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Responses of cutaneous mechanoreceptors to the shape of objects applied to the primate fingerpad

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The present study is one of a series whose aim is to determine how shape is represented in the activity of cutaneous mechanoreceptive peripheral nerve fibers. Cylindrical bars of varying curvature were indented into the receptive fields of slowly and rapidly adapting mechanoreceptive afferent nerve fibers (SAs and RAs respectively) supplying the fingerpad of the anesthetized monkey. The evoked pattern of nerve impulses in single nerve fibers was recorded electrophysiologically. SAs responded to differences in the curvature, both during the ramp and static phases of the skin indentation. RAs responded only during the ramp phase of the indentation, but their responses were not modulated by differences in curvature. Evidence from the present and previous studies is used to support the following hypotheses: Spatial parameters (such as the 'shapes' or 'widths' of response rates plotted over the skin surface) of primarily SAs in a spatially distributed population of fibers govern the recognition of the overall object shape as a distribution of curvatures; Intensive parameters (such as the magnitude of discharge rates) of only SAs under static indentations, and both SAs and RAs under stroking, are important for discriminations of small differences in curvatures of objects belonging to the same category of shape.

1. Introduction

In order to explore and identify tactually the shape of a small object in your coat pocket, you might first assess its overall size and form with the hand. At the same time, the orientation of the object is changed as the fingerpads, containing the highest density of mechanoreceptors (Darian-Smith

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and Kenins, 1980), explore the smaller scaled variations in surface contour. In order to reconstruct the object shape accurately in three dimensions, the tactile information from small contact regions, each typically less than a centimeter in diameter, must be integrated from several fingerpads via proprioceptive input from skin, joints and muscles, as well as knowledge of intended movements. In this article, we focus on the tactile information about shape that can be obtained from a single contact region on the fingerpad and assess how the important geometrical features of shape are represented ('encoded') in the responses of cutaneous mechanoreceptors.

The shape of a three-dimensional object is described by the distribution of curvatures on its surface. From a cross-sectional view through any point on the surface of an object, the local curvature is the reciprocal of the radius of the circle that can be fitted to the surface at that point, and the object shape can be represented as a function relating curvature to distance along the surface. While exploring a rigid object with the hand, it is clear that the tactile perception of shape remains constant despite changes in the orientation, velocity and direction of movement of the fingerpads, as well as variations in the contact forces exerted against the surface of the object. Indeed, human subjects can scale tactual information about the contact force independently from that about the curvature of spherical objects of different radii pressed against the passive fingerpad (Goodwin et al., 1991). Thus, there is evidence that shape can be encoded in the somatosensory system such that it is invariant with respect to many of the stimulus parameters that depend greatly on the way in which the object contacts the skin.

We are interested in relating the physical properties of objects, in this case the geometrical features of rigid objects, to observable biomechanical events on the surface of the skin and then, in turn, to the responses of mechanoreceptors. The skin is compliant and will generally conform to the shape of an object within the region of contact. Pressure peaks occur at points of highest skin curvature, for example at the sharp edge of an object and/or greatest depth of indentation (Phillips and Johnson, 1981; Srinivasan and LaMotte, 1991; Srinivasan and Dandekar, 1992). In the case of a rigid cylinder indenting the skin modeled as an elastic medium, the peak pressure for a specified force varies inversely as the square root of the radius, so that all the stresses and strains occurring at a given mechanoreceptor within the skin should increase with increases in curvature (Srinivasan and LaMotte, 1991). In a study of the neural encoding of shape, we recorded the responses of single mechanoreceptive peripheral nerve fibers to differently shaped steps indented into and stroked across the primate fingerpad. We found that the discharge rates in these fibers (number of nerve impulses/sec) were directly related to the amount and rate of change in the curvature of the skin in the region of contact (LaMotte and Srinivasan, 1987a,b; Srinivasan and LaMotte, 1987).

In the present study, we extended these experiments to test further the hypothesis that the curvature changes in the skin produced by object curvatures are encoded in mechanoreceptor responses and are important for processing tactile information about shape. Instead of the more complex shape of a step, we used shapes that can be described in terms of a single curvature (cylindrical bar) or a simple pattern of curvatures (parallel cylindrical rods of differing spacing).

2. Methods

2.1. Construction of objects of differing shape

Eight individual cylindrical bars were fabricated from plexiglass cylindrical rods. Each bar was one inch in length along the cylinder with a radius of curvature of 1/32, 1/16, 3/32, 1/8, 3/16, 1/4, 3/8 and 1/2 inches. The resulting curvatures (reciprocal of the radius in inches) varied from 2 to 32. These surfaces were easily discriminated by human observers. One experiment was performed using an aperiodic pattern of cylindrical bars each having a diameter of 2 mm with center-to-center spacings that ranged from 2 to 7 mm.

2.2. Application of stimulus objects

The hand of the monkey was oriented palm up and kept stationary by plasticine molded to the back of the hand. Each object was applied to the stationary distal fingerpad. The finger was typically angled upward by approximately 25 degrees from the horizontal plane. The objects with single curvatures were each vertically indented into the skin by means of an electromechanical stimulator that provided servocontrol over compressional force (±0.7 g-wt) (Chubbuck, 1976). The indentation rate was 150 g-wt/sec and the steady force 20 g-wt, applied for 2 sec. The pattern of cylindrical rods was applied by means of a stimulator with hydraulic actuators that were servocontrolled to provide precise control over position and velocity in the vertical and horizontal axes (LaMotte et al., 1983). The object was indented into the skin to achieve a force of approximately 20 g after which the vertical position was held constant as the object was stroked across the skin.

2.3. Electrophysiological recordings

Evoked discharges were recorded from single mechanoreceptive peripheral nerve fibers after microdissection of the upper median or ulnar nerve in the anesthetized monkey (e.g. LaMotte and Whitehouse, 1986). The time of occurrence of each nerve impulse was recorded by a computer. Only fibers with receptive fields centrally located on the distal fingerpad of the 2nd, 3rd or 4th finger were studied. Two types of fibers were included in the experiments, slowly adapting type I (SA) and rapidly adapting, Meissner-corpuscle type (RA) fibers, characterized respectively by a tonic and phasic response to the application of the stimuli. The Meissner RAs were distinguished from fibers with Pacinian corpuscles, not included in the study, by their lesser sensitivity to high frequency, low amplitude vibratory stimuli (e.g. Mountcastle et al., 1972). The receptive field of each fiber was mapped using von Frey type monofilaments. The orientation of the fingerpad was adjusted slightly so that the most sensitive spot in the receptive field was located directly under the cylindrical bar or rod pattern.

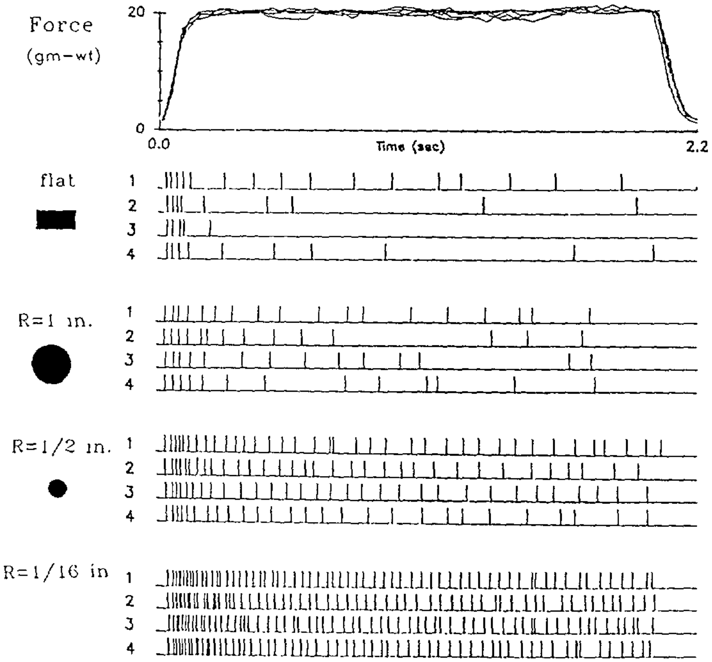

Fig. 1. Responses of an SA fiber to a flat plate and to selected cylindrical bars of different radii of curvature indented in the skin. The skin was indented at a rate of 150 g-wt/sec after which the force was kept at 20 g-wt prior to retraction. Each vertical tick represents the occurrence of an action potential. Each stimulus was delivered four times. Responses are shown for four objects: a flat plate, and cylinders with radii of 1, 1/2, and 1/16 in.

3. Results

3.1. Responses of mechanoreceptive fibers to cylindrical bars indented into the skin

Each cylinder was vertically indented four times into the center of the cutaneous receptive fields of 9 SAs and 3 RAs. As illustrated for an SA and an RA in Figs. 1 and 2, the SAs responded continuously during both the ramp and the plateau portions of the trapezoidal waveform of force generated during each vertical indentation, whereas the RAs responded only during the ramp phase.

The mean discharge rate (impulses per sec) of each SA was always higher during the ramp-up than during the plateau phase. The response during both phases was modulated by changes in the curvature of the bars (Fig. 1), with higher curvatures (smaller radii) evoking greater discharge rates. In contrast, most of the RAs responded with very few impulses to each cylinder, with a

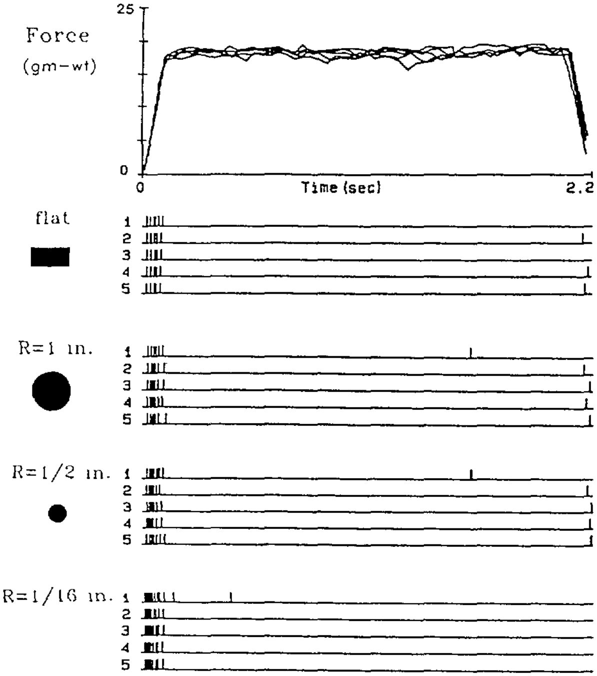

Fig. 2. Responses of an RA fiber to a flat plate and selected cylindrical bars of different radii of curvature indented into the skin. Same format as in Fig. 1.

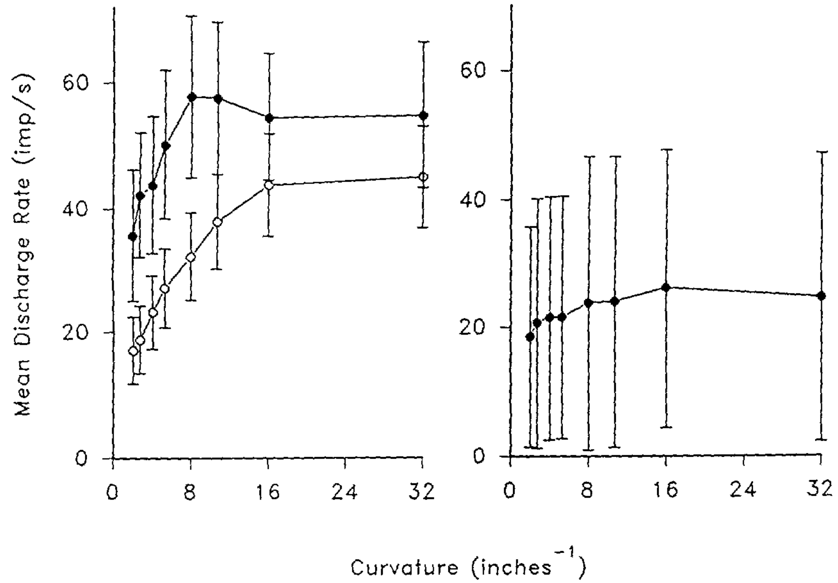

Fig. 3. Mean responses of SA and RA fibers during the rising (ramp-up) (●) and steady (plateau) (○) phases of the indentation of skin by cylindrical bars of different curvature. Left panel: Mean discharge rate (±1 SEM) evoked in 9 SAs. Right panel: Mean discharge rate (±1 SEM) of 3 RAs during the ramp up. RAs did not respond during the plateau.

weak discharge that was modulated very poorly or not at all by changes in curvature (Fig. 2).

The mean discharge rate was averaged separately for the SAs and RAs tested (Fig. 3). Responses of RAs were variable and did not change reliably with curvature. The discharge rates of SAs, however, increased with increasing curvature over a range of 2 to 8 for the ramp and 2 to 32 for the plateau. While a majority of SAs continued to exhibit increases in discharge rates with increases in curvature beyond 8–16 a few did not or even decreased their rates. In the latter instances, it is possible that the centers of the cylindrical curvatures were slightly misaligned with the most sensitive spot in the receptive field, giving rise to lower discharge rates.

Another feature of SA responses was that the discriminability between curvatures increased with time during the indentation. This is illustrated for an SA in Fig. 4. Functions plotting discharge rate against curvature became steeper when rates were taken over successively longer periods of time from the beginning of the indentation. Thus, if there is a central integrator that can accumulate nerve impulses over time, its input would come primarily from SAs and its output would be progressively better modulated by curvature with the passage of time during stimulation.

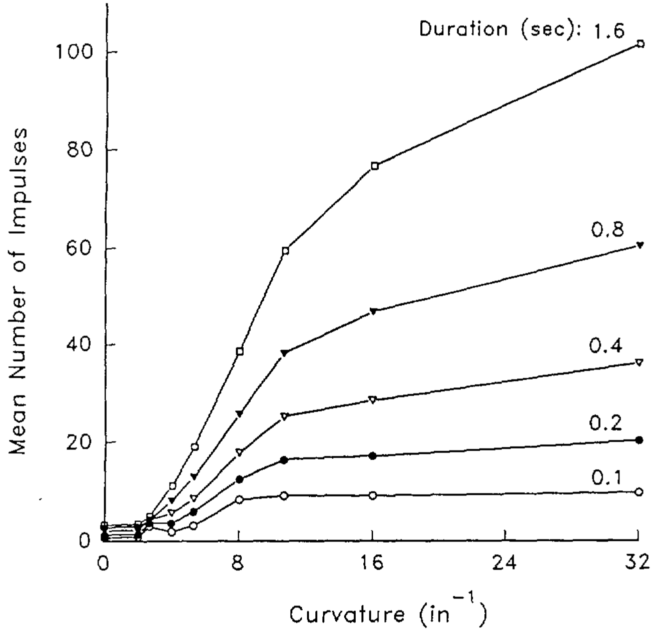

Fig. 4. Cumulative number of nerve impulses evoked in an SA during the first 0.1 to 1.6 sec of indentation produced by cylindrical bars of different curvature. Each point is the mean number of impulses evoked during the indicated time period averaged from the 4 applications of each bar.

3.2. Responses of an SA to a pattern of cylindrical bars stroked across the skin

The temporal sequence of nerve impulses evoked in an SA in response to the aperiodic pattern of identical cylinders stroked across its receptive field is plotted in Fig. 5 as a spatial sequence. Each tick mark indicates the horizontal location of the center of the receptive field on the surface of the object each time an action potential occurred. This 'spatial event plot' represents the response of a hypothetical population of SAs with identical biomechanical and neural response properties and distributed across the surface of the skin. The SA responded with bursts of impulses to each cylinder as it passed over the most sensitive spot in the receptive field. The important geometric features of this shape pattern, i.e. the size, shape and spacing of the cylinders, were represented respectively in the spatial width, shape and magnitude (discharge rate) of each burst, and the width of the pause between successive bursts. The discharge rate within a burst decreased as the cylinders became more closely spaced together most likely because the skin was

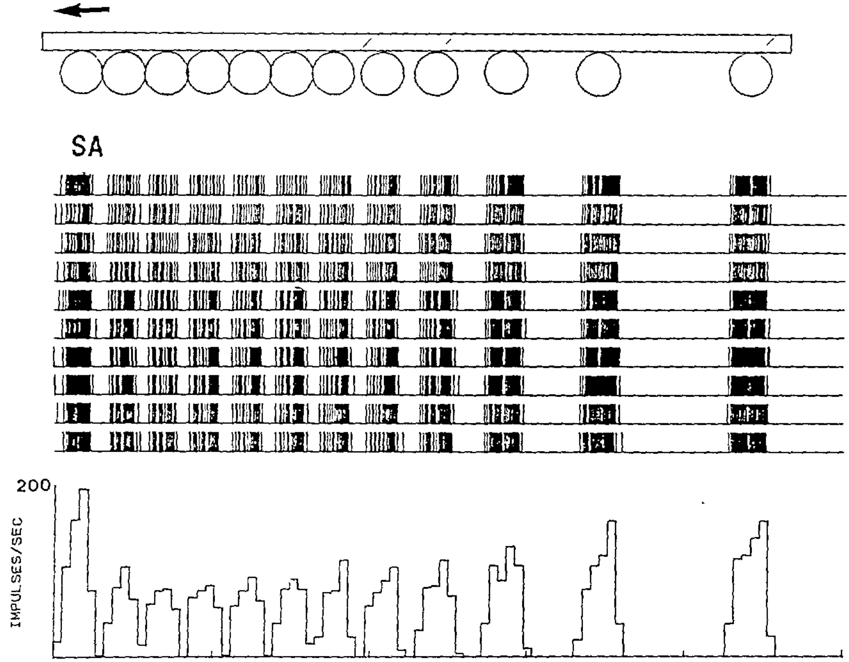

Fig. 5. Responses of an SA fiber to a pattern of cylindrical bars stroked across the skin. Each small vertical line represents the position on the bar pattern of the most sensitive spot in the fiber's receptive field each time a nerve impulse occurred. The stroke occurred in the direction of the arrow at a velocity of 10 mm/sec, and stopped on the last bar.

less able to conform to each shape, resulting in less depth of indentation and less skin curvature.

4. Discussion

As the compliant skin comes in contact with a rigid object, its shape is changed within and around the regions of contact. The magnitude and rate of change in the curvature of the skin are directly related to the curvatures that characterize the shape of the object. In an earlier study, we found that the amount and rate of change in the curvature of the skin produced by a small step pressed against or stroked across the fingerpad were well represented in the responses of both the RA and SA fiber population (LaMotte and Srinivasan, 1987a,b; Srinivasan and LaMotte, 1987). These responses contained both intensive and spatial information that was relevant for the identification of step shape, and discriminations between steps of different shape. The cross-sectional shape of the step approximated that of a half-cycle of a sinusoid such that it could be varied, for different steps, from gradual to steep.

The spatial event plot for the SA revealed a medium rate of discharge to the flat portions on either side of the central step, the highest rate to the point of maximum curvature on the step and a cessation of firing at the gap between convex upper portion of the step and the lower flat part. This rate pattern provided spatial information about the sinusoidal nature of the shape which would be required for identification or recognition. The spatial pattern of discharge was obtained both when the step was stroked over the skin as well as when it was statically indented at each of a succession of laterally shifted locations across the receptive field. In addition, the responses of the SAs were very sensitive to differences in wavelength (or maximum curvature) between the different step shapes as indicated by differences in the widths and discharge rates of the bursts.

The results of the present study in which individual cylindrical shapes or a pattern of such shapes were used, confirm those obtained from experiments using step shapes. SAs responded to differences in the curvature of cylindrical shapes statically indented into the skin. The shapes and spacings of a pattern of cylinders stroked across the skin were well represented by the shapes of the SA discharge rates plotted as functions of distance. These histograms, interpreted as spatial distributions of discharge rates in an idealized population of active SAs, demonstrate the direct relationship between object curvature and response rate as a neuronal mechanism for encoding changes in surface contour.

In the earlier studies of step shapes it was found that the responses of RAs did not discriminate the differences in step shape when the steps were indented into the skin without stroking. This is confirmed by the results of the present study in which cylindrical bars were used. However, differences in step shape were represented by differences in discharge rate during the single burst evoked by each step stroked across the skin. Differences in step shape had little effect on the width of the burst which remained more or less the same with different shapes and directions and velocities of stroking. Thus, it was concluded that RA discharge rates encoded intensive information about the sharpness of the steps, but conveyed little spatial information about shape per se, such as its half-sinusoidal pattern and the width of the region of maximum curvature.

In the present study, RAs did not respond well to differences in curvature when the cylindrical bars were staticly indented into the skin. Our earlier experimental results with steps, as well as more recent data on neural encoding of curvature patterns and three-dimensional objects, show that RAs respond well when shaped objects are stroked over the skin at sufficiently high velocities. However, the responses to stroking reflect the changes in curvature – primarily the onset of each convexity but often to the offset as well – and do not typically reflect the spatial features of the shapes (LaMotte and Srinivasan, 1987, and unpublished observations).

Both types of fibers were more responsive to moving shapes (indenting or stroking) than to shapes that were stationary. SAs gave greater discharge rates during the ramp than during the steady phase of a vertical indentation. RAs, as expected, responded only during the ramp. In accordance with this finding, studies in which objects of different curvature were stroked acrosss the skin found that the discharge rates of both fiber types increased with increasing stroke velocity to all curvatures, but more so for higher curvatures (unpublished observations). This result confirms earlier findings that the frequencies of responses of SAs and RAs to spatially patterned surfaces (Johnson and Lamb, 1981) or to step shapes (LaMotte and Srinivasan, 1987a,b; Srinivasan and LaMotte, 1987) were higher when the objects were stroked across as opposed to merely indented into the skin with the same force. For step shapes, the differences in discharge rate evoked by gradual as opposed to sharp steps were greater at higher stroke velocities than lower, especially for the RAs.

The studies of the peripheral neural encoding of shapes through the sense of touch confirm the hypotheses that the geometrical properties of shape are well represented in the spatial and temporal properties of mechanoreceptor responses brought about by changes in the curvature of the skin in contact with the object. One property of these responses is ‘intensive’, i.e. the discharge rates of SAs and RAs. The discharge rates of SAs are a function not only of the magnitude and velocity of vertical indentation, but also the amount and rate of change in the curvature of the skin produced by the object within its receptive field. The discharge rates of RAs are related not only to the indentation velocity but also to the rate of change in the curvature of the skin.

Other properties of mechanoreceptor response are ‘spatial’. The spatial pattern of changes in contour are best represented in the shape of the spatial distribution of discharge rates in the SAs. The widths of regions of skin curvature produced by contact with the object are represented in the corresponding widths of the regions of activity in the SA and RA population.

It is likely that the spatial parameters of mechanoreceptor responses are more important for the classification (recognition, identification) of an object as belonging to a particular category of shape (e.g. cylindrical bar or sinusoid step). These parameters seem most likely to remain invariant with small changes in the force exerted by the object against the skin, changes in orientation or in the direction and velocity of movement of the object relative to the skin. The associated intensive parameters are probably most relevant for discriminations of small differences in shapes belonging to the same category.

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