Monkey Cutaneous SAI and RA Responses to Raised and Depressed Scanned Patterns: Effects of Width, Height, Orientation, and a Raised Surround

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Blake, David T., Kenneth O. Johnson, and Steven S. Hsiao. Monkey cutaneous SAI and RA responses to raised and depressed scanned patterns: effects of width, height, orientation, and a raised surround. J. Neurophysiol. 78: 2503–2517, 1997. The aim of this study was to examine the slowly adapting type I (SAI) and rapidly adapting (RA) primary afferent representation of raised and depressed surface features. Isolated, raised, and depressed squares and small raised squares with a circular surround were scanned across the receptive fields of SAI and RA mechanoreceptive afferents innervating the distal fingertips of the rhesus monkey. Pattern height ranged from 0.620 to 6.20 mm and width ranged from 0.2 to 7.0 mm. The surround radii ranged from 3.0 to 7.0 mm. Previous combined psychophysical and neurophysiological studies have provided evidence that SAI afferent responses are responsible for the perception of spatial form and texture and that RA afferents are responsible for the detection of stimuli that produce minute skin motion (flutter, slip, microgeometric surface features). Our results strengthen these hypotheses. Response properties shared by both SAI and RA afferent types were that both responded only to the edges of the larger raised and depressed patterns, both responded to falling edges half as vigorously as to rising edges, both responded to rising and falling edges with impulse rates that were proportional to the sine of the angle between the edge and the scanning direction, and both had suppressed responses to a small raised surface feature when a raised surround was closer than 6 mm. Response differences consistent with the hypothesis that SAI afferents are specialized for the representation of form were that SAI responses were confined to areas around the features that evoked them in areas that were 40–50% smaller than the comparable RA response areas. SAI responses were more than four times more sensitive to stimulus height than were RA afferents over the range from 280 to 620 μm, and SAI (but not RA) afferents responded 20–50% more vigorously to corners than to edges. Response differences consistent with the hypothesis that RA afferents are specialized for the detection of minute surfaces features were that only RA afferents responded to very small surface depressions, depressed squares 0.8 mm wide, that were detectable by palpation. Mechanisms underlying the many differences in SAI and RA response properties are discussed.

INTRODUCTION

When a finger is scanned across a surface, the surface features evoke a neural image that moves across the afferent population response in register with the features. Studies in monkeys (Gardner and Palmer 1990; Johnson and Lamb 1981) and humans (Phillips et al. 1990, 1992) show that neither slowly adapting type II (SAIL) nor Pacinian afferents provide a signal that could account for the human ability to discriminate Braille characters (Loomis 1981; Stevens et al. 1996) or raised letters (Vega-Bermudez et al. 1991). It is clear that surface feature discrimination depends on one or both of the neural images conveyed by the SAI or rapidly adapting (RA) afferent populations. An intriguing hypothesis that, if true, would have implications for the CNS mechanisms underlying the processing of information from the SAI and RA afferents is that the SAI system is specialized for form processing and the RA system for motion processing (Johnson and Hsiao 1992). Investigations concerned with the relative roles of the two afferent fiber types in surface feature perception depend on quantitative hypothesis testing. There have been many quantitative studies of the neural responses to textured surfaces (i.e., repetitive or quasirepetitive stimuli) but fewer quantitative studies of the SAI and RA responses to isolated surface form (Goodwin et al. 1995; Johnson and Lamb 1981; LaMotte and Srinivasan 1987a,b; LaMotte and Whitehouse 1986; LaMotte et al. 1996).

Previous studies provide a partial picture of the responses of SAI and RA afferents to scanned stimuli. They demonstrate that both SAI and RA afferent populations provide an isomorphic image of the stimulus scanned over the skin surface, that the SAI image is more acute than the RA image, and that the spatial structure of the afferent neural image is affected little by wide changes in scanning velocity and force (Johnson and Lamb 1981). In a study similar to the one reported here, LaMotte and Srinivasan (1987a,b) scanned rising and falling edges over the receptive fields of SAI and RA afferents and varied scanning velocity and edge slope while they held the height, width, and force constant. In this study, we vary the height and width of square patterns while holding the scanning velocity, edge slope, and force constant. We also study the effect of a raised surround on the responses to a raised pattern. The squares range from 0.2 to 7.0 mm in width and from −620 to +620 μm in height. Both SAI and RA afferents respond vigorously to leading and trailing edges of both raised and depressed patterns. SAI afferent discharge rates are sensitive to pattern height, width, and corners whereas RA discharge rates are relatively insensitive to all three pattern components. Both afferent types are sensitive to the orientation of an edge; each responds with a discharge rate proportional to the sine of the angle between the scanning direction and the edge.

METHODS

Stimuli

The stimuli were fabricated from sheets of photosensitive plastic that are water-soluble until exposed to UV light (Toyoba Printight...
plastics, EF-series). A stimulus pattern was produced by laying a photographic negative of the pattern over the plastic sheet and exposing it to UV light. The portion of the surface layer not exposed to UV light was scrubbed off lightly in water. The height of the resulting raised pattern was determined by the thickness of the water-soluble layer, which was 280, 370, 470, and 620 μm in this study. The sides of the patterns fell away to the background at 60° relative to the plane of the surface. Three sets of stimulus patterns were used. The first set, constructed at all four heights, consisted of seven raised squares, 0.2, 0.8, 1.5, 2.5, 4.0, 5.5, and 7.0 mm wide, which were separated by 30 mm, center to center, in the scanning direction (see Fig. 3). The second set consisted of seven depressed squares, 620 μm deep, with the same widths as the raised squares (see Fig. 10). The third set consisted of seven circular wells, 620 μm deep, 3.0–7.0 mm in radius and separated by 30 mm center to center in the scanning direction (see Fig. 13).

In the center of each well was a raised square, 620 μm high and 0.4 mm wide. After exposure and washing, the patterns were trimmed to strips 20 mm wide and 240 mm long and fixed to a drum, 240 mm in circumference (Johnson and Phillips 1988).

**Neurophysiological experiments**

Experiments were performed on barbiturate anesthetized rhesus monkeys (*Macaca mulata*) weighing 4–5 kg (Mountcastle et al. 1972). Single cutaneous mechanoreceptive fibers were dissected from the median or ulnar nerves using conventional methods (Mountcastle et al. 1972). Afferents were classified as SAI, RA, or Pacinian (PC) on the basis of responses to indentation and vibration with a point probe (Talbot et al. 1968). Only SAI and RA afferent fibers with receptive fields on the distal glabrous pads of digits two to five were studied. After mapping the receptive field with von Frey monofilaments, the fiber was positioned so that the point of maximum sensitivity was located at the center of the region of contact between the skin and the stimulus. Neurons were not studied when the fiber could not be positioned appropriately because, for example, the receptive field was on the side of the finger or too close to the nail. The patterns always were scanned from proximal to distal. The stimulus pattern was presented to the skin (see below) with a contact pressure and scanning velocity chosen to match the motion and subsequent skin distortions that typically occur when human subjects palpate a patterned surface (Johnson and Lamb 1981; Vega-Bermudez et al. 1991).

The drum with the stimulus glued to its surface was mounted on an apparatus that lowered the drum onto the surface of the skin with a constant force (30 g) and rotated it at an angular velocity that produced a scanning velocity of 40 mm/s (Johnson and Phillips 1988). The contact force was controlled by a servocontrolled torque motor whose shaft was the fulcrum of a balance beam with the drum and drive motor at one end and counterweights on the other. The contact surface between the drum and the monkey’s finger was an oval, 7 mm wide by 9 mm long or more. After each full rotation of the drum containing the stimulus pattern, the drum was shifted 0.2 mm in the axial direction (at right angles to the direction of rotation). This sequence was repeated ≥75 times, producing a total transverse of 15.0 mm in the direction orthogonal to rotation. The occurrence times of action potentials and drum position signals were recorded with a precision of 0.1 ms.

**Analysis**

The action potential times were converted to spatial coordinates by interpolating between the times of drum position signals (200 per revolution) to obtain the horizontal, X, coordinate and assigning each action potential a vertical, Y, position based on the axial position of the rotating drum at the time of the action potential. The resulting rasters (e.g., Fig. 2) are referred to as spatial event plots (SEPs). Apart from a constant, unknown error due to action potential conduction delay between the receptors and the recording site, the action potentials were located with a precision of 8 μm (Johnson and Phillips 1988). Then the SEPs were converted into two-dimensional firing rate arrays of 0.2 × 0.2 mm bins with a two-dimensional, adaptive Parzen estimator (Twombly et al. 1996), which replaces each impulse with a two-dimensional Gaussian function with unit volume. The ratio and orientation of the Gaussian major and minor axes are determined by the covariance of the locations of all impulses within 1.0 mm of the target impulse in the SEP. The spread (standard deviation of the major axis) is scaled so that it is inversely proportional to the square root of the number of impulses within this 1.0 mm radius. Thus an impulse in a region of high firing rate is represented by a tall, narrow Gaussian, whereas an isolated impulse is represented by the widest allowable Gaussian function, which, in this application, was a circular distribution with a standard deviation equal to 0.63 mm in all directions. Then the Gaussian volume overlying each 0.2 × 0.2 mm bin was calculated to generate a two-dimensional array of firing rates. This binning method was used because extensive analyses with simulated spike trains show that this method generates impulse rate estimates with lower standard errors than conventional bucket binning or fractional interval binning. These two-dimensional arrays of firing rate were used to compute response areas and mean firing rates.

The analyses of the independence of height and width effects were done two ways, either using the multiplicative model specified in RESULTS or its logarithmic equivalent where the multiplicative effects of height and width become additive effects. Then the heights and widths were coded as dummy variables (Hays 1981) and solved using multiplicative or additive regression. All regression analyses and tests of significance were done with SPSS for Windows, Version 7.0.

**Response area and impulse rate**

The method of computing the areal extent of a response to a particular pattern is a modified version of the 10% rule used by Johnson and Lamb (1981) and Phillips et al. (1992). The original method included all histogram bins where impulse rates evoked by a particular pattern exceeded a threshold defined as 10% of the peak impulse rate evoked by that pattern. In this study, we modified the method of estimating this threshold because the peak rate in 0.2 × 0.2 mm bins can be quite variable. The new method yields the same threshold on average but is less variable. A new estimate of the peak rate was obtained by searching and finding the circular region, 1 mm in diameter, within each response region that contained the maximum number of impulses and, therefore, the maximum mean impulse rate. The coefficient of variation of the new peak rate measure was <0.1% when applied to repeated scans of the same pattern. Because this rate was, on average, 40% of the peak rate measured in single bins (i.e., by the old method) the threshold for measuring response area was set to 1/4 of this value. These thresholds were, on average, 10% of the peak rate within the small, 0.2 × 0.2 mm bins, but were less variable than the thresholds based on the original method.

A SEP, spatial rate plot (instantaneous impulse rates estimated with the Parzen algorithm), and response area for a typical SAI response are shown in Fig. 1. The mean rate was computed as the mean rate in all 0.2 × 0.2 mm bins included in the response area. The total impulse rates in the SAI and RA population responses were calculated as the product of the mean impulse rate, mean response area, and innervation density (Darian-Smith and Kenins 1980) for each afferent fiber type.
RESULTS

Neurophysiological data were collected from 12 SAI and 14 RA afferents in the median or ulnar nerves of three rhesus monkeys. All afferent fibers had receptive fields on the glabrous surface of one of the four distal finger pads. Twelve SAI and 12 RA afferents were studied using raised squares with and without circular surrounds. Seven SAI and 10 RA afferents were studied using depressed squares.

Responses to raised square surfaces

The spatial structures of the responses of the two afferent types are qualitatively similar as can be seen in Figs. 2 and 3. Both afferent types responded vigorously to the rising and falling edges of the raised stimuli. Although Fig. 2 shows an example where the SAI afferent responded to the falling edge rather weakly, it will be shown later that there was no significant difference in the ratio of mean responses to rising and falling edges between SAI and RA afferents (e.g., see also Figs. 3, 4, and 8). Both afferent types responded much less vigorously to the edges running parallel to the scanning direction, and neither responded to the flat, elevated surface. Figure 3 illustrates particularly well the interaction between the afferent fiber’s receptive field and the pattern. The SAI illustrated in Fig. 3 is the same as the one illustrated in Fig. 1. The asymmetry of the receptive field accounts in part for the difference in responses at the top and bottom of the rising edge.

One major difference between SAI and RA responses to these raised patterns was the spread of neural activity around the rising and falling edges, a difference that has been noted before (Johnson and Hsiao 1992). Averaged responses of all SAI and RA afferents to a narrow and wide square are illustrated in Fig. 4.

SAI response areas were smaller than RA response areas over all combinations of pattern height and width, as illustrated in Fig. 4, and less variable. The coefficient of variation (CV, standard deviation of response area between fibers at one combination of width and height divided by the mean area) averaged 0.25 (range 0.11–0.43) for SAI and 0.41 (range 0.18–0.66) for RA. The SAI response areas evoked by the narrowest patterns were very homogeneous with CVs in the range from 0.1 to 0.2; the increasing CVs at greater widths arose mainly from the variation in SAI responses to the trailing edges (see later in text). The CVs for RA area were unaffected by height or width.

A second major difference is that the SAI afferents responded with much higher peak rates than did the RA afferents. The peaks of the SAI mean impulse rate profiles evoked by the rising edges of patterns illustrated in Fig. 3 ranged from 160 impulses/s (ips) for the 7.0 mm wide square to 275 ips for the 0.8 mm wide square. The comparable range for the RA mean rate profiles was 120–170 ips. The peak rates evoked by the falling edges were less variable partly because the falling peak rates were less than the rising rates and partly because the falling responses didn’t emerge as separate entities until the squares were >2.5 mm wide. The mean peak rates at the falling edge were ~100 ips for the RA and 125 ips for the SAI mean rate profiles illustrated in Fig. 3.

Effects of pattern height and width

Although SAI impulse rates were very sensitive to changes in pattern height, the RA rates were not. The qualitative effects of changes in pattern height can be seen in Fig. 2, the quantitative effects in Fig. 5. SAI impulse rates and areas were affected similarly by changes in pattern height; increasing the pattern height from 280 to 620 μm caused an average 44% increase in mean SAI impulse rate (range 36–49%) and a 38% increase in response area (range 24–55%). In contrast, RA impulse rate was affected only slightly by
FIG. 3. SAI and RA responses to raised squares of varying width. Patterns were raised 470 μm above the background and were separated from one another in the scanning direction by 30 mm center to center. A: stimuli. B: SEPs for a typical SAI and RA afferent and the mean rate profile over all afferents of a single type (SAI or RA) for the sweep where the center of each square passed over the afferent’s point of maximum sensitivity.

the same change in pattern height (10% mean increase, range 1–13%), whereas response area was affected strongly (53% mean increase, range 30–78%).

Although neither SAI mean impulse rate nor response area was directly proportional to pattern height, the effects combined to produce a total population discharge rate that was proportional to pattern height. The SAI population impulse rate, defined as the product of mean impulse rate, response area, and innervation density, doubled on average when the stimulus height increased from 280 to 620 μm (98% mean increase, range 76–130%). The total RA population impulse rates increased as height doubled but not proportionately (67% mean increase, range 45–98%); for example, the SAI population impulse rates evoked by the 4.0-mm-wide raised squares increased from 2,800 to 5,400 ips, whereas the RA population rates increased from 4,900 to 7,600 ips when the pattern height increased from 280 to 620 μm.

Changes in pattern width had similar effects on SAI and RA response areas (see Figs. 3 and 6). To a first approximation, SAI and RA response areas increased linearly with pattern width for both SAI and RA afferents because they responded almost exclusively to the rising and falling edges not to the interiors as illustrated in Figs. 2–4. Pattern width also had a large effect on SAI but not RA mean impulse rates (Fig. 6). For example, the mean rates evoked by the squares 620 μm high declined from 226 to 176 ips as widths grew from 0.2 to 7.0 mm. The comparable RA rates were 117 and 122 ips.

The implication of the findings presented so far is that when the finger is scanned over a raised pattern, it is tracked by a neural image, which highlights the leading and trailing edges and whose total impulse rate is several thousand impulses per second. The SAI neural image contains higher peak rates that are concentrated tightly around the leading and trailing edges. The RA neural image also highlights the edges but is more diffuse. The response variable most strongly related to pattern height is SAI mean impulse rate, and thus it would be a strong candidate for the signal underlying the perception of pattern height. The response variables most strongly affected by pattern size are SAI and RA response area and both provide an effective signal for the perception of pattern size. The SAI and RA population im-
SAI AND RA RESPONSES TO RAISED AND DEPRESSED PATTERNS

FIG. 5. Mean response area, mean impulse rate, and population impulse rate versus pattern height for raised squares 0.2, 4.0, and 7.0 mm wide. Other widths produced responses intermediate between those shown here. Response areas were measured as in Fig. 1 (see METHODS). Mean response rate for each afferent was measured as the total number of impulses within the response area divided by the total scanning time within that area. Normalized mean impulse rates for individual afferent responses to the raised squares, 4.0 mm wide, are shown to illustrate the variation between afferents. Normalization for each afferent fiber was achieved by dividing the mean response rate evoked by each square by the fiber’s mean rate for all four 4.0 mm wide raised squares. Population rate was calculated as the product of the mean response area, mean impulse rate, and innervation density (1.2 afferents/mm² for SAI, 1.5 for RA; Darian-Smith and Kenins 1980).

Pulse rates are ambiguous cues since they are affected strongly by both pattern height and width.

Height and width have independent effects on mean impulse rate

Analysis of the effects of pattern height and width on mean impulse rate revealed that changes in pattern height and width had completely independent effects; that is, the SAI and RA mean impulse rates, illustrated in Figs. 5 and 6, can be separated into multiplicative height and width effects with no detectable interaction. The mean rates of both SAI and RA afferents can be expressed as the product of three terms—one for the rate at one combination of height and width (the reference stimulus), one for the effect of changing height, and one for the effect of changing width:

mean impulse rate = reference rate · height effect · width effect

The smallest raised square, 0.28 mm high and 0.2 mm wide, that evoked mean impulses rates of 155.2 and 113.4 ips in SAI and RA afferents, respectively, was adopted as the reference stimulus. The independent height and width effects are listed in Table 1 and displayed in Fig. 7.

Those data show that the effects of height on SAI impulse rates were about four times greater than on RA rates; for example, squares 0.62 mm high evoked SAI impulse rates that were, on average, 44% greater (1.440 times) than

FIG. 6. Mean response area, mean impulse rate, and population impulse rate versus square width. Format is the same as in Fig. 5.

FIG. 7. Height and width effects on mean impulse rate. Pattern height and width had independent, multiplicative effects on the mean impulse rate (see text). Points in the left graph represent the normalized mean impulse rates evoked by raised squares, 0.2 mm wide (±SE). Points in the right graph represent the effect of pattern width on the mean impulse rate. Mean impulse rate evoked by any combination of pattern width and height is given by the product of the height and width effects. The dashed lines represent the model values.
TABLE 1.  *Effects of height and width on impulse rate*

<table>
<thead>
<tr>
<th>Effect of Height Relative to a Pattern</th>
<th>Reference Rate, ips</th>
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<tbody>
<tr>
<td>0.28 mm high</td>
<td>0.37</td>
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<tr>
<td>SAI rate</td>
<td>1.000</td>
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<tr>
<td>RA rate</td>
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<thead>
<tr>
<th>Effect of Width Relative to a Pattern</th>
<th>0.2 mm wide</th>
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<tbody>
<tr>
<td>SAI rate</td>
<td>1.000</td>
</tr>
<tr>
<td>RA rate</td>
<td>1.000</td>
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Height and width have independent effects; mean impulse rate = reference rate \times height effect \times width effect. SAI, slowly adapting type I; RA, rapidly adapting; ips, impulse per second. *Not significantly different from 1.0 \( P > 0.05 \).

squares 0.28 mm high, whereas RA impulse rates were only 9.7% greater. The effects of height on both SAI and RA impulse rates were highly significant \( P < 0.001 \), analysis of variance on the logarithm of mean rate). The standard errors of the SAI height effects were all close to 0.011. The standard errors of the RA height effects were all close to 0.013. The width effects, listed in the lower half of Table 1, were highly significant for SAI afferents \( P < 0.001 \) but not RA afferents \( P = 0.15 \). The standard errors of the SAI width effects were all close to 0.01.

The correlations between predicted impulse rates based on the assumption of independence and actual rates (see Table 1) were 0.997 and 0.826 for SAI and RA rates, respectively. The difference in correlation values is not because the RA impulse rates were predicted less accurately than the SAI rates, but rather because the range of impulse rates being predicted was so much smaller (RA range: 109–127 ips; SAI range: 124–226 ips). The standard deviations of differences between predicted and actual rates were 2.05 and 2.12 ips for the SAI and RA data, respectively; for example, the mean SAI rate evoked by the square 0.47 mm high and 4.0 mm high was 166.5 ips, whereas the predicted rate was 168.3 ips \( (155.2 \times 1.296 \times 0.837) \). The differences between predicted and actual mean rates are so small that there is little room for interactive effects. Indeed, neither inspection of these differences nor regressions of the differences on height and width revealed any systematic deviation from independence.

The curves of impulse rate versus pattern height (Figs. 5 and 7) have only a slight negative curvature, suggesting a near linear relationship between impulse rate and pattern height. However, if the curves are extrapolated to the ordinate, they predict high discharge rates for smooth surfaces; this is not consistent with the observed rates. The smooth parts of the surfaces evoked minimal discharge (see Figs. 1, 2, 10, and 13); this suggests that if surfaces with heights <0.28 mm had been used, the relationship between mean firing rate and pattern height would have been much steeper in the region between 0 and 0.28 mm height, and the overall result would be a highly nonlinear relationship between pattern height and impulse rate in both SAI and RA afferents.

**Responses to corners**

SAI afferents responded more vigorously to the corners than to the central sections of the rising and falling edges, producing impulse rates near the corners that were 20–50% greater than at the middle sections of the rising and falling edges. The RA afferent responses were less sensitive to corners; their impulse rates near the corners were, on average, within 10% of the rates at the middle sections of the rising and falling edges. Profiles of the mean SAI and RA afferent impulse rates in a cross-sectional view of firing rates parallel to the rising and falling edges of the 7.0 mm squares, 280 and 620 μm high, are shown in Fig. 9. There was a 10% elevation in mean RA firing rates at the leading corners of the 620 μm high square (Fig. 9, top right) but also a small drop in mean firing rates at the trailing corners. The mean
this elevation may be due more to the summation of the effects of leading and trailing edges than to the corners.

These elevated peak rates at small pattern widths are reflected in elevated SAI but not RA mean rates (see Fig. 6). The mean SAI rates evoked by the patterns 0.2 and 0.8 mm wide are, on average, 27% higher than the mean rates evoked by the patterns 7.0 mm wide, and the difference is highly significant. The RA rates are, on average, 4% higher but the difference is not significant at any height. The explanation for the increased mean SAI rates as the patterns narrow is that the corner responses become a progressively larger part of the total discharge. The reason that the mean rate increases by a smaller amount (27%) than the peak rate (65%) as the patterns narrow from 7.0 to 0.2 mm is that the neural activity is spread more widely around the features of the narrower stimuli (see APPENDIX). This effect accounts as well for the nearly complete lack of any effect of pattern width on RA mean rate: the 33% increase in peak RA rate associated with the narrow patterns is offset by a comparable growth in the spread of neural activity around the stimulus.

Receptive field areas

Receptive field areas have been measured frequently with punctate stimuli (Johnson and Lamb 1981; Phillips et al. 1992; Talbot et al. 1968) but not with complex stimuli of the kind used here. A complication associated with the analysis of cutaneous mechanoreceptors is that receptive field size depends on the stimulus and its intensity. The data presented so far show that RA receptive fields are larger than SAI fields, that both depend on stimulus height, and that both are smaller at falling than at leading edges (by 30%). Because SAI and RA impulse rates evoked by the edges parallel to the scanning direction were <10% of the peak rate, the response area was determined exclusively by the responses to the leading and trailing edges. Consequently, we modeled the response areas as convolutions of a circular receptive

![Fig. 8. Leading and trailing responses to raised squares 7.0 mm wide in 12 SAI and 12 RA afferents. Abscissa and ordinate in each graph represent the total number of action potentials evoked by the rising and falling edges summed over all scans. \( + \), sample means.](image)

![Fig. 9. Leading and trailing peak edge responses to raised squares 7.0 mm wide. Profiles illustrated here were obtained by selecting a vertical slice 1 mm wide around the peak leading and trailing rates in each SEP and averaging the rates at each vertical location. Top: responses shown to squares 620 \( \mu \)m high. Bottom: responses shown to squares 280 \( \mu \)m in height. Responses to the squares 370 and 470 \( \mu \)m high were intermediate between those illustrated here and were omitted for clarity.](image)
field with the leading and trailing edges (see APPENDIX). The field diameter was adjusted to fit the data at each height and was reduced by 30% at the trailing edge to account for the observation that the spread of activity at the trailing edge was 30% less than at the leading edge. Table 2 shows the receptive field diameters and areas that account most effectively for the observed response areas. The modeling results show that response area is predicted accurately by such an analysis, that both SAI and RA receptive field areas depend strongly on pattern height, and that RA receptive field areas are about twice as large as SAI field areas. Analysis of the responses to the smaller raised squares showed that when the response areas produced by the leading and trailing edges overlap, there is only partial (50%) summation of the two response areas, which accounts for the nonlinearity at the lower left of the curves relating response area to pattern width in Fig. 6.

Responses to depressed squares
The second stimulus set, illustrated along with the responses of typical SAI and RA afferents in Fig. 10, consisted of depressed squares that varied in width. The responses of SAI and RA afferents to the wider squares were similar to their responses to the wider raised squares (cf. Figs. 3 and 10, also Figs. 4 and 12). The afferents responded primarily to the leading and trailing edges, producing population responses that outlined the depressed patterns. However, the quantitative details were quite different. The responses evoked by the depressed patterns were less intense, and the more intense response occurred at the trailing rather than the leading edge. Another major difference in the responses of SAI and RA afferents to the two pattern types lay in their responses to the corners. In the responses to depressed squares, the discharge rates at the corners were decreased relative to the rates at the leading and trailing edges. Also, both SAI and RA afferents responded more vigorously to the edges that run parallel with the scanning direction than to the similar edges in the raised patterns. Other differences, evident in Figs. 3 and 10, are that RA afferents and to a lesser degree SAI afferents tended to fire in the middle of the depressed patterns, which increased the pattern width required for complete separation of the leading and trailing responses.

The quantitative effects of changes in pattern width are
SAI AND RA RESPONSES TO RAISED AND DEPRESSED PATTERNS

The outlines of the depression. A major difference between the responses to raised and depressed squares was that the SAIs responded more vigorously to the edges running parallel to the scanning direction in the depressed patterns, thus providing a more complete image of the pattern (cf. Figs. 4 and 12).

Effects of a raised surround

The third stimulus set, illustrated in Fig. 13, comprised 0.4 mm wide squares, 620 μm high, surrounded by plateaus, also 620 μm high, at distances of 3.0–7.0 mm from the center of the raised square. Typical SAI and RA responses are displayed in Fig. 13. The responses to the circular depressions were like the responses to square depressions; both afferent types responded to the trailing, rising edge more vigorously than the leading, falling edge, and the RAs tended to respond in the center of the depression whereas the SAIs did not. Also, both SAI and RA afferents, but particularly SAI afferents, provided a clear neural image of the entire depressed pattern, including the edges parallel to the scanning direction.

Raised surrounds at distances of 3–6 mm had larger depressive effects on the SAI than on the RA responses. The threshold for the effect on SAIs was ~6 mm (see Fig. 14). At distances >6 mm the response to the raised square was as vigorous (244 ips) as when there was no surround. The comparable threshold for RAs was ~5 mm. At 3 mm, the SAI impulse rate evoked by the raised square declined by 50%, from 244 to 121 ips, and the RA impulse rate declined by ~30%, from 167 to 115 ips. Earlier, it was shown that the minimum depression widths registered by SAI and RA afferents were ~0.8 and 0.2 mm. Thus the response rates shown in Fig. 14 should drop to zero at surround radii of 1.2 and 0.6 mm for SAIs and RA afferents. Note that the SAI and RA rates in Fig. 14 are closer to peak rates (see METHODS).
FIG. 13. SAI and RA responses to a raised square with a raised circular surround. Squares, 0.4 mm wide and 620 μm high, were surrounded by raised plateaus, also 620 μm high. A: black areas represent raised parts of the pattern. B: SEPs for typical SAI and RA afferents and the mean rate profile over all afferents of each type for the sweep where the center of each square passed over the afferent’s point of maximum sensitivity.

Effects of edge orientation

The responses evoked by the leading and trailing edges of the raised surrounds illustrated in Fig. 13 clearly are related to the orientations of the edges relative to the scanning direction. This effect was analyzed by removing the response to the central, small square and counting action potentials in 30° segments around the response to the rising and falling edges. The result is shown in Fig. 15 together with a rectified sine wave with a constant offset. The result suggests that both SAI and RA responses are proportional to the sine of the angle between the edge and the scanning direction. The main lack of fit, which applies more to the RA than the SAI responses, is a reduction of the measured responses at 90° and 270° relative to the predicted responses. The reason appears to be that during the few scans where the small raised squares pass over the center of the receptive field, the RA response is depressed. Otherwise, the responses to the trailing, rising edge (90°) would have been larger than to the leading, falling edge (270°) as in the responses to the depressed squares illustrated in Fig. 10.

DISCUSSION

The responses of SAI and RA afferents to raised and depressed patterns were studied. Many of the details of the responses of the SAI and RA afferents to raised and depressed patterns were similar. They show that both afferent types responded strongly to the rising and falling edges of both raised and depressed patterns and neither responded to the flat central portions of the scanned, raised patterns. Both responded to edges running parallel to the scanning direction much less vigorously than to edges that are orthogonal to the scanning direction. The responses to rising and falling edges were approximated closely by the sine of their orientation relative to the scanning direction. The result of these response properties is an intense neural image in both the SAI and RA population responses that tracks the stimulus pattern and highlights spatial details.

However, there were significant differences in the responses of the two afferent fiber types that are consistent with the hypothesis that the SAI afferents are specialized for the transmission of spatial information, whereas the RA afferents are specialized for the detection of stimuli that produce minute skin movement (Johnson and Hsiao 1992). The most striking difference was the effect of pattern height. The primary effect of increasing pattern height on the SAI neural image was to intensify it by increasing the firing rates of individual afferents. The effect on the RA neural image mainly was to increase the spread of neural activity, thus

FIG. 14. Impulse rate vs. distance to a raised circular surround (see Fig. 13). Abscissa in each graph represents the radius of the raised surround. Top: ordinates represent the mean impulse rate measured in a circle, 2 mm in diameter, centered over the response to the raised square. Bottom: ordinates represent the response rates of individual neurons normalized with respect to the mean response to all the patterns with a surround.
The stimuli employed here produce complex patterns of skin deformation, and some discussion of terminology is required. Surface curvature is multidimensional and typically has an infinite number of values at a single point on a surface (Hilbert and Cohn-Vossen 1952), one for each plane passing through the point. Once the plane is defined, curvature at a point is defined by the circle best fitting the line of intersection between the surface and the plane (more precisely, it is the circle with the same rate of change of direction at that point). The center of curvature is the center of the circle, and curvature is defined as the reciprocal of the radius. We will refer to curvature in the plane of the skin as horizontal curvature and curvature in planes orthogonal to the skin as vertical curvature. We will refer to stimulus curvature whose center lies toward the interior of the stimulus as stimulus convexity and skin curvature whose center lies beneath the skin as skin convexity. Also, when a surface contacts the skin, two profiles of surface curvature are important—the profile of the stimulus where it contacts the skin, which we will call the contact profile, and the skin profile where it leaves the stimulus, which we will call the free skin profile. In regions of contact, the skin profile and the contact profile are, of course, the same. In regions where the skin is free of the stimulus, the stimulus profile is irrelevant but not the skin profile. The total skin profile is the contact profile plus the free profile.

**Rising and falling edges**

The study reported here complements one by LaMotte and Srinivasan (1987a,b), who scanned rising and falling edges over the receptive fields of SAI and RA afferents. Both studies controlled force rather than displacement and used similar contact forces (20 and 30 g). LaMotte and Srinivasan varied scanning velocity and edge slope, whereas we varied pattern height and width. Where our stimulus conditions and theirs overlap, the results are nearly identical. The only significant difference is that they observed low SAI firing rates on completely flat surfaces, and we did not. This difference is likely explained by the longer interstimulus interval in their study relative to ours (2 vs. 0.175 s).

Although the SAI and RA afferents responded in a similar way to the patterns presented in this study, it seems clear from previous studies that the mechanisms underlying those responses were different. Those studies provide no single mechanism to account for the robust response of both afferent types to the trailing, falling edges. The withdrawal of indentation at the falling edge can account for the RA but not the SAI responses because only the RA afferents respond during withdrawal (Knibestol 1973; Pubols 1980; Talbot et al. 1968). Conversely, sensitivity to edges accounts well for the robust SAI responses but not the RA responses (LaMotte and Srinivasan 1987b; Phillips and Johnson 1981a). However, one study that used vibratory stimuli found that RAs respond more vigorously near an edge than under a flat surface but that the ratio was less than for SAI afferents (Johansson et al. 1982). All these facts suggest that the RA responses to rising and falling edges are due mainly to the dynamic vertical displacement produced by edges rather than the local curvature, whereas the SAI responses are due mainly to the skin curvature produced by edges.
The difference in discharge rates between the rising and falling edges, which averaged 25% for both afferent types in our study, has several possible explanations. The intense burst of impulses at the rising edge a few tens of milliseconds earlier could account for the reduced response (Werner and Mountcastle 1968). That must have been a factor, however, if that was the main cause the impulse rates evoked by the trailing, rising edges of the depressed patterns would have been lower than those evoked by the leading, falling edges, but they were not (cf. Figs. 4 and 12). Moreover, although LaMotte and Srinivasan (1987a) allowed 2 s between stimulus presentations, their results and ours are nearly identical.

A more likely explanation is that skin displacement rates and reaction forces were higher at the rising than at the falling edges. The forces driving the cutaneous and subcutaneous displacements are completely different at the rising and falling edges. At rising edges, the skin is driven down by the mass of the advancing edge. At falling edges, skin displacement is driven back up by the skin’s hydraulic and elastic reaction forces. Although this is the more likely explanation for the difference in responses at the two edges, it does not explain the large variation between afferents (see Fig. 8), for which we have no explanation. Studies of on-and off-responses in RA afferents (Knibestål 1973; Pubols 1980; Talbot et al. 1968) and of the sensitivity of SAI responses to edges relative to flat surfaces (Phillips and Johnson 1981a) have noted similar wide variation in response properties.

Corner responses

A striking finding is that SAI afferents are even more sensitive to corners than edges. Previous studies (Goodwin et al. 1995; Johansson et al. 1982; LaMotte et al. 1996; Phillips and Johnson 1981b; Srinivasan and LaMotte 1987; Vierck 1979) have shown that SAI afferents are sensitive to convex, vertical stimulus curvature. This study shows that SAI afferents are also sensitive to horizontal stimulus curvature. Taken together, the results suggest that SAI afferents are sensitive to stimulus curvature in all directions.

Our present understanding of the biomechanical principals that underlie the response properties of SAI and RA afferents are sufficient to explain difference in their sensitivity to corners. SAI afferents are ≈20 times more sensitive to dynamic vertical indentation at an edge or region of vertical stimulus curvature than at the center of a flat stimulus, whereas RA afferents are relatively insensitive to displacement near an edge (Goodwin et al. 1995; Phillips and Johnson 1981a; Srinivasan and LaMotte 1987; Vierck 1979). The difference can be accounted for by differences in transduction mechanisms. Two studies (Phillips and Johnson 1981b; Srinivasan and LaMotte 1991) have shown that SAI impulse rates are correlated highly with strain components due to shear stresses that occur at regions of high curvature. Those studies also have shown that RA impulse rates are correlated with a different strain component that is sensitive to local vertical deformation but is less sensitive to the stresses produced by curvature.

The greatly increased stress at an external corner can be appreciated by considering the loads borne by surface elements at different locations within the stimulus contact pro-
skin rises and falls at a constant angle around a raised pattern with steep sides, the expected effect is a constant discharge rate that is independent of pattern height. That is consistent with LaMotte and Srinivasan’s data (1987b), which showed that the RA burst rate at the rising edge of their stimulus was predicted closely by the product of the edge slope and scanning velocity until the edge slope exceeded 25–30°. Steeper edge slopes produced only small increases in firing rates, suggesting that the skin was not conforming to those surfaces but was rising free of the surface at a constant angle near 25–30°.

SAI afferents respond to both indentation velocity and depth (Pubols and Pubols 1976). Consequently, the prediction of the hypothesis that the skin rose and fell at a constant angle would be that SAI mean impulse rates would contain two components— one constant and one proportional to pattern height. In fact, that description fits the relationship between mean SAI impulse rate and pattern height well (see Fig. 5).

Another prediction of this hypothesis concerns the spread of neural activity. The angle where the skin breaks free from the deforming surface, its conformal limit, determines not just the maximum indentation velocity produced by a scanning stimulus but also the spread of deformation. If the skin sloped away at a constant angle of 25–30° from the rising edge of the advancing, raised pattern, as suggested by the LaMotte and Srinivasan study (1987b), the spread of deformation would be about twice the pattern height. In fact, an increase in stimulus height of 0.34 mm (0.26–0.62 mm) yielded an increase in RA response width of 0.77 mm (see Table 2), which corresponds to a ramp angle of 24°. The skin would not, of course, rise as a perfect linear ramp (LaMotte and Srinivasan 1987a; Phillips and Johnson 1981a; Srinivasan 1989) but would exhibit some curvature that would translate to increasing deformation velocity with increasing pattern height. In fact, the RA response rate did rise modestly with increasing pattern height.

Depressed patterns

SAI and RA responses to depressed patterns were, in some respects, like their responses to raised patterns. Both afferent types responded vigorously to the rising and falling edges of the wider depressed patterns and both, especially the SAI afferents, represented the boundaries clearly. In some cases, the overall impulses rates were very similar to the overall rates evoked by the raised squares. For example, the raised square, 7 mm wide and 280 μm high, evoked SAI and RA responses whose total rates and response areas were almost identical to those evoked by the depressed square, 7 mm wide and 620 μm deep.

Although some raised and some depressed squares were matched closely for responses rates and areas and the population responses were qualitatively similar (cf. Figs. 4 and 12), the percepts evoked by the raised and depressed patterns were clearly different. These differences must have been based on the quantitative differences between the responses evoked by the two pattern types. Both afferent types responded more vigorously to the trailing than the leading edges of the depressed patterns, both responded more vigorously to the edge of the depressed pattern running parallel to the scanning direction than to the same edge in the comparable raised pattern, and the SAI afferents responded less vigorously to the corners than to the leading and trailing edges. These differences must account for the different percepts produced by raised and depressed patterns that evoke similar total impulse rates.

At smaller square widths, the neural responses to raised and depressed squares were very different. As the patterns narrowed, the response rates evoked by the raised patterns rose rapidly whereas the responses rates evoked by the depressed patterns fell rapidly. The RAs were much more sensitive to the narrowest depressions than were the SAs. The depression 0.8 mm wide in this study can be perceived by tactile scanning, and it is clear from the neural responses that this must be due to activity in RA afferents or possibly PC afferents. This conclusion is consistent with previous studies of the neural mechanisms underlying the detection of patterns with very low relief (LaMotte and Whitehouse 1986; Srinivasan et al. 1990).

The main differences between the responses of SAI and RA afferents to raised and depressed patterns are accounted for by two main differences in the mechanical interactions between skin and the raised and depressed patterns. First, as discussed earlier, interior corners produce much lower stress and strain levels than do external corners. More important is that even though the average application force (30 g) was the same for both raised and depressed patterns, the instantaneous forces deforming the skin would have been very different. Because the drum assembly is relatively massive and has built-in damping mechanisms (Johnson and Phillips 1988), which resist rapid movements of the entire assembly, the assembly would produce whatever force was required to drive the skin down and around the advancing raised pattern. The force driving the skin into the depressed pattern is, by contrast, only the skin’s reaction force to the flat surface, which was ~0.6 g/cm² (30 g force distributed over 50-60 square mm of skin). These differences account for the generally lower impulse rates evoked by the depressed patterns, but they also account for the higher impulse rates along the depressed edges running parallel to the scanning direction.

A problem with this study is that we should have varied force when applying the depressed patterns. Force has been shown to have little effect on responses to patterns raised above a flat background (Johnson and Lamb 1981). The reason is that once sufficient force is exerted to force the skin around the raised object and onto the flat background, additional force causes little additional deformation around the raised object. Additional force clearly causes increased stress (pressure) but not strain (deformation) because, in incompressible tissues, strain depends on stress gradients not stress per se. Thus the responses of mechanoreceptive afferents are sensitive to the height of a raised, rigid object but are much less sensitive to the application force (Johnson and Lamb 1981). A similar consideration of the interaction between the skin and a depressed pattern suggests a complete reversal of the roles of force and displacement. When the pattern is depressed, the only force driving the skin into the depression is the pressure in the subcutaneous tissues, which is proportional to the application force. Thus the skin deformation and the neural response evoked by a depressed pattern is almost certainly sensitive to the force of application.
but not the depth of the pattern unless that depth is slight and the skin is supported by the bottom of the depression.

Circular surround

The SAI and RA responses to a small raised square with a circular surround were consistent with their responses to the raised and depressed squares. When the surround was >6 mm distant, the SAI and RA responses to the small raised square were similar to their responses to the same isolated raised square. At the smaller surround radii where skin conformation to the depression rather than the raised central element became the determining factor, the RA afferents were more responsive than the SAIIs. The distance where the surround first began to affect the response to the central element, ~6.0 mm, is similar to the center-to-center distance where responses to single dots first began to decline in a study of the responses of human primary afferents to an array of equally spaced dots (Phillips et al. 1992).

APPENDIX

The data (see Figs. 4 and 6) suggest that SAI and RA afferents have receptive fields with functional radii that depend on the stimulus height and edge orientation. The functional receptive field radius is defined here as the maximum distance at which a particular stimulus evokes a response. The data show that the total activity at the trailing edge is less than at the leading edge and that it evokes activity over a distance that is 70% of the distance at the leading edge. So, we assumed that the functional radius at the trailing edge was 70% of the function radius at the leading edge. We ignored the responses to the edges running parallel to the scanning direction because they contributed <1% of the total discharge for SAI and RA responses to the squares 5.5 and 7.0 mm wide. These assumptions lead to the response model illustrated in Fig. A1. For squares with widths >4.0 mm where there is no overlap between the leading and trailing response areas, this leads to the prediction that total area = leading area + trailing area; leading area = 2 • r • w + π • r²; and trailing area = 2 • (0.7 • r) • w + π • (0.7 • r)² where w represents the stimulus pattern width (0.2–7.0 mm) and r represents the functional radius of the receptive field, which varies with stimulus height. This results in a linear relationship between pattern width and total response area.

For any single stimulus height, which fits the observed response areas (Fig. 6) closely for pattern widths of ≈4.0 mm. However, at smaller pattern widths, this formulation counts the overlapping leading and trailing response areas twice; this results in an overestimate of the total response area. If the overlapping area is counted only once (complete occlusion), the formulation underestimates the observed response areas. The over- and underestimate produced by assumptions of no occlusion and complete occlusion were almost exactly the same, suggesting that there was ~50% occlusion. So the model accounting for response area was formulated as total area = leading area + trailing area – k • overlapping area where k represents the degree of occlusion. The two variables, r and k, were adjusted by nonlinear regression (SPSS) to fit the relationship between response area and pattern width at each pattern height. Since the occlusion parameter was not significantly different from 0.5 in any of the regressions (at 4 pattern heights for each of the afferent types), the occlusion parameter was fixed at 0.5. Since the corners evoke different response rates than the leading and trailing edges, at least in the SAI afferents, they are clearly different stimuli and may require different functional radii. However, when the response radius associated with the corners was treated as a separate variable, it did not improve the fit significantly and was never significantly different from the functional radius for the leading and trailing edges. So the model was reduced to one with a single variable at each pattern height: the functional radius of the receptive field.

The estimated receptive field diameters (twice the estimated radii), their standard errors, the correlation between predicted and observed areas, and the standard deviations of the differences between predicted and observed areas are listed in Table 2. The overall standard errors of prediction for this model with just one estimated parameter at each height rose insignificantly from 0.427 to 0.448 mm² for the SAI response areas and from 1.084 to 1.107 mm² for the RA response areas relative to the predictions with separate parameters for corner radii and occlusion.

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