of this is stepwise transformation, in which each stage of processing performs a partial transformation aimed at producing the final representation. The approach that we have adopted is to map the neural representations of a defined set of spatially structured stimuli in the periphery and in areas 3b and 1 in primary somatosensory cortex (SI) of the alert rhesus (*Macaca mulatta*) monkey. By comparing the response patterns at different levels of processing we aim to discover (*i*) which neuronal populations carry the information that underlies tactual form discrimination, (*ii*) what form of neural representation is employed, and (*iii*) what transformations are effected between successive levels.†

MATERIALS AND METHODS

Neural responses were recorded from single afferent fibers in the median and ulnar nerves of anesthetized monkeys and from neurons in Brodmann's areas 3b and 1 of the primary somatosensory (SI) cortex of awake monkeys, using standard techniques (9, 10). The tactile stimuli consisted of embossed, sans serif, uppercase letters of the alphabet and dot patterns raised 500 μm above the background, which were attached to the surface of a drum. The patterns were produced by exposing a photosensitive nylon polymer to ultraviolet light through a mask consisting of a photographic negative of the desired pattern. The alphabets ranged in height from 3.0 to 8.0 mm. These heights were used because they are near the limits of tactile spatial resolution for humans but are still discriminated effectively (11, 12); therefore, at least one population at each level of processing within the somatosensory system must convey sufficient information to account for the psychophysical performance, assuming cross-species equivalence (13). The tetragonal dot patterns consisted of 0.5-mm (diameter) dots with center-to-center spacings varying continuously from 0.9 to 6.2 mm over a distance of 211 mm. These dot spacings, like the letter heights, were chosen to span the range of tactile spatial acuity (11).

During the neural recording sessions the monkey's arm and hand were held immobile in a simple cast while the stimuli were scanned across the neuron's receptive field by rotating the drum at a controlled velocity (20–80 mm/sec) and applying it to the skin with a controlled force (10–100 g). During cortical recording sessions the monkey performed a

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Abbreviations: SA, slowly adapting; RA, rapidly adapting; PC, Pacinian; SEP, spatial event plot.

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†Recent studies indicate a serial flow of information through postcentral somatosensory cortex to higher levels of processing (6). Previous studies of the responses of somatosensory cortical neurons to spatiotemporal stimuli are described in refs. 7 and 8.

diversionary visual task to ensure that it remained still but alert.

Spatial Event Plots (SEPs). The responses from a slowly adapting (SA) cortical neuron in area 3b to the letter K are shown in Fig. 1. The rotating drum was applied so that the finger initially contacted a smooth circumferential band with no embossed patterns. Then, at one point during each revolution, the drum was stepped 200 μm along its axis of rotation (vertically in Fig. 1) causing the letters to advance incrementally across the receptive field of the neuron under study on each successive parallel sweep (14). A similar technique for reconstructing spatial neural images has been used for the study of visual cortical neurons (15). Drum location and action potential timing were monitored continuously and saved for subsequent analyses. In Fig. 1, the responses evoked when the letter K passed through the receptive field of a cortical neuron on successive scans have been plotted as horizontal rows of ticks, with each tick representing an action potential and each row of ticks representing the action potentials evoked in one sweep. Each tick is plotted with respect to the position of the stimulus at the time of occurrence of the action potential, forming what we refer to as a SEP.

We interpret the SEPs reconstructed from single neuron responses, like that in Fig. 1, in two ways. The conservative interpretation, which is always applicable, is that the SEP characterizes the spatiotemporal properties of the single neuron's response to complex moving stimuli. For example, a sharp, well-defined isomorphic image implies high temporal and spatial resolution and limited convergence. An additional interpretation, which is warranted under some conditions, is that the single neuron SEP approximates a spatiotemporal neural image of the stimulus as it would

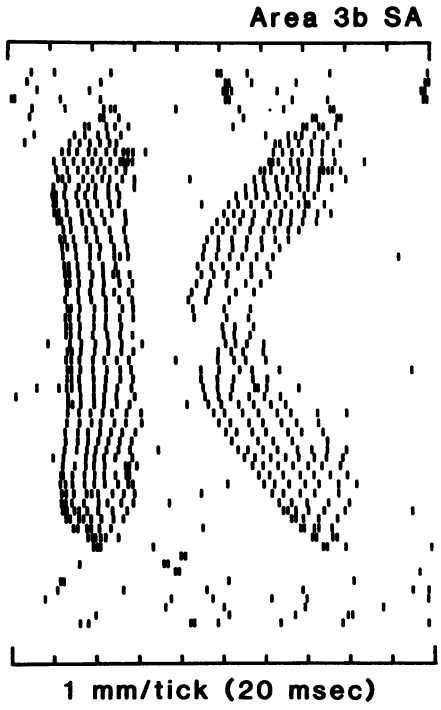

FIG. 1. Method of assigning impulse locations (vertical ticks) in a SEP. The embossed letter K (8.0 mm high, 500 μm relief) was repeatedly scanned (64 times at 50 mm/sec) across the receptive field of a SA cortical neuron (area 3b) innervating the finger pad of an awake monkey. The stimulus moved from right to left across the receptive field (i.e., the vertical bar of the K entered the receptive field first on each scan). The stimulus was shifted (vertically in this figure) by 200 μm on each scan. The time of occurrence of each action potential relative to adjacent stimulus position markers was used to assign it a spatial location relative to the stimulus surface.

appear distributed across a population of similar neurons. This second interpretation is based on three assumptions: (*i*) that there exists a population of neurons with similar response properties, (*ii*) that their response loci are distributed more or less uniformly across the skin surface, and (*iii*) that they are distributed with sufficient density to convey an image. The validity of these assumptions is known at the level of the peripheral nerve. Tactile stimuli evoke activity in three classes of mechanoreceptive afferents in the monkey (16); the SA, rapidly adapting (RA), and Pacinian (PC) afferents. The sparse PC innervation density (17, 18) suggests that the neural image interpretation is not justified for PC afferents. On the other hand, the receptive fields of SA and RA afferents are regularly and densely arrayed across the skin surface (17, 18) and their responses are quite homogeneous within their respective classes. Therefore, we believe that the neural image interpretation is justified for the peripheral SA and RA afferents. Recent mapping studies demonstrate fine-grained somatotopy within areas 3b and 1 of the rhesus monkey (19), suggesting that the neural image interpretation may also be valid in SI cortex.

RESULTS

Peripheral Responses. Eighty-nine peripheral afferents (34 SA, 36 RA, and 19 PC) were studied by using a variety of letter sizes, scanning velocities, and skin contact forces. All fibers studied had receptive fields on the distal finger pads. Fig. 2 shows SEPs derived from responses of single representative peripheral afferents of each class; the SEPs within classes are quite homogeneous. Fig. 2 illustrates the general finding that SA and RA afferents yield isomorphic images of the scanned stimuli, whereas PC afferents do not. The images from SA and RA afferents look like spatially filtered versions of the stimuli, which, for primary afferents, is due to the mechanics of the skin and the way in which the receptors are embedded within it (20). Images reconstructed from SA responses resolve the fine spatial details of the stimulus more successfully than those reconstructed from RA responses. The least spatially acute SA response produced a more acute image than the best RA response (the RA response illustrated in Fig. 2). SA responses are relatively unaffected by changes in scanning velocity, whereas the acuity of RA responses deteriorates with increasing velocity in the range 20–80 mm/sec. Neither SA nor RA responses are significantly affected by varying the application force of the stimulus within the range 20–80 g. The internal details of the letters tend to be less well represented than the general outlines in both SA and RA responses. In particular, horizontal elements (i.e., bars oriented parallel to the direction of movement) are poorly represented and often missing altogether from the images, whereas elements of the letters oriented at right angles to the direction of movement appear enhanced. Particularly for SA responses, the leading edge (the edge first contacting the receptive field) results in a greater response than the trailing edge. The sweep-to-sweep variability in SA responses for parts of the pattern that remain constant (e.g., near the middle of the letter I) is extremely low. An example of this variability can be seen by examining the SA response in the middle of the letter I in Fig. 2. In that response region (central 80%) there is no variability in response count from trial to trial and very little variability in impulse latency. A linear regression on the latencies of the leading impulses yields a residual standard deviation of only 10 μm. In contrast to the SA and RA responses, the PC responses are quite heterogeneous and resolve the letters poorly. The response illustrated in Fig. 2 is an example from a small group of PCs (4/19) in which the responses were related, though weakly, to the structure of

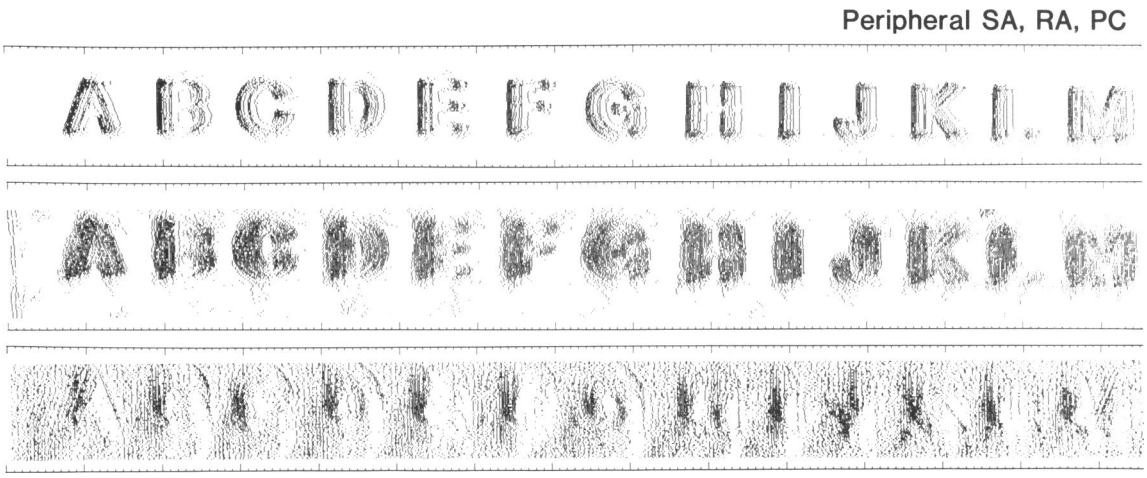

FIG. 2. SEPs reconstructed from one SA (top), one RA (middle), and one PC (bottom) primary afferent fiber. Letter height, 6.5 mm; scanning velocity, 50 mm/sec; contact force, 60 g.

the individual letters. The remainder produced responses unrelated to spatial form.

Cortical Responses. We have studied 199 neurons in SI cortex with receptive fields on the distal finger pads, using embossed patterns as stimuli. Single neurons were assigned to cytoarchitectonic area 3b or 1 on the basis of the orderly progression of receptive fields within penetrations, the mirror-image relationship between representations of the hand in areas 3b and 1, and histological reconstructions of electrode penetrations (21, 22). One hundred ten neurons were localized to area 3b and 68 were localized to area 1. Twenty-one cells could not be assigned reliably. Neurons responding with a maintained increase or decrease in impulse rate to a steady indentation of the skin were classified as SA; those that responded transiently were classified as RA (23). A small number of the neurons with transient responses were extremely sensitive, with large receptive fields like peripheral PCs, and were classified as PC.

Area 3b. Our observations show that the response properties of neurons in area 3b are remarkable for their heterogeneity and fine spatiotemporal structure. Fig. 3 illustrates the responses of five SA neurons from area 3b to letters scanned across their receptive fields. The reconstructions are arranged, from top to bottom, on the basis of decreasing subjective similarity to the stimulus letters. The responses of the neuron displayed in the top record exhibit fine, isomorphic structure that is at least as acute as any we have seen in peripheral afferents. The remarkable resolution of spatial

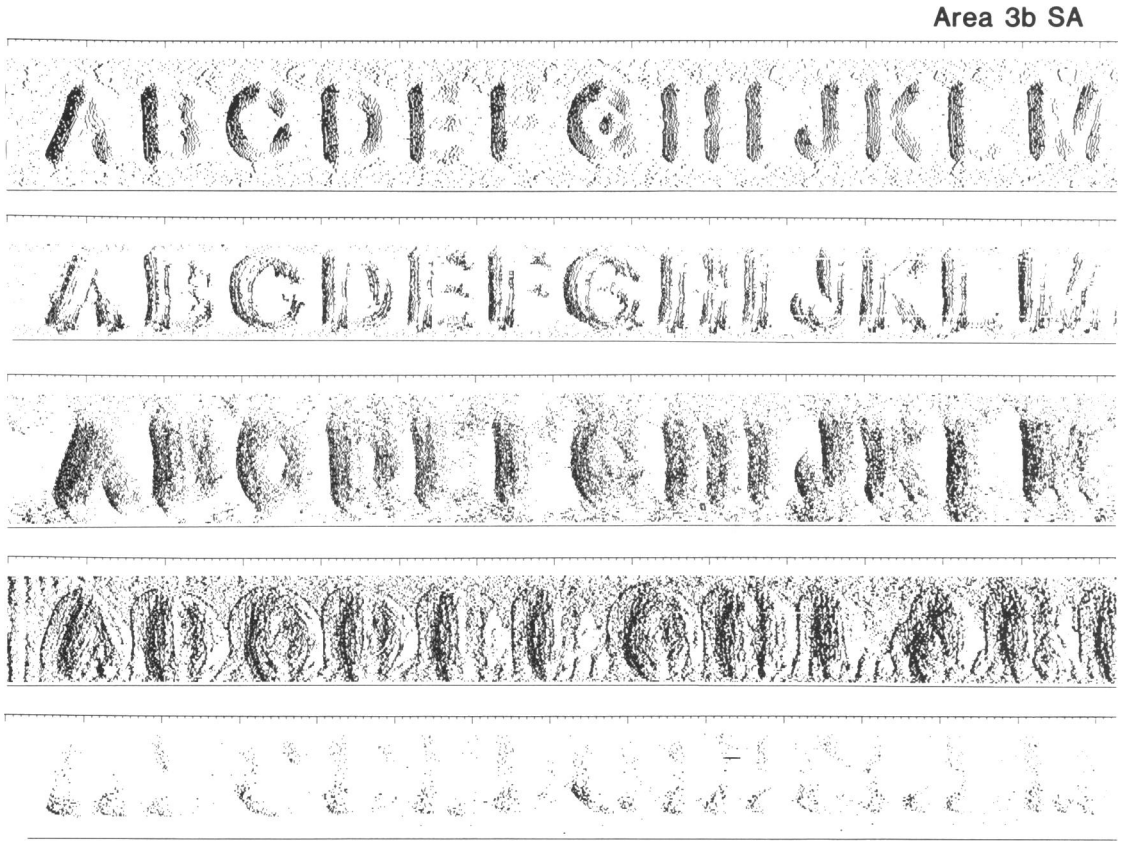

FIG. 3. SEPs reconstructed from five single SA neurons in area 3b of awake monkey. Letter height, 8.5 mm; scanning velocity, 50 mm/sec with the exception of panel 4, for which letter height = 6.5 mm and scanning velocity = 20 mm/sec; contact force, 60 g.

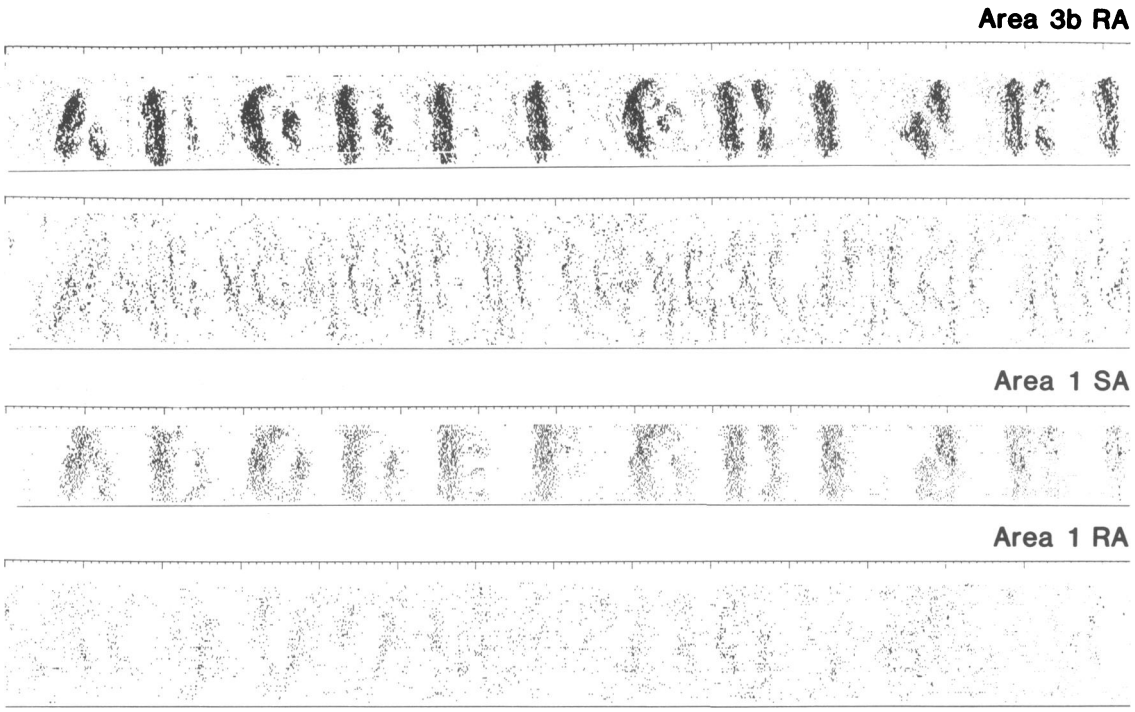

FIG. 4. SEPs reconstructed from single neurons in areas 3b and 1. Letter height, 8.5 mm; scanning velocity, 50 mm/sec; contact force, 60 g.

detail and sweep-to-sweep repeatability is illustrated in Fig. 1, where the responses to the letter K from this neuron have been displayed at increased magnification. The sweep-to-sweep variability in the latency of the first impulse relative to the leading (left) edge of the stimulus is 15 μm. Comparable spatiotemporal resolution (sweep-to-sweep variability, 15–100 μm) was observed in 15 of the 51 SA neurons in area 3b studied with embossed letters. Rows 1 and 3 of Fig. 3, which have relatively simple isomorphic or near-isomorphic responses, are characteristic of a subgroup (12/51) that are dominated by a single excitatory field. Rows 2 and 4 are characteristic of another subgroup (14/51) in which the responses are highly structured, not necessarily isomorphic, and appear to be the result of some process with mixed excitatory and inhibitory components. The fifth row is characteristic of another group (10/51) in which the neuron represents only parts of letters. Another subgroup (8/51, not shown) consists of neurons with structured, differentiated responses in which the dominant response feature is inhibition. A small group (7/51, not shown) yielded weakly structured responses. These subgroups do not constitute homogeneous classes: the SEPs of neurons within these subgroups are generally quite different from one another. RA neurons in area 3b exhibited less spatiotemporal structure and were less responsive to embossed letters than were the SA neurons. The responses illustrated in the top two panels of Fig. 4 were the most structured responses to letters that we observed among 29 area 3b RA neurons.

Area 1. The majority of the SEPs obtained from 52 neurons (SA, RA, and PC) in area 1 exhibited little or no structure (36/52); of those with clearly structured responses (16/52) only three produced isomorphic images. The most structured SA and RA images from this group are shown in Fig. 4. SA responses in area 1 are more acute than RA responses but the difference is not as striking as the difference between SA and RA responses in area 3b.

The data presented so far show that the spatial structure of letters is registered in the spatiotemporal responses of cortical neurons in somatosensory cortex. However, from the responses to letters alone it is not possible to determine whether any of the cortical neurons that we have studied convey fine spatial information sufficient to account for tactile spatial resolution near threshold, which corresponds (in the human) to a separation of stimulus elements of $\approx$0.8

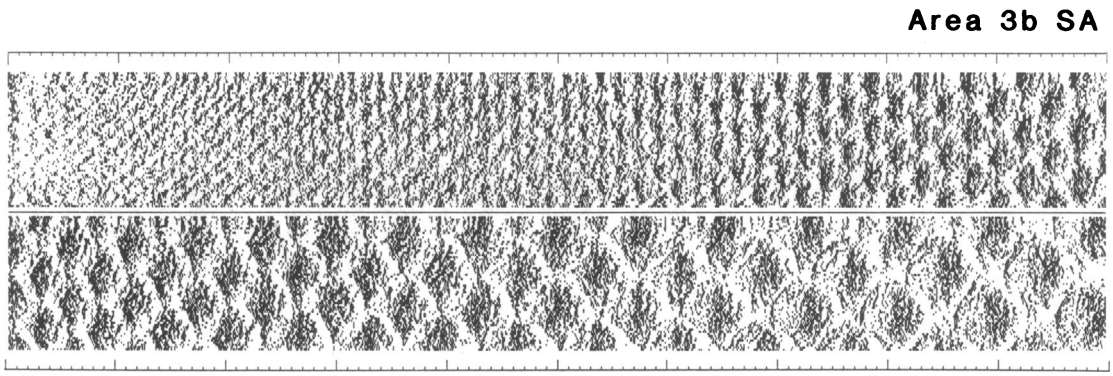

FIG. 5. SEP reconstructed from one SA neuron in area 3b. The raster is displayed in two halves. The stimulus consisted of a tetragonal array of embossed dots in which the gap between dots increased linearly from 0.4 mm at one end (top left) to 6.2 mm at the other (bottom right). Scanning velocity, 20 mm/sec; contact force, 60 g.

mm for stationary (11) and scanned (12) stimuli. Therefore a more direct measure of the limits of each neuron's spatial resolution was made by scanning an embossed tetragonal dot pattern with continuously varying edge-to-edge dot spacing (ranging from 0.4 to 5.5 mm) across the skin. To account for the psychophysics, spatial structure should be evident in the responses of at least one cortical population for dot separations of about 0.8 mm edge-to-edge. The response of a representative cortical SA neuron from area 3b to the dot pattern is illustrated in Fig. 5. The SEP from this neuron is modulated at all dot spacings down to about 0.4-mm gaps between the 0.5-mm (diameter) dots (i.e., below the psychophysical threshold). One-third of the SEPs (10/31) from SA neurons in area 3b exhibited spatial modulation at dot spacings below 0.8 mm. The comparable figures for the remaining populations were 3/24 for area 3b RA neurons, 1/8 for area 1 SA neurons, and 0/14 for area 1 RA neurons. The differences between these proportions are statistically significant (χ^2, $P = 0.05$), and these data suggest that SA neurons in area 3b carry spatial information with sufficient acuity to account for fine form recognition near threshold.

DISCUSSION

Representation and Transformation. In the periphery, RA and SA afferents yield isomorphic SEPs and, within each class, the SEPs are similar; the main difference between primary afferents within a single class is the locus of sensitivity. The response properties and the dense, regular distribution of these afferents imply that the SA and RA population responses each convey isomorphic imagery to the central nervous system. The relatively sparse innervation by PCs and the lack of structure in their SEPs imply that they do not transmit isomorphic imagery. In the cortex, the fact that some SEPs from area 3b SA neurons are highly isomorphic suggests that a subpopulation of these cortical neurons carries isomorphic neural imagery. However, the variety of response types within area 3b implies that the representation does not remain strictly isomorphic. In the intermediate stages of a series of stepwise transformations leading to a nonisomorphic representation of form, one would expect responses that demonstrate vestiges of isomorphism together with a variety of emerging nonisomorphic characteristics. This is the sort of response we observe among area 3b SA neurons. The relative lack of isomorphism in the area 3b RA neurons and area 1 neurons suggests either that fine spatial form is not represented effectively in these neuronal populations or that the representation of fine spatial form is quite nonisomorphic.

Critical Pathways for Form Recognition. In psychophysical experiments using exactly the same embossed letters, scanning speeds, and stimulating apparatus used in these neurophysiological experiments, human subjects perform at a median level of 60% correct identifications (6.0-mm letters, unpublished observations), which implies highly structured neural responses in at least one pathway. In the periphery, although the SA neurons respond to these complex spatial patterns with significantly greater acuity than the RA neurons, the SEP data suggest that either population could account for the human capacity for letter recognition. In the cortex, the acute spatiotemporal structure of the area 3b SA responses as compared with area 3b RA or area 1 responses makes area 3b SA neurons the primary candidates for the transmission of spatial information underlying tactile letter recognition. The relative lack of structure in area 3b RA neurons and area 1 neurons may mean that they process information related to some other facet of tactual perception—e.g., texture (24, 25). Alternatively, it could mean that these neurons are engaged in the representation of spatial form but are further along the pathway from an isomorphic to an abstracted representation in which each single neuron represents some distributed property of the stimulus geometry. We cannot, as yet, distinguish between these possibilities.

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