INTRODUCTION

Stimulation of different sites on the body surface evokes responses at different loci in somatosensory nuclei (somatotopic organization). Therefore, stimulus locations and geometries must be reproduced to some extent by the spatial patterns of responding neurons, providing a spatial representation of stimuli. Reciprocally, the locations of responding neurons should be an adequate indication of the location of the stimulus (place code). In principle, spatial relations between or within stimuli may be sufficiently well preserved in this representation that discriminations can be performed by looking for features of the stimulus pattern in the central representation (feature preservation). Under this scheme, for example, size (area) of stimulus may be reflected in size of representation (number of responding neurons) and two-point discrimination could be mediated by detecting separate peaks of neural activity separated by an area with less activity. We wish to determine the degree to which this assumption is tenable for the spinal dorsal horn. To examine place coding in the dorsal horn, we have chosen to model the spatial pattern of responses to simple stimuli, as predicted by the excitatory low-threshold receptive fields (RFs) of cells in dorsal horn laminae III and IV. These cells receive almost exclusively input from low-threshold cutaneous mechanoreceptors (e.g., Brown et al. 1977, 1978; Vierck 1973, 1977). We would like to be able to use a small sample, e.g., 500 neurons, as a basis for modeling the representations of stimuli by the entire population. These modeled representations then can be used to predict localization, size, and two-point discrimination on the basis of various putative discrimination mechanisms acting on them. First, we have approximated RFs of observed cells as ellipses, which can be described with five parameters. In a second stage, these five parameters were described as mean and variance surfaces in the RC, ML plane according to the locations of the cells, so that the entire population of ~122,000 cell RFs (Wang et al. 1997) could be simulated according to their locations in the plane. The following measures of goodness of fit of the model were obtained: fractional overlaps of best-fitting ellipses and real RFs; spatial correlations of the segmental representations of sampled and simulated cells; fractional overlaps of the RFs of observed cells and cells simulated at the same RC, ML locations; and spatial correlations of geometric properties (area and length/width ratio) of the RFs of simulated and observed cells as a function of their RF locations on the hindlimb.

In this preliminary investigation, only the place coding capacity of the dorsal horn was examined. It was not the purpose of this research to determine the roles of discharge patterns (e.g., action potential patterns elicited during movement of a stimulus across the skin), or variations in discharge rate elicited by stimuli impinging on different portions of cells’ RFs. We have simulated representations of stimuli with varying location, size, and two-point separation to determine whether the dorsal horn spatial representations of the stimuli reflect these three stimulus properties. A preliminary report of these results has been published in abstract form (Brown et al. 1996).
METHODS

Combining data across animals

It is not possible, using present techniques, for us to characterize the RFs and reconstruct recording sites of 500 neurons in one animal. Therefore single-unit data must be combined across animals. One requirement for combining data across animals is the need to compensate for random rostral and caudal shifts of the map due to random RC shifts of dorsal root dermatomes. To compensate for these shifts, we have devised a method of shifting data from individual animals relative to the aggregate of data across animals, for best fit of each animal’s RF locations (D, distance of RF center from tips of toes) as a function of RC and ML cell locations (Koerber and Brown 1995; Koerber et al. 1993; Wang et al. 1997). Such shifting procedures require enough cells in each animal to obtain a goodness-of-fit measure [root mean square deviation of D (RC, ML) in an individual animal relative to the model surface for all animals combined]. We have chosen as a rule of thumb at least six cells with characterized RFs and reconstructed recording sites per animal. Using these criteria, 356 cells were available from previous studies (Koerber and Brown 1995; Koerber et al. 1993; Wang et al. 1998).

Single-unit recording

Additional cells were recorded from adult cats of either sex, anesthetized with 0.3 mg/kg ketamine and 0.025 mg/kg xylazine or with 0.17 mg/kg telazol (Fort Dodge Laboratories). This was replaced with ≤30 mg/kg alpha chloralose as the original anesthetic wore off. In later animals, we maintained cardiac function with 0.05 mg/kg glycypyrrolate im every 3 h to counteract the cardiodepressor effects of the drugs used for induction. The fur of the hindlimb was clipped to a length of ~1 mm. Intubations of trachea, internal carotid artery, and jugular vein were used for artificial respiration and expired CO2 monitoring, blood pressure measurement, and the administration of drugs, respectively. Expired CO2 was maintained at 4% by controlling respirator parameters. Temperature was maintained at 38°C via rectal probe-controlled heating pad and heat lamps. The animal was mounted on a rigid frame and the lumbosacral enlargement was exposed at the bottom of a mineral oil pool. Paralysis was induced with 20 mg gallamine triethiodide (Flaxedil), maintained with 10-mg supplements every half hour. Maintenance doses of 0.1 times the initial dose of chloralose were administered intravenously every 2 h or earlier when blood pressure responded to surgical manipulations. A slow lactated Ringer drip was used to maintain fluid volume. When necessary, mean blood pressure was maintained at 90 mg Hg with slow infusions of dopamine.

Single units were recorded using stainless-steel microelectrodes in segments L4–S2 in rows of tracks spaced 200 µm apart across the width of the dorsal horn, at quarter-segment intervals. Each excitatory RF was characterized with hand-held probes, applying mechanical stimuli that barely displaced the skin, defining the perimeter of the RF to an accuracy of approximately ±1 mm. The excitatory RFs of lamina III–IV cells are defined sharply, and different investigators can obtain quantitatively repeatable measures of their sizes, shapes, and locations. The RFs were transferred to standard leg drawings using distances of borders from bony landmarks. Each RF was drawn as a planar projection with the horizontal position on the unfolded skin drawing. The ellipse center was placed at the RF geometric center. The location of the RF center on the leg was expressed as y (unfolded skin coordinate, identical to D, the distance from tips of toes), and x, the horizontal position on the unfolded skin drawing. The ellipse area A (cm²) was set equal to the RF area and the ratio of major/ minor axis was set equal to the ratio of the longest axis of the RF (longest line from 1 edge to the other, through the center) to the perpendicular axis (longest line perpendicular to the long axis, from 1 edge to the other, not necessarily through the center of the RF). The angle of orientation of the ellipse φ was equal to the angle of the long axis of the ellipse relative to the x axis of the standard skin outline. Goodness of fit was determined by placing a grid of points i, j with 0.5-mm spacing on the skin outline, and setting values within each area (original RF and elliptical approximation) equal to 1, values outside each area equal to 0. The fractional overlap f was determined as follows:

\[ f = \frac{\sum_{i} \sum_{j} R_{ij} S_{ij}}{\sum_{i} \sum_{j} R_{ij}^2 \sum_{i} S_{ij}^2} \]

where \( R_{ij} = \begin{cases} 1 : & \text{original RF covers grid point } i, j \\ 0 : & \text{original RF doesn't cover grid point } i, j \end{cases} \)

and \( S_{ij} = \begin{cases} 1 : & \text{simulated RF covers grid point } i, j \\ 0 : & \text{simulated RF doesn't cover grid point } i, j \end{cases} \)

At the end of each experiment, animals were perfused with 1 L 38°C physiological saline, followed by 2 L of 10% formalin at room temperature. Relevant segments were removed and blocked at intersegmental boundaries, and stored in 10% formalin for ≥1 wk. Frozen transverse sections were cut and mounted on subbed slides. Sections were stained with Cresyl Echt violet and Luxol fast blue (Kluver-Barrera). Electrode tracks and lesions were visualized under dark field, and the relative ML, RC, and laminar locations were determined.

Generation of the descriptive model

SHIFTING DATA. The procedure for shifting animals to eliminate interanimal variation due to pre- and postfixation has been explained in detail elsewhere (Wang et al. 1997). All the data from an animal were shifted in trial steps of 0.1 segment rostral and caudal. At each shift, the unshifted data D (RC, ML) from all animals were combined and exponential smoothing was used to obtain model D' (RC, ML) at each shifted recording site in order measure the deviation of each shifted D (RC, ML) from the model D' (RC, ML). The shift at which the root mean square deviation of D (RC, ML) from D' (RC, ML) was minimized was taken as the best shift for aligning the animal’s data with the aggregate of all animals. This process was repeated for each animal. Then all animals’ data were shifted by their best shifts, and the process of modeling and shifting was repeated until the best shifts were all zero; shifts converged to zero in no more than four iterations.

GEOMETRIC DESCRIPTION OF RFs. One objective in modeling RFs was for individual RFs to be represented by geometric figures that have a high fractional overlap with the original RFs. To model RFs as best fitting geometric figures, we chose to use ellipses, which can be described by five parameters. We chose as parameters three measures that we have used already for analysis of RFs plus two new ones. We already are using D, distance of RF center from tips of toes; A, area; and L/W, length/width ratio (e.g., Brown et al. 1975). In addition, we need another position parameter θ, the circumferential angle of RF center around the leg, and φ, the orientation of the ellipse. RFs were translated from the standard leg drawings to an unfolded skin representation of the leg, and D and θ were measured as y and x positions, respectively, on the unfolded skin drawing (Fig. 1A).

Each RF was approximated as an ellipse as follows (Fig. 1B): the ellipse center was placed at the RF geometric center. The location of the RF center on the leg was expressed as y (unfolded skin coordinate, identical to D, the distance from tips of toes), and x, the horizontal position on the unfolded skin drawing. The ellipse area A (cm²) was set equal to the RF area and the ratio of major/ minor axis was set equal to the ratio of the longest axis of the RF (longest line from 1 edge to the other, through the center) to the perpendicular axis (longest line perpendicular to the long axis, from 1 edge to the other, not necessarily through the center of the RF). The angle of orientation of the ellipse φ was equal to the angle of the long axis of the ellipse relative to the x axis of the standard skin outline. Goodness of fit was determined by placing a grid of points i, j with 0.5-mm spacing on the skin outline, and setting values within each area (original RF and elliptical approximation) equal to 1, values outside each area equal to 0. The fractional overlap f was determined as follows:
where 0° was taken as the left edge and 360° the right edge, of the skin outline at y corresponding to D, the distance of the RF center from the tips of the toes. Mean and variance θ's were computed and translated back to values of x. Clearly, it was mandatory that trends in the RC, ML plane for these variables should agree with trends already reported in the literature. Covariances among the five parameters as a function of RC, ML were not adjusted for. Although such adjustments might improve the accuracy of the model, the accuracy obtained was adequate for our purposes.

**SIMULATION OF MODEL RFs.** Using the mean and variance surfaces, it was possible to generate populations of elliptical RFs at each grid square, the number of simulated RFs at each square being equal to the number of cells estimated from cell counts of laminae III and IV (Wang et al. 1997). At each grid square, each simulated RF parameter was generated by adding the fitted mean to a random variable with variance equal to the fitted variance, for the required number of cells.

**Validation of the model**

**AGGREGATE RFs.** To test the aggregate simulated RFs against the aggregate RFs of the data sample, we compared the segmental distribution of RFs for observed and simulated populations. Different smoothing factors (space constants used to produce the five parameter surfaces) were tested to determine which gave the best match between observed and simulated segmental representations. This was done by computing spatial correlations of stacked RFs, plotted on a grid with 0.5-mm spacing on the unfolded skin. Each grid point on the grid was initialized to zero and was incremented by one for each RF that overlapped it. This is equivalent to stacking all the RFs on the skin, each RF contributing unit elevation, and counting the number of RFs stacked at each grid point. Separate stacked RFs were generated for the observed and simulated populations. The stack height at each point on the simulated and observed set of RFs then were cross-correlated.

**INDIVIDUAL RFs.** Because the representations of stimuli are dependent on adequate modeling of individual RFs, it was desirable to know how well individual RFs compared with modeled RFs at the same RC, ML locations. Values of means of the five descriptive parameters at recording sites were estimated from values at grid squares in the model, and these means were used to simulate RFs at these sites. Fractional overlap was computed using different space constants for smoothing of the parameter surfaces.

**RF GEOMETRIES AS A FUNCTION OF POSITION ON THE LEG.** As a final test of the model, we assessed the ability of the model to predict RF geometries as a function of location on the leg: Area A and length/width ratio L/W were plotted for all cells in the observed and simulated populations as a function of x and y, the RF center locations on the leg. These properties of the cell RFs were determined in the modeled cells entirely by their locations in the RC, ML plane, and there should be poor agreement if the model is not accurate. The variables A and L/W therefore were averaged at grid points on the leg corresponding to their RF centers, and values then were interpolated by exponential smoothing on the unfolded skin. Corresponding grid points obtained from the observed and simulated data then were cross-correlated in the same fashion as the stacked RFs used to compare observed and simulated segmental representations.

**Dorsal horn spatial representations of simple stimuli**

The immediate purpose of these simulations was to model the spatial representation of simple stimuli. This was accomplished by placing simulated stimuli on the unfolded skin and determining which cells' RFs overlapped the stimuli. If a grid point was overlapped by both a cell's RF and a stimulus, the cell was excited by...
Even though the 551 data points plotted in this way generate chaotic pictures, certain trends are apparent. The lowest values of $D$ (shown as $Y$), $A$, and $L/W$ are found in medial dorsal horn of segments L_6 and L_7 where the toes are represented, and $X$ varies with segmental location reflecting the shift from preaxial to postaxial skin from rostral to caudal. These trends all agree with earlier reports (e.g., Brown et al. 1975).

Surface plots of model means and variances for the five ellipse parameters are plotted as functions of RC, ML in Fig. 4, plotted using $\lambda_{RC} = 0.03$, $\lambda_{ML} = 0.01$. These were the surfaces used to simulate the RFs of dorsal horn cells. For each simulated cell, the values of the variables’ means and variances at the cell’s RC, ML locations were obtained from these surfaces.

**Validation of the model**

**SEGMENTAL REPRESENTATIONS.** Stacked RFs are illustrated in Fig. 5 for the five segments studied. In each set of four stacked representations, the segmental span of dorsal horn cells sampled is illustrated (left). In each segmental representation, the four unfolded skin outlines, going from $a$ to $d$, are observed data, least ($\lambda_{RC} = 0.03$, $\lambda_{ML} = 0.01$), intermediate ($\lambda_{RC} = 0.15$, $\lambda_{ML} = 0.05$), and greatest ($\lambda_{RC} = 0.3$, $\lambda_{ML} = 0.1$) smoothing. Fractional overlap analysis revealed that the smallest smoothing factor produced the highest fractional overlap (0.84) between observed and simulated segmental representations (Table 1). In the three greatest smoothings, the highest fractional overlap was observed when the calculated variances were used rather than 10 times or one-tenth the variances. In the least smoothing, all three variances gave essentially identical results. This indicates that covariance among the five parameters is not an important factor for our purposes. Zero $\lambda$’s would produce the best fractional overlap, perfect except for the nonelliptical shapes of original RFs and in rare instances where differing RFs were encountered at the same RC, ML location in the shifted original data.

**RESULTS**

**Single-unit recording**

Recording sites were reconstructed successfully for 195 characterized cells. These were added to the original database of 356 cells, and the optimal shifts for all animals were determined, as described in METHODS. The resulting database had 3 cells in L_3, 20 in L_4, 81 in L_5, 209 in L_6, 150 in L_7, 83 in S_1, and 5 in S_2. Because of small sample sizes in L_1 and S_2, only segments L_4–S_1 were used for modeling purposes.

**Generation of the descriptive model**

Original RFs and their fitted ellipses based on the five RF parameters are illustrated in Fig. 2, $A–C$, for the best and worst-fitting ellipses, and an ellipse the fit of which was equal to the average fit. Average fractional overlap of best fitting ellipses and original RFs was $0.90 \pm 0.092$ (SD). The distribution of fractional overlaps is illustrated in Fig. 2D.

The five parameters for all the observed cells are plotted as five sets of elevations as a function of RC, ML in Fig. 3. Even though the 551 data points plotted in this way generate chaotic pictures, certain trends are apparent. The lowest values of $D$ (shown as $Y$), $A$, and $L/W$ are found in medial dorsal horn of segments L_6 and L_7 where the toes are represented, and $X$ varies with segmental location reflecting the shift from preaxial to postaxial skin from rostral to caudal. These trends all agree with earlier reports (e.g., Brown et al. 1975).

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with their best fitting ellipses. Visual inspection reveals a very close agreement among most of the original and simulated RFs, on a cell by cell basis, although there are a few instances where original and simulated RFs do not overlap at all.

For purposes of quantitative analysis, corresponding observed and modeled RFs were compared by computation of fractional overlap. All observed and modeled cell pairs were compared, regardless of whether they were included in Fig. 6. The distribution of fractional overlaps is plotted in Fig. 7 for all the smoothing factors of Table 1 (the 2nd smallest smoothing of Fig. 7 was the 1 used to generate Fig. 6). Again, best fractional overlaps were obtained with lowest smoothing (Fig. 7A). The distribution in Fig. 7A was bimodal: the mean of the bimodal distribution is 0.64 and the higher mode peaks between 0.80 and 1.0. Small fractional overlaps were produced where there were clusters of two or more cells very close together in the original data, and their parameter values described nonoverlapping RFs. The mean locations computed from these cells produced RFs that were intermediate in location and that overlapped the original RFs poorly if at all. The peak at zero overlap consists of 116 cells or ∼21% of the total. The high fractional overlaps were found at locations where cells were relatively isolated from other cells or clustered cells had similar RFs so that the observed and simulated RFs overlapped well.

The second smallest smoothing, Fig. 7B, was the one used for Fig. 4. The peak at zero overlap consists of 174 cells or ∼26% of the total; the rest of the distribution is relatively flat, and the mean for the histogram was 0.49.

**RF GEOMETRIES AS A FUNCTION OF POSITION ON THE LEG.**

The final test of the validity of the descriptive model was perhaps the most challenging: a comparison of simulated and observed RF area and length/width ratio as a function of RF position on the skin. These relationships were not direct consequences of the model because none of the five parameters was modeled as a function of any of the others (specifically, A and L/W were not modeled as a function of D and θ). Therefore these relations are only indirectly determined by the model, in that the four parameters A, L/W, D, and θ were all modeled as functions of RC, ML.

Figure 8 illustrates A and L/W as a function of position on the leg, using pseudocolor for A and L/W. The space constant λs, for smoothing on the unfolded skin was 5 mm (10 grid points). Visual inspection indicates a high degree of similarity, which correlation analysis confirms: \( r(A) = 0.50, r(L/W) = 0.66. \)

**Spatial representation of simple stimuli**

OVERALL ORGANIZATION OF THE MAP STUDIED WITH SIMULATED STIMULATION OF BANDS OF SKIN. Figure 9 illustrates the spatial distributions of dorsal horn cells responding to simulated stimulation of bands of skin. The 4 panels in the left portion of A–D, represent the densities of responding original cells (left to right) at all grid points and the densities of modeled cells using least smoothing, intermediate, and most smoothing of Fig. 5, respectively. The band on each skin outline represents the simulated stimulus, 5 cm in proximodistal extent, with distal edges at 0, 7, 14, and 21 cm from tips of toes. Note that, as the band is moved up the leg, the pattern of responding cells moves from the toe region in medial L7 and S1 to more lateral, rostral, and caudal locations, as would be expected from previous studies (e.g., Brown and Fuchs 1975). This indicates an orderly organization of the map that is similar for original and simulated cells. Note that the representations of bands of skin consist of discontinuous clusters of responding cells (patchy representation) for the two most proximal stimuli.

As would be expected from an orderly map in which some RFs are bound to overlap more than one stimulus band, the degree of overlap between representations decreased as a function of distance between bands. However, it should be noted...
that even widely spaced bands (e.g., on toes and thigh) had some overlap of their representations, presumably because of variances in the location parameters ($D$ and $\theta$) and large RFs. The degree of spatial correlation of the different representations was calculated (Table 2). The two most similar representations, for bands 14 and 21 cm from tips of toes, have a positive correlation of 0.49. These areas have the lowest map scale and the largest RFs, so it is not surprising that they have the most similar representations. Poorly overlapping representations (e.g., 0 and 7, 7 and 14 cm) have essentially zero correlations. Representations that are roughly complementary (e.g., 0 and 14; 0 and 21) have strong negative correlations. Generally, correlations become less positive (or more negative) with increasing distance between stimuli.

**REPRESENTATION OF PUNCTATE STIMULI.** The simulation of Fig. 9 involved the use of large simulated stimuli to study overall organization of the representation of the hindlimb. It is also of interest to know the effect of stimulus location for punctate stimuli. Figure 10 illustrates the responses of dorsal horn cells to simulated $2 \times 2$ mm stimuli at 32 different locations on the leg. To accommodate 32 dorsal views in a single figure, only the intermediate smoothing of Figs. 4–7 was used. Note that, at several sites, a single point on the skin is represented by more than one cluster of responding cells. Also these constant-area stimuli clearly do not activate equivalent numbers of cells (Table 3: cells counts based on modeled cells used for dorsal views).

**REPRESENTATION OF STIMULUS SIZE.** The representations of punctate stimuli of Fig. 10 are discernibly smaller (involve fewer responding neurons) than the representations of Fig. 9, as expected from the fact that the simulated stimuli are much smaller and therefore overlap fewer RFs. To study explicitly the effect of stimulus size on representation size (number of responding neurons), the simulated stimulus area was varied at three different locations on the hindlimb over a 100-fold range, from $0.5 \times 0.5$ to $5 \times 5$ mm, and representations were...
FIG. 5. Segmental representations for each of the 5 segments. A: L_{4}; B: L_{5}; C: L_{6}; D: L_{7}; E: S_{1}. In A–E, the bar on the left represents the segment sampled; the 4 unfolded skin representations (a–d in A) are original data, least smoothing, intermediate smoothing, and most smoothing. In each unfolded skin representation, the RFs are stacked and autoscaled, and depth of stack at each point is indicated by pseudocolor (pseudocolor scale on right).
depicted on dorsal views (Fig. 11). Although there is clearly some effect of stimulus size, the representation size does not change as much as the stimulus size. This is illustrated quantitatively in Fig. 12, where it can be seen that for a 100-fold range of stimulus area, there is only a 1.6-fold range of representation size for a given site on the leg. Representation size also varies as a function of location: more dorsal horn cells respond to a given area stimulus on the distal limb than on the proximal limb. In fact, there is greater variation of representation size with stimulus placement than with stimulus area over the ranges tested.

**TABLE 1. Correlations of stacked RFs for real vs. simulated RFs**

<table>
<thead>
<tr>
<th>Lamdbas</th>
<th>ML = 0.001, RC = 0.003</th>
<th>ML = 0.010, RC = 0.001</th>
<th>ML = 0.050, RC = 0.150</th>
<th>ML = 0.0010, RC = 0.300</th>
</tr>
</thead>
<tbody>
<tr>
<td>var-wt</td>
<td>0.1</td>
<td>1</td>
<td>10</td>
<td>0.1</td>
</tr>
<tr>
<td>L4</td>
<td>0.72</td>
<td>0.73</td>
<td>0.73</td>
<td>0.60</td>
</tr>
<tr>
<td>L5</td>
<td>0.90</td>
<td>0.85</td>
<td>0.82</td>
<td>0.65</td>
</tr>
<tr>
<td>L6</td>
<td>0.87</td>
<td>0.88</td>
<td>0.87</td>
<td>0.60</td>
</tr>
<tr>
<td>L7</td>
<td>0.87</td>
<td>0.89</td>
<td>0.89</td>
<td>0.59</td>
</tr>
<tr>
<td>S1</td>
<td>0.85</td>
<td>0.87</td>
<td>0.88</td>
<td>0.76</td>
</tr>
<tr>
<td>Average</td>
<td>0.84 ± 0.07</td>
<td>0.84 ± 0.07</td>
<td>0.84 ± 0.06</td>
<td>0.64 ± 0.08</td>
</tr>
</tbody>
</table>

Spatial fractional overlaps (Pearson correlation) of segmental representations for real versus modeled data, showing variation of fractional overlap with segment, smoothing, and different multiples of observed variances. RF, receptive fields; ML, mediolateral; RC, rostrocaudal.

**FIG. 6.** Figurine drawings of a representative sample of original RFs (cyan) and simulated RFs (light brown) at the same RC, ML locations. Areas of overlap between original and simulated RFs are colored magenta. Dorsal view of left dorsal horn, segments L5–S1. Left edge, lateral edge; right edge, medial edge. Normalized RC and ML dimensions. All cells, regardless of which side they were recorded, are plotted as left side.
representation. To test this concept with regard to the dorsal horn representation, we simulated two-point stimuli on the leg and the corresponding representations (Fig. 13). Stimuli were placed on the plantar foot and posterior knee; two-point stimuli were compared with separate presentations of the two points for pairs with distoproximal and mediolateral orientations. The feature preservation hypothesis would predict different single-zone responses for the two points presented separately and a combination resulting in two discernible zones of responses when the pair is presented simultaneously. This was not the case for any of the four stimulus pairs, even though paired stimulus representations were always recognizable as composites of the representations of individual point stimuli.

The surprising conclusion is that a discrimination mechanism operating on the representations of Fig. 13 could not use a peak detecting procedure to determine whether one or two points is (are) being stimulated. Many one-point stimuli give rise to multiple zones of discharge, (e.g., medial point on foot, medial and lateral points on knee, distal point on foot, proximal and distal points on knee), and addition of a second point does not result in the addition of a new zone or fragmentation of an old response zone. In fact, two-point representations sometimes appear more continuous than single-point ones (e.g., medial + lateral vs. medial foot) or very similar to one of the single point representations (e.g., medial + lateral vs. lateral knee). We must conclude that insufficient information about the structure of the stimulus is preserved in the simulated spatial representation for such a discrimination mechanism to work.

**Discussion**

**Adequacy of the model**

For most purposes, this first-order model should be an adequate simulation of “average” dorsal horn cells’ RFs and their variation with location in the map of the hindlimb. The simple elliptical approximation of RFs is good enough, for example, so that simulations of the spatial distribution of cells responding to tactile stimuli is in good agreement with the spatial distributions based on real data. Insofar as the model is based on actual distributions of cells rather than a potentially biased distribution of sampled cells (e.g., due to surface blood vessel patterns), the simulated distributions of responding cells actually may be more realistic than that deduced directly from the sample of observed cells.

There are, however, some known sources of error that might produce artifactual results in simulations of spatial patterns of responding cells. First, not all interanimal variation has been eliminated. Ideally, the representation of an “average” animal’s map should include the average within-animal variation but should exclude interanimal variations. We have eliminated some of the interanimal variation due to pre- and postfixation by shifting data from individual animals, but we have not eliminated variation that cannot be compensated for by shifting. In principle, this could be done with appropriate analysis of variance. Our initial analysis (Koerber et al. 1993) indicates that intra-animal variation is about one-third of the total variance measured in data combined across animals, so this could have a significant effect.

Our samples of the most rostral and caudal segments with very proximal hindlimb input are not yet adequate for modeling. This deficit can be remedied by more extensive sampling in these segments. In the meantime, conclusions about the spatial patterns of cells activated by stimulation of the proximal leg only should be accepted tentatively.

Although elliptical approximations have a fractional overlap of 0.9 with the original RFs, it may be that in some applications a higher approximation is required. In
FIG. 8. \(L/W\) and \(A\) as a function of location on the leg for original and simulated cells. 

- **A**: original unsmoothed \(L/W\).
- **B**: original smoothed \(L/W\).
- **C**: simulated unsmoothed \(L/W\).
- **D**: simulated smoothed \(L/W\).
- **E**: original unsmoothed \(A\).
- **F**: original smoothed \(A\).
- **G**: simulated unsmoothed \(A\).
- **H**: simulated smoothed \(A\).

That case, additional RF descriptors will be required, such as curvature of the principal axis of the ellipse or shifting of the center of the minor axis away from the center of the major axis.

One clear source of potential error is the presence of co-variation of RF parameters. The \(L/W\), \(A\), and \(D\) tend to covary, so independent simulation of their variances could introduce more scatter in the geometries of RFs than actually exists. A covariance model would be needed to compensate for such effects.

This model does not include dynamic factors such as differences of discharge pattern (including rate) evoked by stimulating different parts of a cell’s RF, inhibitory portions of RFs, or spatial interactions. Although there is little doubt that such factors are important in spatial discriminations (e.g., Johnson and Phillips 1981; LaMotte and Srinivasan 1993; Loomis 1979; Wheat et al. 1995), our first objective is to study the adequacy of classical place coding for such discriminations. Any inadequacies in a simple place code would suggest either that other types of representation are involved or that the dorsal horn does not have an adequate representation for some discriminations.

**Multiple zones of response to single-point stimuli**

A large fraction of the single-point stimulus simulations produced multiple response zones in the dorsal horn. We do not believe that this implies multiple maps of the skin because of the orderly migration of response zones as circumferential stimuli are moved up the leg. The most obvious cause of such fractionation is the discontinuity required to represent a closed surface (the skin) on an open surface (the horizontal plane of the dorsal horn). The discontinuity appears to approximate the boundary between pre- and postaxial skin (viz., Brown et al. 1992). Individual dorsal horn cell RFs overlap the axial line, both in the pre- and postaxial portions of the skin representation. Therefore it is necessary for substantial projections of preaxial skin near the axial line into postaxial areas of the map and for some postaxial skin to project into preaxial map. This should be discernible in axonal marking studies. Although it is evident in the projections of some cutaneous nerves (Koerber and Brown 1980, 1982), there are no reports of two-part projections of individual axons (Brown et al. 1977, 1978, 1980, 1981). This may mean that the discontinuity is bridged by postsynaptic axons or axonal marking methods have not been adequate to reveal existing two-part projections.
FIG. 9. Simulated spatial distributions of responding cells activated by simulated annular stimuli applied at different distances from tips of toes. In each portion of the figure, the 4 dorsal views at the left represent densities of responding cells based on original data, least smoothing, intermediate, and greatest smoothing (left to right). Unfolded skin representation at right depicts simulated stimulus location. Each dorsal view is autoscaled to the same maximum; pseudocolor scale at right indicates range of colors from minimum to maximum.

Although the single-point stimuli that give rise to clearly separated pre- and postaxial responses are most commonly near the axial line, there are other, smaller clusters and voids in the response patterns that may be due to experimental errors in localization of cells in the dorsal horn (including recordings from dorsal horn cell axons) or RFs on the skin or that may represent real anomalies. A larger sample might reveal that such "anomalies" are more ubiquitous than these data suggest, in which case they should simply be considered part of the normal variation of somatotopy.

The multiple patches of cells activated by some small stimuli and the small changes produced by the introduction of a second punctate stimulus suggest that a literal interpretation of one model of two-point discrimination, where the

<table>
<thead>
<tr>
<th>Distances From Tips of Toes, cm</th>
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<th>7</th>
<th>14</th>
<th>21</th>
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<td>-0.62</td>
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<td>-0.53</td>
<td>-0.37</td>
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<td>1.00</td>
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Fractional overlap of dorsal horn representations of simulated stimulation of 5-cm bands of skin, corresponding to the simulations of Fig. 7.
TABLE 3.  Stimulus locations for the 32 standard stimulation sites of Fig. 12 and the numbers of responding cells using the intermediate smoothing

<table>
<thead>
<tr>
<th>Site No.</th>
<th>X_{min}</th>
<th>X_{max}</th>
<th>Y_{min}</th>
<th>Y_{max}</th>
<th>Responding Cells</th>
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<td>72</td>
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<td>82</td>
<td>84</td>
<td>7</td>
<td>9</td>
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<td>95</td>
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<tr>
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<td>103</td>
<td>105</td>
<td>9</td>
<td>11</td>
<td>4,989</td>
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<tr>
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<td>114</td>
<td>116</td>
<td>7</td>
<td>9</td>
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<td>127</td>
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<td>4,913</td>
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<td>139</td>
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<td>7</td>
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<td>143</td>
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<td>27</td>
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<td>58</td>
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<td>28</td>
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<td>162</td>
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<td>193</td>
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</table>

X_{min} and X_{max} and Y_{min} and Y_{max} are in millimeters.

CNS detects two clusters of responding cells (Mountcastle and Darian-Smith 1968), is not tenable, especially if such fragmentation exists in other somatosensory nuclei. However, the CNS still could perform two-point discriminations if a “same/different” judgment is made regarding distributions of cells responding to a one-point standard versus a two-point comparison stimulus or if a mechanism exists for construction of a central representation in which features such as numbers of stimulus points are well preserved. Thus the CNS could judge whether there is a significant difference in the distribution of responding cells engaged by one or two points: such a difference measure presumably would increase with distance between points, as the sets of cells activated by standard and comparison stimuli diverged.

Application of the model to studies of discrimination

A long-standing interest regarding the function of the dorsal horn concerns the extent to which it contributes to spatial tactile discriminations such as localization and two-point discrimination (e.g., Noordenbos and Wall 1976; Vierck 1973, 1977). This can be broken down into two questions: what is the representation of stimuli in the dorsal horn and what use is made of this representation by the nervous system in performing discriminations? We have begun to address the first question in this account so as to address the second question in later studies.

We are interested initially in studying the neural correlates of localization and two-point discrimination, two elementary discriminations that have been tested in a variety of lesioned preparations and in human (e.g., Adani et al. 1994; Brown et al. 1989; DeMaio-Feldman 1996; Fuchs and Brown 1984; Keunen and Slooff 1983; Kim and Choi-Kwon 1996; Matsen et al. 1986; McCracken 1975; Ogunro 1984; Poppen et al. 1979; Shimokata and Kuzuya 1995; Song et al. 1993; Van Boven and Johnson 1994; Wilson and Wilson 1967). It classically has been supposed that the primary representation of stimulus location and shape is the spatial pattern of neurons driven to discharge (place code). Our results indicate that the assumption that the spatial representation of even simple stimuli, however, is not necessarily a simple transformation of the stimulus pattern. It is therefore likely that we cannot perform simulated discriminations such as two-point discrimination by looking for features in the representation that mirror similar features of the stimulus, such as presence of two peaks of activity corresponding to two discrete stimulated points. However, we can ask whether there is a quantitative relation between the performance of subjects asked to make same/different judgments about two stimuli and the degree of similarity of the spatial representations evoked by the two stimuli.

Application of the first-order model to studies of development and plasticity

We have proposed a developmental model that is amenable to quantitative testing (Brown et al. 1997). Among its other features, this model postulates invariant divergence/convergence ratios for the connections of primary afferent to dorsal horn cells. Recent quantitative analyses have supported this postulate for annular rings of skin 1 cm in proximodistal length for the full length of the leg (Wang et al. 1997). In these analyses, we showed that the calculated ratio of map scale to innervation density was invariant for different D. We proposed that initial (‘‘prototype’’) RFs are formed during the initial ingrowth of peripheral axons and that these prototype RFs then are modified to some unknown extent by further ramification of afferent axons, activity-dependent competitive mechanisms, and such sculpting influences as pre- and postsynaptic inhibition. We also suggested that the map scale and geometries of prototype RFs at any level of the dorsal horn are determined by the distribution of afferent input available through axons growing into the gray matter at that level. It soon will be possible to model the prototype RF formation once we have determined afferent input densities (analogous to innervation densities) of primary axons growing in at different rostrocaudal levels.
in the adult. These prototype RFs then can be compared statistically [e.g., using the distributed $t$-test, which we recently have validated (Brown and Millecchia 1997b)] with the model developed here to determine the magnitude of changes that would be necessary to go from the predicted prototype RFs to the adult RFs.

It is striking that no strong theories of the mechanisms underlying plastic change in the dorsal horn have been established. One reason may be the lack of agreement concerning the sorts of changes that occur as result of such maneuvers as partial deafferentation, spinal transection, and spinal injury. Another may be the lack of good quantitative methods of describing changes that do occur and the absence of a model of the normal organization of the dorsal horn. Such a model now exists, and appropriate statistical methods are now available (Brown and Millecchia 1997b). The only requirement for quantitative descriptions of changes of somatotopy and dorsal horn RF geometries is a sample of perhaps 500 neurons from an appropriate animal model with at least half a dozen cells recorded from the normal side of the spinal cord in each animal to shift data into register across animals. Such quantitative descriptions are essential before we can pose testable hypotheses about changes occurring during reorganization.

**Implications for spatial discriminations based on place code**

The most startling conclusion from this simulation study is that the classical place code isn’t much good for discrimination of numbers of stimuli placed on the skin. The assumption that spatial features of the stimulus are reflected accurately in corresponding features of the representation is not correct. Localization, size (area) discrimination, and two-point discrimination all would be served poorly by a discrimination mechanism that performs feature detection on the spatial representation.

It can be argued that somatotopic organization is not re-
required for representation of the spatial features of tactile stimuli. This is verified easily by a simple thought experiment: shuffle the locations of cells in a somatotopic map without changing any of their afferent or efferent connections. Because all the cells still have the same connections, they will have the same RFs and the same projections, so their function will not be altered, in spite of the fact that their spatial organization has been changed from somatotopic to random. We have suggested, instead (Brown et al. 1991, 1997), that somatotopic organization is a remnant of developmental processes responsible for the formation of concise RFs. The results of this investigation go further by demonstrating that feature preservation in the somatotopic map of the skin is not adequate for spatial discriminations known to be subserved by the dorsal horn. It would be of great interest to know whether this is the case for other somatosensory nuclei; we are inclined to suspect that it is, given the similarities of somatotopic organization and RF geometries.

The lack of feature preservation in the spatial patterns of discharge evoked by simulated cutaneous stimuli does not, of course, preclude a role for a dorsal horn place code in spatial discriminations. The dorsal horn cell spatial patterns of discharge must contain the information necessary for higher somatosensory nuclei to perform spatial discriminations.

**FIG. 12.** Log-log plot of representation size (number of responding cells) as a function of stimulus size (area of skin contacted) for the simulations of Fig. 14. Separate curves for stimulus/response relationships for foot, calf, and thigh.

**FIG. 13.** Comparison of representations of simulated 1- and 2-point stimuli. Rows, top to bottom: plantar foot mediolateral orientation of stimulus pair; posterior knee, mediolateral orientation of stimulus pair; plantar foot, proximodistal orientation of stimulus pair; posterior knee, proximodistal orientation of stimulus pair. Columns, left to right: single stimulus, lateral or distal of pair; single stimulus, medial or proximal of pair; both stimuli combined. Each dorsal horn representation is autoscaled.
tions because cats and humans with dorsal column sections still can perform such discriminations. An alternative worth investigating is the possibility that the central representation actually used for discrimination is an aggregate of the RFs of cells activated by a stimulus, which we have called the referred representation (Brown and Millecchia 1997a).

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