Cutaneous neural codes for shape[1]

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Received August 4, 1993

LAMOTTE, R.H., SRINIVASAN, M.A., LU, C., and KLUSCH-PETERSEN, A. 1994. Cutaneous neural codes for shape. Can. J. Physiol. Pharmacol. **72**: 498–505.

In the pursuit of peripheral neural representations of shape for the sense of touch, a series of two- and three-dimensional objects were stroked across the fingerpad of the anesthetized monkey and responses evoked in cutaneous mechanoreceptive primary afferent nerve fibers recorded. Responses of slowly adapting fibers (SAs) and rapidly adapting fibers (RAs) were recorded to the stroking of a cylinder, a sphere, several ellipsoids, and a pattern of alternating convex and concave cylindrical bars. The compressional force was maintained constant during a stroke, and the stroke velocities as well as orientations of the objects and stroke trajectories were varied between separate sets of trials. The major geometrical properties of the shapes were well represented in the spatiotemporal responses of the afferent fiber populations, particularly those of the SAs. Intensive parameters of shapes, such as the magnitude of change in skin curvature produced as a result of contact with the object surface, were encoded in the discharge rates of SAs and RAs, but this neural code was also influenced by changes in stroke velocity. Spatial parameters of shapes such as the extent of contact and the changes in contour that characterize a shape as belonging to a particular category (such as a sphere as opposed to a cylinder) are encoded in the spatially distributed discharge rates of the SA population. This spatial response profile provides a neural code that is probably invariant with moderate changes in the way the object comes in contact with the skin, such as the contact force or the orientation of the object.

Key words: shape, cutaneous mechanoreceptors, primates, touch.

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Pour étudier la représentation neurale périphérique de formes pour le sens du toucher, on a frotté légèrement une série d'objets à deux ou trois dimensions sur la pulpe des doigts du singe anesthésié et enregistré les réponses induites dans les fibres afférentes primaires des mécanorécepteurs cutanés. On a enregistré les réponses de fibres s'adaptant rapidement (AR) et lentement (AL) à l'effleurement d'un cylindre, d'une sphère, de plusieurs ellipsoïdes et d'un montage de barres cylindriques concaves et convexes alternantes. La force de compression a été constante durant l'effleurement, et les vitesses d'effleurement ainsi que les orientations des objets et les trajectoires de l'effleurement ont été variées d'une épreuve à l'autre. Les propriétés géométriques majeures des formes ont été bien représentées dans les réponses spatio-temporelles des populations de fibres afférentes, particulièrement celles des fibres AL. Les paramètres intensifs des formes, tel le degré de variation de courbure de la peau produite lors du contact avec la surface des objets, ont été encodés dans les taux de décharge de fibres AL et AR; toutefois, ce code neural a aussi été influencé par les variations des vitesses d'effleurement. Les paramètres spatiaux des formes, tels que la superficie de contact et les variations de contour qui caractérisent une forme pour l'identifier à une catégorie particulière (par exemple une sphère par opposition à un cylindre), sont encodés spatialement dans les taux de décharge de la population de fibres AL. Ce profil de réponses spatiales fournit un code neural qui demeure probablement invariant en présence de faibles fluctuations de la manière dont l'objet entre en contact avec la peau, telle la force de contact ou l'orientation de l'objet.

Mots clés : forme, mécanorécepteurs cutanés, primates, toucher.

[Traduit par la rédaction]

Introduction

What tactile information is required to recognize the shape of an object? When we reach out in the dark to pick up a drinking glass, fingerpads contact and explore the surface of the glass. Tactile signals about shape guide the movements of the hand in manipulating the glass, not only to identify it but also to provide a stable grasp. Normal mobility of the hand in the absence of tactile sensation is insufficient to find and grasp a desired object without adequate visual cues. Tactually guided manipulation and associated sensations normally involve the integration of motor commands with tactile and kinesthetic signals. However, for small shapes of typical wavelengths and amplitudes of a few millimetres, the tactile signals seem to provide the dominant information. Therefore, the method we have chosen to study the role of tactile information in signalling shape is to apply small objects of different shape to the passive skin in a controlled manner.

Even while restricting shape information to the sensory sig-

[1]This paper was presented at the Symposium of the Centre de recherche en sciences neurologiques entitled Sensorimotor Control of the Hand, held May 6 and 7, 1993, at Montréal, Que., and has undergone the Journal's usual peer review.

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Printed in Canada / Imprimé au Canada

nals from the skin within and around the contact region, it is obvious that the responses of mechanoreceptors depend not only on the physical features of the object's shape but also on the manner in which it is applied to the skin. An important question, then, is how the shape of an object is preserved in the responses of cutaneous receptors despite variations in the force of the object against the skin and changes in the orientation, velocity, and trajectory of the object as it moves over the surface of the skin.

What are the critical geometric features of shape that govern the patterns of stresses and strains in the skin, consequent mechanoreceptor responses, and ultimately object recognition despite gross differences in the way the shape contacts the skin? The shape of an object can be represented as a unique distribution of the curvatures of its surface. If one takes a cross section through any point on the surface, the local curvature is defined as the reciprocal of the radius of the circle that can be fitted to the surface at that point. Thus, object shape can be represented as a function relating curvature to distance along the surface (Srinivasan and LaMotte 1991). This intrinsic description of the object surface is invariant with respect to translation and rotation of the object. When the object is applied to the skin, its pattern of curvatures that define its shape will produce a characteristic geometric pattern of stresses and strains in the skin that enable populations of cutaneous mechanoreceptors to contain, in their responses, a representation of the object's shape.

Previously, we have recorded the responses of cutaneous mechanoreceptors to indentations and stroking of a variety of shapes such as sinusoidal steps, cylindrical bars, a pattern of cylindrical rods, and wavy surfaces, together with psychophysical discrimination experiments on some of these shapes (LaMotte and Srinivasan 1987*a*, 1987*b*, 1993; Srinivasan and LaMotte 1987, 1991). The results supported the following hypotheses. The spatially distributed pattern of neural discharge rates in a population of mechanoreceptors represents an object's overall shape as a distribution of curvatures. The sizes of convex regions of the object in contact with the skin and the concavities between them are encoded by the sizes of the regions of skin containing active and inactive mechanoreceptors, respectively. These are spatial measures of neural response. In addition, the magnitude and rate of change in the curvature of the skin produced by an object are encoded by the discharge rates of individual fibers, an intensive measure of neural response.

The following pages describe the results of ongoing studies concerning how two- and three-dimensional shapes of objects moving across the fingerpad are represented in the responses of cutaneous mechanoreceptors. We are particularly interested in the spatial and intensive measures of this neural representation that remain invariant with respect to changes in the orientation, velocity, or direction of movement of the object.

Methods

Stimulus objects and tactile stimulators

Two types of rigid objects were constructed whose shapes were made to vary along a continuum of changing curvature in a carefully controlled manner. One was two dimensional in that its surface height changed as a function of length alone: a smoothly changing wavy surface of alternating convex and concave circular cylinders of differing curvature (reciprocal of radius). The curvatures were 8, 5.33, 4, 2.67, 2, 1.33, 1 and 0.67 in.$^{-1}$ (1 in. = 25.4 mm). A servocontrolled stimulator with 2 degrees of freedom (LaMotte et al. 1982) stroked the object across the skin at a constant velocity of 1 to 40 mm/s while maintaining compressional force approximately constant. The object was stroked back and forth along a single trajectory that was perpendicular to the long axis of the finger.

The second class of objects was three dimensional, consisting of two ellipsoids, a sphere, and a cylinder. Both ellipsoids had a radius of 5 mm along one axis and, for the orthogonal axis, a radius of either 1 or 3 mm. The sphere and cylinder each had a radius of 5 mm. For some of the experiments, a 0.5 mm high section was cut off the top of each of these three-dimensional shapes and mounted on a plate. These will be referred to as ellipsoids in relief. Each stimulus object was mounted on a servocontrolled torque motor. The motor was mounted to a six-axis force–torque sensor that allowed measurement of the contact force vector. The sensor, in turn, was attached to a servocontrolled stimulator with 3 degrees of freedom. The orientation of the object relative to the finger was adjusted by hand. After bringing the object into position on the stationary fingerpad, the stimulator controlled the motion of the object along a linear trajectory in the horizontal plane, while the torque motor controlled the compressional force of the object against the skin. The object was stroked from one side of the receptive field to the other. Typically the contact locations of the object at the beginning and end of each stroke were outside the receptive field. In some experiments, the orientation of the trajectory and (or) the orientation of the object were varied.

Electrophysiological recordings

The methods of fiber microdissection and single unit analysis were used to record from mechanoreceptive afferent nerve fibers innervating the fingerpad of the anesthetized monkey (*Macaca fascicularis*) (LaMotte and Srinivasan 1987). Responses to each object stroked across the fingerpad were recorded in single, slowly adapting, type I, and rapidly adapting, Meissner corpuscle mechanoreceptive nerve fibers (henceforth referred to as SAs and RAs, respectively). The number of SAs and RAs studied were 7 each for the wavy surface and 6 each for the ellipsoidal objects.

Video recording

Each object was transparent, allowing the contact between the object and the skin to be viewed through a microscope at 20× and recorded on video tape. When playing back the tape in slow motion, the amount of skin stretch that occurred during each stroke was measured. It was found that the skin stretch occurred only during the initial portion of a stroke before the object started slipping against the skin and remained constant until the end of the stroke. The measurement of skin stretch enabled us to allign the spatial plots of neural responses to strokes in opposite directions and at different velocities.

Results

Two-dimensional shapes

The responses of both SAs and RAs were modulated by the resulting changes in skin curvature produced by the aperiodic curvature pattern as it was stroked across the skin. The temporal sequences of nerve impulses evoked in an SA and two RAs are shown in Fig. 1 as spatial sequences. The object was stroked beginning with the lowest (broadest) curvature and ending with the highest (sharpest) curvature. The recorded neural response can be viewed in three ways. First, it is the response over time of a single nerve fiber during the passage of the object over its receptive field. A plot of the temporal sequence of impulses would appear as the impulse rasters in Fig. 1, with the origin of time at the left end for each stroke and the time scale given by dividing the distance by the stroke velocity. Second, the data can be viewed as the result of a hypothetical experiment where the object was stationary and the skin of the fingerpad was moving over it. Then, each tic mark in Fig. 1 indicates the horizontal location of the center of the receptive field on the surface of the object when an action potential occurred. Here, the fingerpad should be imagined as

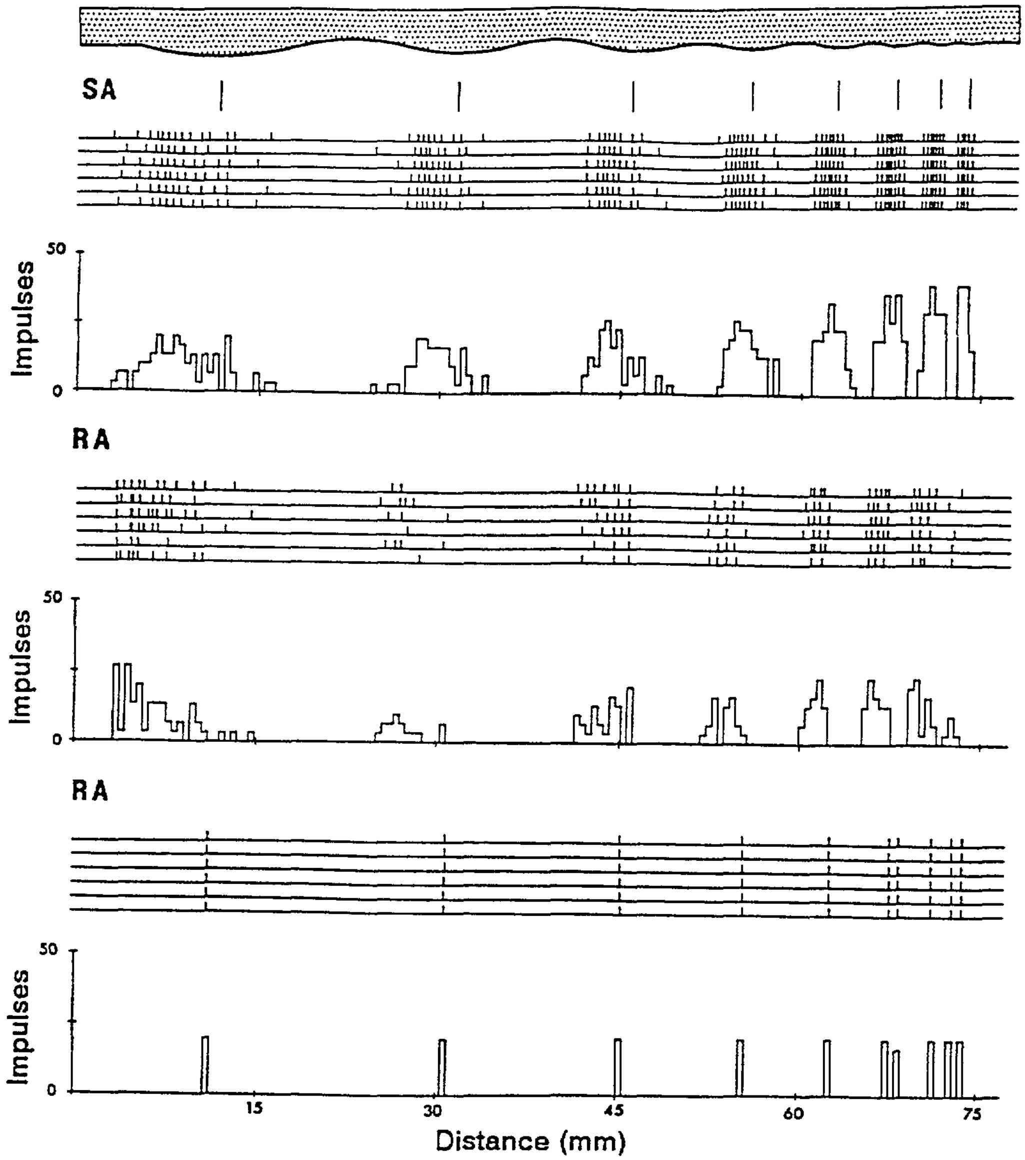

FIG. 1. Responses of slowly adapting and two rapidly adapting mechanoreceptive afferent fibers (SA and RA, respectively) to an aperiodic pattern of curvatures stroked across the stationary fingerpad. The temporal sequence of impulses is plotted as a spatial sequence (see Results). The tic marks can be interpreted as the locations of active receptors in a hypothetical population of receptors. Shown beneath is the spatial profile of discharge rate averaged over six strokes (bin size is 0.5 mm). Responses are shown to each of six strokes in the same direction along the same trajectory oriented perpendicular to the long axis of the finger. The stroke velocity was 10 mm/s and the compressional force 20 g wt.

moving from left to right underneath the object with a velocity equal to the stroke velocity. Third, we can imagine the skin surface to be large (much bigger than the length of the whole wavy surface), flat, and covering a continuous sheet of identical mechanoreceptors. Then, at any instant of time during a stroke of the wavy surface, all the convexities will be in contact with the skin, and the tics shown for each stroke in Fig. 1 can be viewed as the locations of the active receptors at that time. Thus, the widths of bursts and pauses represent active and inactive receptor regions, with the discharge rate at each location representing the instantaneous frequency of discharge of the receptor at that location. This "spatial event plot" (Johnson and Lamb 1981; Johnson and Hsaio 1992), shown in Fig. 1, and the discharge rate profile derived from it represent a snapshot of the instantaneous response of a hypothetical population of spatially distributed continuous sheet of SAs with identical biomechanical and neural response properties. In this view, which is the one we will adopt, the fact that the skin contacts the wavy surface at only a few of the convexities implies that the variation of the population response over time is given by moving a window of width equal to the skin contact width from left to right in Fig. 1, with a velocity equal to the stroke velocity.

As shown in Fig. 1, the SA responded with bursts of impulses to each cylindrical convexity as it passed over the most sensitive spot in the receptive field. The responses are repeatable over multiple strokes. Several important geometric features of the shape pattern are contained within these responses and are consistent with our previous results (e.g., Srinivasan and LaMotte 1991). The widths of the bursts and the pauses between bursts represent the widths of afferent activity and inactivity corresponding to the widths of the convexities and concavities of the curvature pattern. The discharge rate during each burst is directly related to the rate and amount of curvature (see also LaMotte and Srinivasan 1987*a*, 1987*b*; Srinivasan and LaMotte 1987, 1991). Finally, the dome-

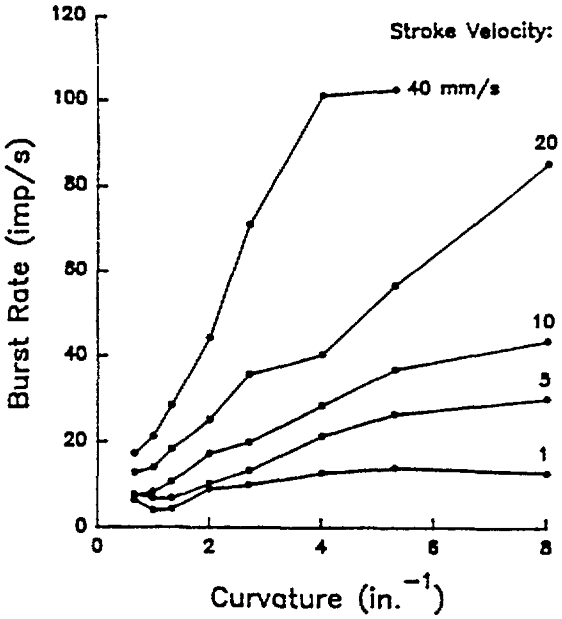

FIG. 2. Mean discharge rate of an SA during the burst of impulses (imp) evoked by each convexity in the aperiodic pattern stroked at 1, 5, 10, 20, and 40 mm/s. Each data point is an average of responses to 12 strokes in the same direction.

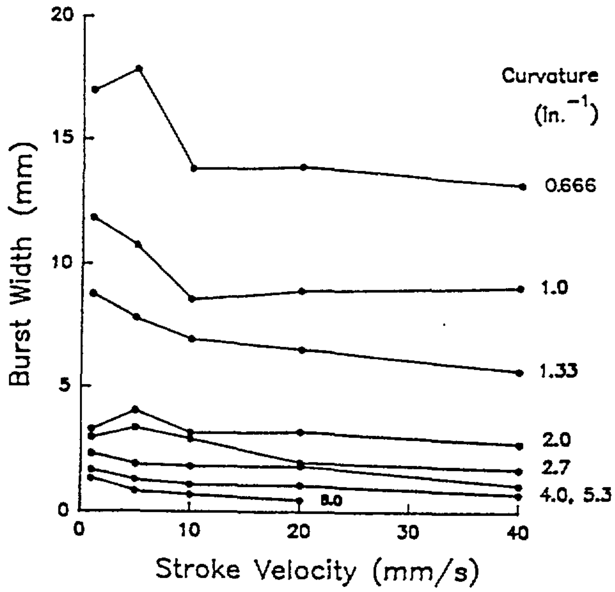

FIG. 3. Mean width of the burst of impulses evoked from an SA by each curvature in the aperiodic pattern stroked with velocities of 1, 5, 10, 20, and 40 mm/s. Each data point is an average of responses to 12 strokes in the same direction and was obtaiined from a spatial event plot such as the one shown in Fig. 1.

shaped pattern of discharge rates in the spatial profile reflects the cylindrical shape of each convexity. Thus, the overall shape, as a distribution of curvatures, is represented by the spatially distributed pattern of peripheral discharge rates.

For certain RAs, the discharge rates and widths of impulse bursts evoked by the stimulus shape are well modulated by the changes in curvature, as shown for the RA in the middle of Fig. 1. In separate experiments with an indenting probe, this fiber was responsive to relatively low velocities of vertical indentation. Some of the RAs, such as the one whose responses to the curvature pattern are shown in the bottom of Fig. 1, required higher velocities of indentation before they responded. Their abilities to encode the width or magnitude of object curvatures were less reliable or absent at sufficiently low curvature rates produced by the broad curvatures or when the stroke velocity was too low and only a few or no impulses were evoked by each curvature. However, RAs that respond with very few impulses may nevertheless accurately encode the distance between peaks of convexities (bottom panel of Fig. 1).

The mean discharge rates and the mean burst widths, averaged from 12 strokes in the same direction, are plotted in Figs. 2 and 3 for a typical SA. The discharge rate increased as the curvature of each convexity increased. The mean rates of the more responsive RAs (not shown) increased as well with increasing curvature. However, the discharge rate of either receptor type was not invariantly related to curvature because it was also modulated by changes in stroke velocity. The mean discharge rate during each burst increased with stroke velocity for both SAs and RAs over the range of 1 to 40 mm/s, as illustrated for the SA in Fig. 2. The increase was greater for higher than for lower curvatures. This was true as well for the more responsive RAs but, again, only for sufficiently high rates of change in skin curvature produced by higher curvatures and stroke velocities.

The widths of bursts were less susceptible to changes in stroke velocity. The mean widths of the bursts in the SAs and the more responsive RAs decreased monotonically with increasing curvature. Unlike discharge rate, which changed with stroke velocity, the widths of the bursts of SAs changed little over a wide range of velocities. This is illustrated for an SA in Fig. 3. Burst widths of RAs also remained constant with respect to stroke velocity but were a reliable neural code only for sufficiently high stroke velocities since many RAs did not respond to low stroke velocities (typically greater than 5 mm/s).

Three-dimensional shapes

The spatial profiles of responses of SAs to three-dimensional shapes provided information about the nature of the shape and its orientation. The spatial event plots in Fig. 4 were obtained from an SA under conditions where the orientation of a full ellipsoid was held constant while it was stroked over the receptive field along trajectories of different orientation. The ellipsoid (with 1 × 5 mm radii) was stroked at 10 mm/s in one direction along a series of parallel trajectories, separated by 0.2 mm and oriented at 30, 60, 120, or 150° with respect to the axis orthogonal to the length of the finger. The major axis of the ellipsoid was oriented at 90°, that is, parallel to the long axis of the finger. Each dot in a spatial event plot is the location of the center of the ellipsoid on the skin each time an action potential occurred. As mentioned before, this plot can be interpreted as a snapshot of the SA population response. The results in Fig. 4 illustrate how the orientation of the object and certain features of its shape might be preserved in the responses of a population of SAs despite changes in the orientation of the stroke trajectory and consequently of the skin stretch due to friction.

Responses of another SA to the relief version of the narrow ellipsoid are shown in Fig. 5. In this experiment, the orientations of the shape and the stroke trajectory were 90 and 0°, respectively, while the object was stroked back and forth over the receptive field. Responses to each direction of stroking are shown separately and then combined. The amount of skin stretch produced by strokes in the forward and backward direction, 0.25 and −0.25 mm, have been added to the position of each dot

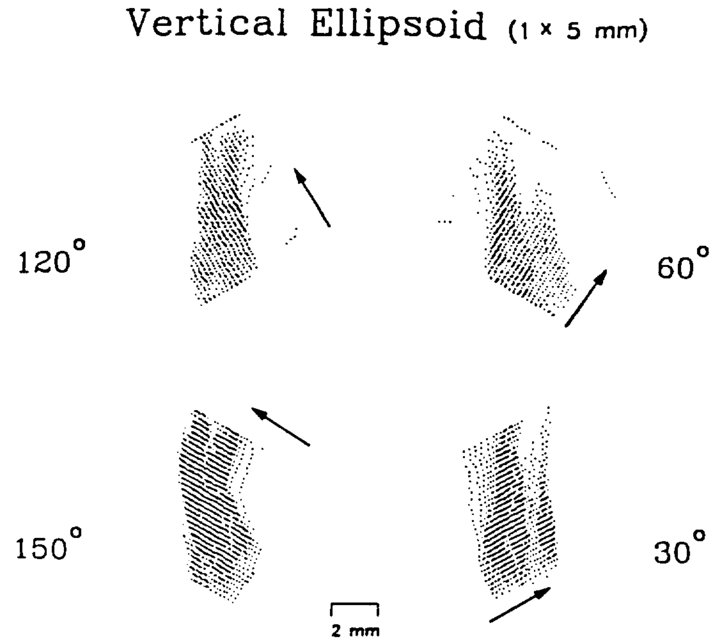

FIG. 4. Responses of an SA to an ellipsoid stroked along four sets of parallel trajectories differing in orientation with respect to the finger. The major axis of the full ellipsoid (principal radii of 1 × 5 mm) was oriented parallel to the finger (vertical in the figure). Each dot represents the position of the center of the object when an action potential occurred. For each of the four spatial event plots, strokes were in the direction indicated by the arrow, beginning at the rear end of the arrow and separated by 0.2 mm along the orthogonal axis. The angle of orientation of each set of trajectories is given in relation to the axis orthogonal to the length of the finger.

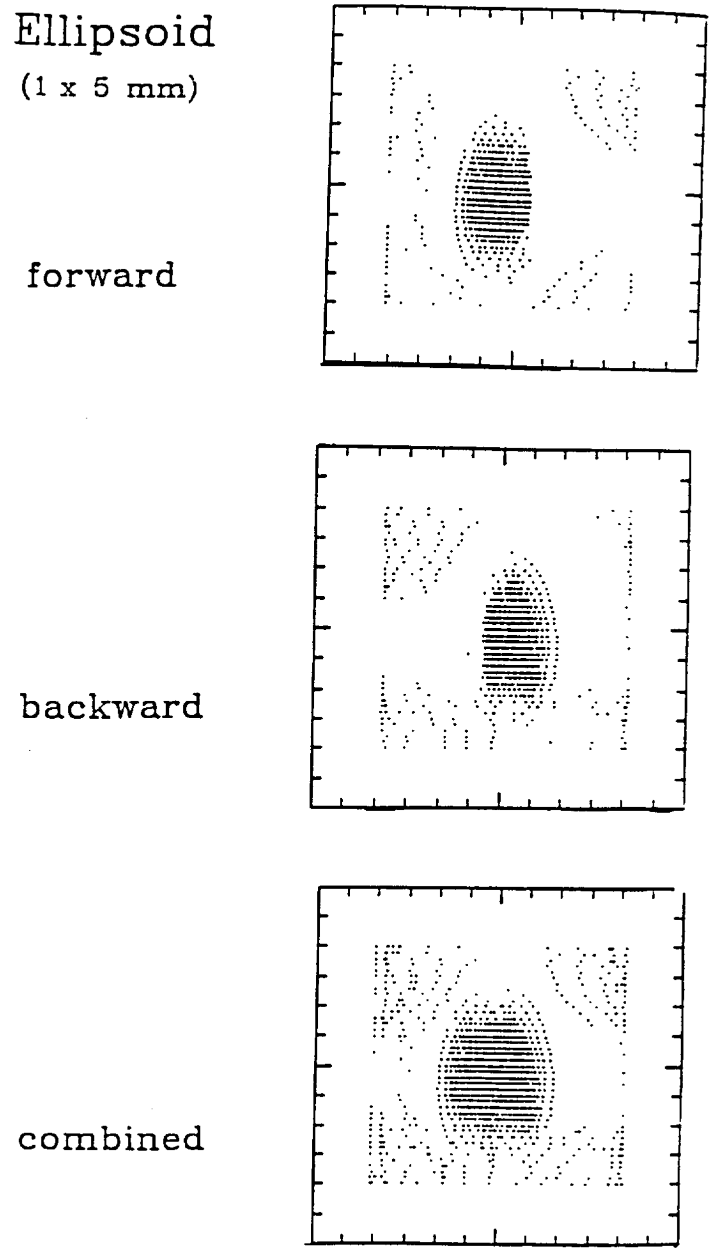

FIG. 5. Responses of an SA to an ellipsoid in relief on a flat plate stroked along a series of spatially shifted, parallel trajectories. The major axis of the ellipsoid was oriented 90° with respect to the direction of stroking and parallel to the finger. The minor axis had a radius of 1 mm. Each tic mark represents the location of the center of the ellipsoid when an action potential occurred during a stroke along a given trajectory. After a single stroke back and forth at 10 mm/s, the object was shifted by 0.2 mm proximal to distal (shifted upward in the figure) and another stroke begun. Responses to strokes from left to right (forward) and right to left (backward) and the superposition of both are shown in the top, middle, and bottom panels, respectively. The three spatial event plots are spatially aligned with respect to a fixed point on the skin by taking into account the amount of skin stretch in the direction of stroking (see main text). Compressional force of the object against the skin was held constant at 20 g wt. Each interval between the marks in the frame represents a distance of 1 mm.

to spatially align each spatial event plot with a fixed point on the skin within the receptive field.

There was no response to the trailing edge of the ellipsoids for strokes in each direction because the finger does not contact the stimulus surface at that location. But, when the responses to the leading edge of the shape stroked in the two opposite directions are combined, a more symmetrical image of the shape is obtained for the combined responses. Therefore, assuming that the brain has an adequate mechanism for storing, recalling, and summing the spatially distributed mechanoreceptor responses obtained from each stroke across an object, multiple strokes along different trajectories and directions of stroking may produce a more accurate tactile image of the object's shape.

In the next experiment, the orientation of the stroke trajectory was kept the same while the orientation of the thinnest ellipsoid in relief was varied. The spatial event plots shown for the SA and RA in Fig. 6 were obtained by combining the data for the forward and backward strokes for each of the parallel trajectories. Both SAs and RAs were capable of coding the shape and orientation of objects, but the spatial images provided by SAs were typically clearer. The distinct lobes seen for the RA responses to orientations of 30 and 0° are likely due to their adaptation to the relatively low rate of skin curvature produced by the middle of the object when its major axis is oriented parallel to the direction of stroking.

In another set of experiments, the orientation of each shape and stroke trajectory were held constant and the shape was varied. Spatial event plots obtained from an SA are shown for combined back and forth strokes in response to two ellipsoids, and a cylinder oriented vertically, together with a sphere (Fig. 7). Three-dimensional mesh plots of the data are shown in the middle column, where the z-axis represents the discharge rate as a function of distance along and perpendicular to the finger axis (the background discharge surrounding the

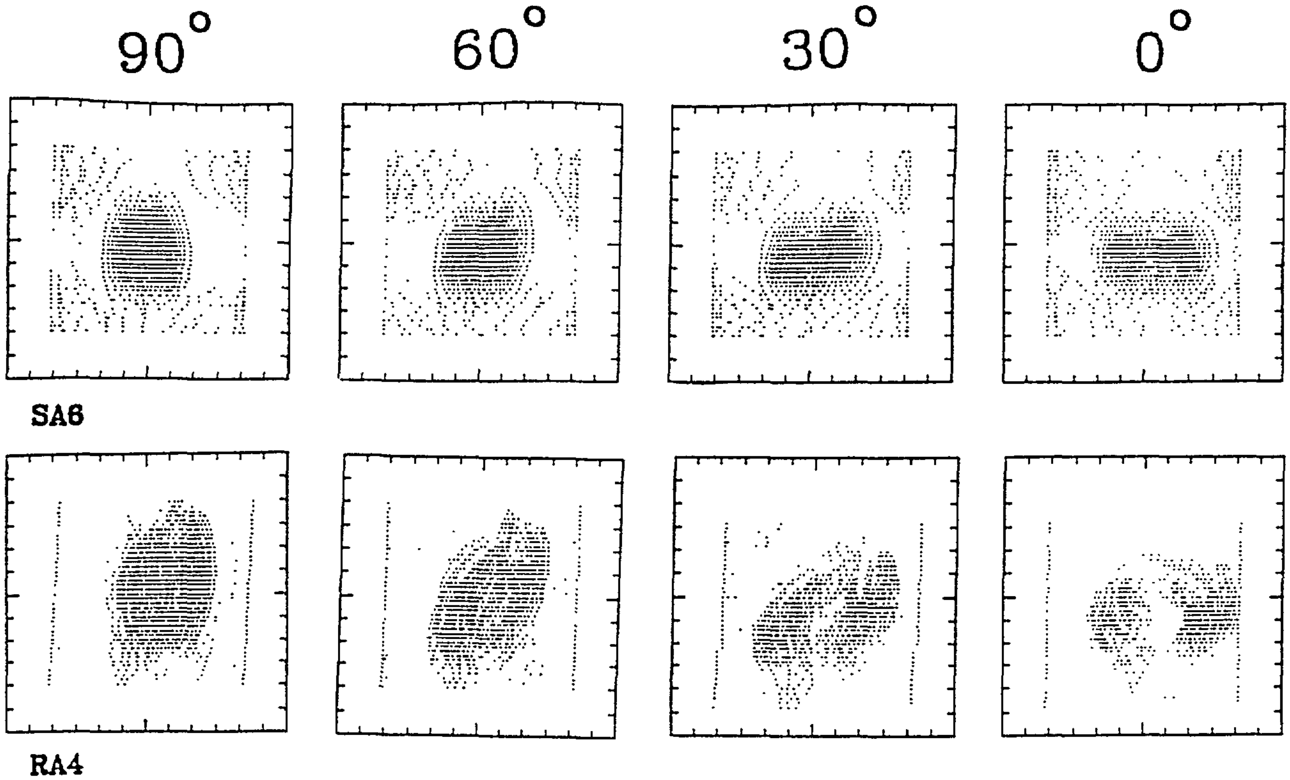

FIG. 6. Responses of an SA and RA to different orientations of the thinnest ellipsoid in relief (1 × 5 mm radii) on a flat plate stroked back and forth over their receptive fields on the fingerpad. Responses to strokes in each direction are combined for each of the spatially shifted parallel trajectories oriented perpendicular to the long axis of the finger (same format as bottom panel in Fig. 5). The ellipsoid was oriented 90, 60, 30, and 0° to the direction of stroking.

shape was removed). These discharge rates provide an idea of how the shape of a surface on the skin could be extracted from the responses of a population of slowly adapting primary afferents or might be represented in the responses of sensory neurons in the central nervous system.

Discussion

The three-dimensional shapes used in the present study were readily discriminable by human observers. Humans could identify perfectly up to six categories of orientation of the thinnest ellipsoid, and it was shown that this capacity diminished as increases in radius of the minor axis (with the radius of the major axis kept the same) made the ellipsoid more spherical (LaMotte et al. 1992).

Studies of neural encoding of two-dimensional spatial patterns in the horizontal plane, such as Braille and embossed letters, support the hypothesis that SAs provide spatial resolution that is about three times greater than that conveyed by RAs (for review see Johnson and Hsiao 1992). The results of the present series of experiments with shapes that smoothly vary in height as well as width and (or) length lend support to the notion of better spatial information processing by SAs.

The discharge rates of SAs and RAs have been shown to be higher in response to sharper objects and to the edges of objects than to broad, flat surfaces (Vierck 1979; Phillips and Johnson 1981). A more general hypothesis is that cutaneous mechanoreceptors are responsive to changes in the curvature of the skin (Srinivasan and LaMotte 1991). Using sinusoidally shaped steps of different curvature stroked across or merely indenting the skin, it was shown that the discharge rates of SAs increase as a function of both the rate and amount of curvature change of the skin brought about by changes in step curvature. RAs respond primarily to the rate of change in curvature (LaMotte and Srinivasan 1987*a*, 1987*b*; Srinivasan and LaMotte 1987, 1991).

When spherical objects of different curvature are pressed against the passive fingerpad with controlled compressional force, human subjects can independently scale the magnitude of subjective contact force and the magnitude of perceived curvature (Goodwin and Wheat 1992). This suggests that cutaneous mechanoreceptors provide independent information about contact force and object curvature.

The results of this and earlier studies (e.g., Srinivasan and LaMotte 1991) demonstrate that the geometrical features of the shape of an object moving across the skin are represented in the evoked responses of slowly adapting and rapidly adapting cutaneous mechanoreceptors. These properties contain both intensive and spatial information. Intensive information is provided in the discharge rates of SAs and RAs. When an object containing a pattern of curvatures is stroked across the skin, the discharge rates of the SAs are modulated by both the amount and rate of change in the curvature of the skin, in addition to the depth and velocity of indentation. The discharge rates of the RAs are related only to the rates of change in the curvature of the skin in addition to the velocity of indentation, provided that the object is stroked at a sufficiently high velocity.

Spatial information about the size and shape of the geometrical features of an object's surface is also contained in the responses of populations of cutaneous mechanoreceptors. Both

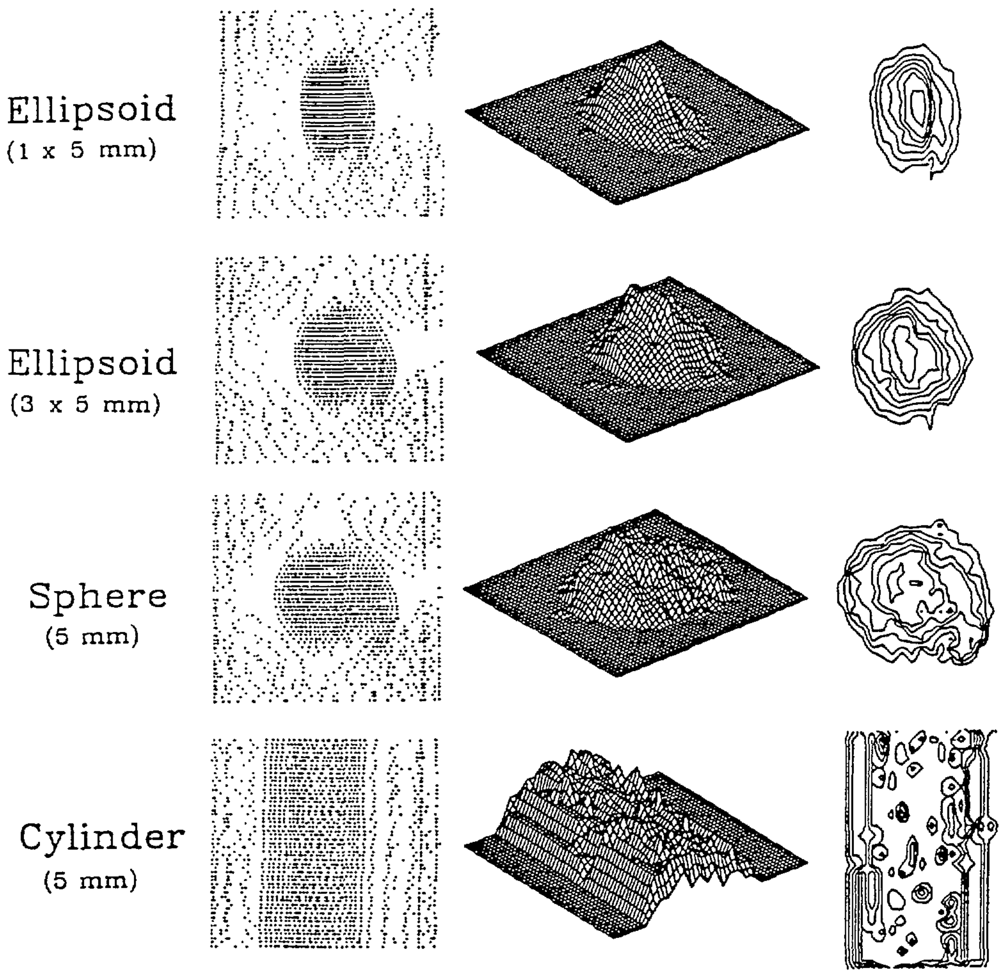

FIG. 7. Responses of an SA to four different shapes in relief. (Left column) Spatial event plots representing the combined responses to strokes in each direction along parallel, shifted trajectories (as in bottom of Fig. 5). The ellipsoids and cylinder were oriented at 90° (major axis parallel to the finger axis). (Middle column) Mesh plots, corresponding to the spatial event plots on the left, where the discharge rate is plotted along the vertical axis for each 0.2 × 0.2 mm bin along and orthogonal to the finger axis, respectively. The background discharge surrounding each shape was removed. (Right column) Boundaries of contour plots obtained from horizontal sections through the mesh plot.

RAs and SAs signal the widths of regions of contact between the object and the skin, but the pattern of curvatures that constitute the object's shape is best represented in the shape of the spatial distribution of discharge rates in the SAs both for static indentation and for stroking. The spatial pattern of discharges in the SA population can be used to characterize the shape as belonging to a particular category such as a sphere, ellipsoid, or cylinder. As demonstrated for differences in the shapes of single steps (LaMotte and Srinivasan 1987*a*, 1987*b*; Srinivasan and LaMotte 1987), intensive response parameters can signal small differences in shapes belonging to the same category, e.g., whether the step is steep or gradual. However, the spatial parameters are more likely to remain invariant with changes in the way in which the object contacts the skin, such as moderate changes in the force exerted by the object against the skin, or with changes in orientation or in the direction and velocity of movement of the object relative to the skin.

Acknowledgments

This research was funded by Office of Naval Research grant N00014-88-K-0604, and National Institutes of Health grants NS 15888 and DC 00625. The authors thank Kiran Dandekar and Catriona McDonald for their assistance.

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