Variability in Hand Surface Representations in Areas 3b and 1 in Adult Owl and Squirrel Monkeys

MICHAEL M. MERZENICH, RANDALL J. NELSON, JON H. KAAS, MICHAEL P. STREYKER, WILLIAM M. JENKINS, JOHN M. ZOOK, MAX S. CYNADER, AND AXEL SCHROPPMANN

Coleman Laboratory and Department of Otolaryngology and Physiology, University of California at San Francisco, San Francisco, California 94143; Department of Psychology, Vanderbilt University, Nashville, Tennessee 37240

ABSTRACT

Detailed microelectrode maps of the hand representation were derived in cortical areas 3b and 1 from a series of normal adult owl and squirrel monkeys. While overlap relationships were maintained, and all maps were internally topographic, many map features varied significantly when examined in detail. Variable features of the hand representations among different monkeys included: a) the overall shapes and sizes of hand surface representations; b) the actual and proportional areas of representations of different skin surfaces and the cortical magnifications of representations of specific skin surfaces, which commonly varied severalfold in area 3b and manyfold in area 1; c) the topographic relationships among skin surface representations, with skin surfaces that were represented adjacently in some monkeys represented in locations many hundreds of microns apart in others; d) the internal orderliness of representations; e) the completeness of representations of the dorsal hand surface; and f) the skin surfaces represented along the borders of the hand representation.

Owl monkey maps were, in general, internally more strictly topographic than squirrel monkey maps. In both species, area 3b was more strictly topographic and less variable than was area 1.

The degree of individual variability revealed in these experiments is difficult to reconcile with the hypothesis that details of cortical maps are ontogenetically specified during a period in early life. Instead, we propose that differences in the details of cortical map structure are the consequence of individual differences in lifelong use of the hands. This conclusion is consistent with earlier studies of the consequences of peripheral nerve transection and digital amputation, which revealed that cortical maps are dynamically maintained and are alterable as a function of use or nerve injury in these monkeys (Merzenich et al., '83a,b, '84a; Merzenich, '86; Jenkins et al., '84; Jenkins and Merzenich, '87).

Key words: monkey, hand, somatosensory representations, cortex, area 3b, area 1, representational variability

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R.J. Nelson's present address is the Department of Anatomy, University of Tennessee, Memphis, TN 38163.

J.M. Zook's present address is the Department of Zoological and Biomedical Sciences, Ohio University, Athens, OH 75501.

M.S. Cynader's present address is the Department of Psychology, Dalhousie University, Halifax, Nova Scotia.

A. Schoppmann's present address is the Abteilung Vergleichende Neurobiologie, Obereer Eselberg, Universität Ulm, 7900 Ulm, Germany.

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Penetration density and map construction

In the earliest experiments, maps of areas 3b and 1 were derived from the receptive fields defined in 150–250 penetrations into these two fields in each individual monkey. Cytoarchitectonically defined boundaries between areas 1a and 3b, 1b and 1, and 1 and 2 were determined, and were found to correspond approximately with functional borders, defined either between cortex devoted predominantly to deep-receptor and predominantly to cutaneous-receptor input (for 3a-b and 2-1) or by a reversal in the sequence of cytoarchitectonic representation (for 3b-1). In more recent studies, maps were derived in more detail. Between 250 and 450 penetrations were used to map the area 3b or area 1 hand representation. The majority of these more recent normal maps were limited to the zones of representation of the fingers in area 3b, and the borders of the area 3b representation were usually defined electrophysiologically but not cytoarchitectonically.

Data from a representative experiment are shown in Figures 1 and 2. The penetration grid is illustrated in Figure 1 (top). The sequences of receptive field centers are illustrated in Figure 1 (bottom), and many of the receptive fields for this case are shown in Figure 2. The penetration density in this map is representative of all of the owl monkey maps illustrated in this report. Squirrel monkey maps were derived at 1.2–1.8 mm thick. The construction of topographic maps from this data has been described previously (Merzenich et al., ’78, ’81; Nelson et al., ’80a). Regions with receptive fields centered on a given body part were outlined (e.g., see Fig. 1). The positions of the borders between body parts on the map are biased to reflect the relative distance of each receptive field defining the border from the boundary of the body part represented. Thus, a border between D2 and D3 is drawn closer to the penetration site yielding a receptive field on D2 when one of the receptive fields that define this border is on the extreme ulnar aspect of D2. In this case, the other is midway to the radial face of D4. All measurements of representational areas were made with a digital planimeter.

Reproducibility and accuracy of cortical maps

We have attempted in two ways to determine the adequacy of the microelectrode sampling methods used in these experiments for determination of map areas. First, the reproducibility of our receptive field determinations for a given cortical locus was evaluated. In experiments reported in the accompanying paper (Stryker et al., ’87), one part of area 3b was mapped 2 or 3 times over the course of a single day in individual monkeys. Different experimenters defined most receptive fields in at least one different map repetition in each experiment. Each of these repeated maps was made without knowledge of the previous findings. Receptive fields defined at nearly identical map locations under different conditions of anesthesia by different experimenters were closely overlapping. These results indicate that the peripheral receptive field defined for given receptive fields are relatively stable and are accurately defined, we considered the precision with which representational territories can be determined from microelectrode sampling points spaced in a grid that is coarse (usually 50–300 μm) compared to the size of cortical neurons. Mathematical analyses and com-
puter simulations demonstrated that only small errors in estimations of representational areas are likely, given sampling grids of the density used in these studies. The differences in area among the hand representations of the monkeys of this study far exceed the possible sampling errors. The maximum error in determining the area representing, for example, a particular digit can be determined from our maps by placing the border of the digit representation through all the recording sites either just within the representation (for a minimum area), or just outside the representation (for a maximum area). The true border must lie between these two extreme borders. In the digit repre-
Fig. 2. All receptive fields defined in penetrations within the 100-mm-wide "vertical zone" demarcated in Figure 1. Numbers in these drawings correspond to the vertical zone numbers in Figure 1. This typical map was limited to the area 3b hand surface representation; the most extreme proximal aspect of the palm was incompletely mapped.
sensations shown in Figure 1, those maximum and mini-
mum areas differ from the borders drawn by about 20%.
It can be shown geometrically that the maximum error
in the determination of a compact area for an evenly spaced
grid of sample sites nearly equals $2 \times 2\%$, where $n$ is the
number of sites within the representation whose area is to
be measured. This maximum error, however, would occur
only extremely rarely, as it is statistically unlikely that the
true border would lie at the same extreme position relative
to all of the points that determine it. The precision of the
area determination is measured by the standard deviation of
repeated determinations of the same true area. This area
measurement is influenced, of course, only by the points
along the perimeter of the area. The number of those perim-
eter points is proportional to area $^2$. From information the-
ory, we know that the precision of a determination based
on repeated imprecise measurements increases with the
square root of the number of measurements. Hence, the
standard deviation is proportional to (area $^2$) $^{1/2}$ or area $^{1/2}$. The
coefficient of variation, which expresses the variation as a
fraction of the mean area, is the standard deviation divided
by the mean. Hence, the coefficient of variation of area
equals $^{1/2}$ divided by area, which equals area $^{-1}$ This relation
is given by sampling theory and holds true irrespective of
whether the sampling grid is evenly spaced.

This predicted statistical distribution of measured areas
was confirmed by a Monte Carlo method. In this computer
simulation of the microelectrode mapping process, the coef-
ficient of variation of the measured area was equal to 0.064
(mean area) $^{1/2}$ ($^{2}$ $^{1/2}$ = 0.8960. In actual practice, the situa-
tion is somewhat better for two reasons: 1) the experimen-
ters sometimes biased the sampling grid for defining the
locations of interesting borders, and 2) border definitions
marked by receptive field overlap were biased at each loca-
tion to reflect the degree of that overlap. Thus, these bor-
ders are determined more precisely than they would be by the
random sampling of equivalent density assumed in the

Given the more conservative equivalent-density model,
the consequence of this degree of variability for our experi-
mental measurements of area illustrated in Figure 1 is as
follows: 1) For the digit 2 representation, consisting of 36
sites, the coefficient of variation of the area measurements
would be 4.3%, yielding 95% confidence limits that the area
as drawn was correct to within $\pm 8.4%$. 2) For the digit 3
representation, with 35 sites, the variation would be 4.4%,
giving 95% confidence limits of $\pm 9.4%$ of the measured
area. We conclude that errors in the measurement of rep-
resentational areas associated with the spacing of these
microelectrode grids are small compared to the map varia-
tions recorded in this study.

RESULTS
The major findings of this paper are drawn from inspec-
tion and measurement of the maps illustrated in Figures 3,
4, 6, and 7. The paragraphs below point out the constant

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**Fig. 3. Patterns of representation of the hand in cortical area 3B in 5
adult owl monkeys. Outlined areas are the cortical areas in which all
receptive fields examined in the skin area shown were recorded. The
border drawing at the right, Areas of representation of dorsal hand nothas
are even hatched in each drawing. The orientation and the area 1 border
was defined in the maps shown in B and D, but not in A-C.**

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and variable features of these maps, tabulate their quantitative aspects, and display the regularities in receptive field sequences that underlie these maps.

**Common features of area 3b maps of the hand among adult owl and squirrel monkeys**

Figures 3, 4, and 6 show nearly complete maps of area 3b derived in a series of adult owl and squirrel monkeys. Several features were common to all maps: a) There was a single and complete or nearly complete representation of the glabrous hand surface in area 3b. b) Tips of digits 2-4 were, with one exception, represented along the extreme rostral margin of the field. c) The digits were always represented in orderly sequence. d) An overall internal topographic order was maintained throughout the field, with very few receptive fields out of topographic sequence. e) The dorsal surfaces of digit 1 (and sometimes 2 and sometimes 3) were represented continuously in the most lateral aspect of most of those maps, as was the dorsum of digit 5 (and sometimes digits 4 and 3) in the most medial aspect. f) Dorsal skin surfaces were represented in a number of fragments, small, discontinuous patches amid a predominately glabrous digital surface representation.

**Variable features of area 3b hand maps**

Maps of hand surfaces were also highly individual with numerous variable features.

The **outlined configuration of the hand representational area**. Note the idiosyncratic shapes of the hand representational zone in area 3b in both species.

The **total cortical area of representation of the hand**. The hand representation in Figure 3E, for example, is approximately 0.6% of the area of representation of the hand in the case illustrated in 3D. In the 9 owl monkeys illustrated in Figures 3 and 4, the glabrous digits occupied from about 3.2 mm² (in 4) to about 5.1 mm² (in 5). Similarly, the hand and digital representations shown in the third squirrel monkey map in Figure 6 were only about 50–60% of the size of the representations in the first monkey illustrated.

The **overall territories of representation of different hand surfaces**. Note, for example, the differences in the area of representation of the individual digits in area 3b in different monkeys. The territory of representation of the thumb is only 0.5 mm² in owl monkey C (Fig. 5); it is 1.4 mm² in owl monkey B. The ranges of areas of digit surfaces in area 3b are indicated by thin vertical lines.

**Fig. 5. Mean area of representation of digital glabrous and dorsal skin surfaces in the nine adult owl monkeys whose maps are shown in Figures 3, 4, and 6.**
3b in both owl monkeys and squirrel monkeys, and palmar surfaces in area 3b in squirrel monkeys are indicated by the thin vertical bars in Figures 5, 8, and 10. Roughly twofold differences have been seen in comparing the cortical areas of representation of most glabrous surfaces.

Proportional areas of representation of given hand surfaces. When the digit representations of different monkeys were normalized by expressing them as a fraction of the total areas of all the 3b digit representations in each animal, strikingly different proportional differences in representation are still present. This can be appreciated by a comparison of cortical maps A, B, D, F, and H in Figures 3 and 4, which are all nearly the same overall size. The magnitude of size differences in areas of representation in this group of monkeys is nearly as great as the full range of absolute areal variation noted above. Similarly great proportional differences were seen in area 3b in squirrel monkeys. Note, for example, the large differences in territories of representation of different hand surfaces between the first and fifth or second and third monkeys' maps in Figure 6. The two in each pair are about the same overall size.

Cortical magnification of representation of different skin surfaces. Representational magnification is defined as the area of cortical territory of representation divided by that of the skin surface represented. Magnifications for all digits of owl and squirrel monkeys illustrated are summarized in Table 1. Of course variations in magnification directly reflect variations in actual cortical representational area, discussed above.

The extents of patches representing different dorsal digital surfaces, and the extents of skin surfaces represented in those patches. One of the most striking features of these maps is the idiosyncratic appearance of the small patches of cortex representing dorsal skin surfaces (cross-hatched zones in Figs. 3, 4, 6). This feature was not noted in our initial descriptions of the hand surface representation in area 3b in the owl monkey (Morrisuch et al., '78), which were based on maps derived with definition on only one-third to one-fifth the grain of present maps. We then described the relatively large, continuous dorsal hand representation along the lateral and medial margins of the hand representational zone, but missed the small but internally homogenous islands of dorsal skin representation that lie amid the larger glabrous digital skin surfaces. No such patches have ever been seen within the palmar representational zone.

These patches of digit dorum representation varied markedly in size among the different digits of the same monkey, as well as among the representations of the same digit in different monkeys. For example, note the territory of representation of dorsal digit 2 (0.400 mm²) in owl monkey 1 (Fig. 4A), as compared with the nonexistent representation of the dorum of digit 3 in the same monkey and the ninefold difference in the territory of representation of dorsal digit 1 vs dorsal digit 5 in monkey 2 (Fig. 4). Note also the wide range of variability of the territory of the dorum.

Fig. 6. Maps of the cortical representations of the hand in area 3b of 5 adult squirrel monkeys. Abbreviations as in Figure 3, hand inset. Dorsal skin representational areas are cross-hatched; the territories of representation of the glabrous surfaces of the digits are marked by diagonal lines. The area 3b-areas 1 borders were defined on an anatomical basis in all illustrated cases.
of the same digits in different monkeys, shown in Figure 5. There, about 15-fold variations in the territories of representation of dorsal digits 2–5 were evident. In the squirrel monkeys studied, these dorsal patches were even less constant, and dorsal representations for some fingers seemed to be absent.

Even in maps from monkeys in which representations of all dorsal digits were found, those representations were highly individual and never complete. Examples from several owl monkeys are shown in Figure 9. There, dotted zones illustrate the entire skin surface represented in the larger, continuous dorsal representational zones on the lateral and medial margins of the hand representation. All of the receptive fields defined in penetrations within islands of dorsal skin representation amid the glabrous digital zone are outlined. The representation of the hand dorsum in the monkey shown in B is one of the most complete seen in this series. Those shown in A and C are more typical. Note as well the marked local differences in the extents of representation of dorsal skin surfaces. Some were represented strongly, others weakly, others not at all. Note also that in some instances skin surfaces were represented both in patches and in the lateral and medial zones.

Topological neighborhood relationships in the maps. Many variants of map topology were evident. Most striking is the split representation of the glabrous thumb in owl monkeys B, D, F, H, and I (Figs. 3, 4) in comparison with the continuous representation in other cases. Discontinuities in A and I were especially striking, because intervening distances were large, and the representation of digit 2 intervened. In both cases, the more caudal zone represented only proximal phalangeal surfaces, while the more rostral zone represented distal phalangeal surfaces. Similar split glabrous surface representations were seen on digits 2 and 3 on monkeys A, G, and I and on digit 5 in F (Figs. 3, 4).
## TABLE 1A. Area 3b Owl Monkeys

<table>
<thead>
<tr>
<th>Glabrous digits</th>
<th>Hairly digits</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment No.</strong></td>
<td><strong>1</strong></td>
</tr>
<tr>
<td>A</td>
<td>.85</td>
</tr>
<tr>
<td>B</td>
<td>1.41</td>
</tr>
<tr>
<td>C</td>
<td>1.86</td>
</tr>
<tr>
<td>D</td>
<td>.86</td>
</tr>
<tr>
<td>E</td>
<td>.74</td>
</tr>
<tr>
<td>F</td>
<td>.90</td>
</tr>
<tr>
<td>G</td>
<td>.53</td>
</tr>
<tr>
<td>H</td>
<td>.71</td>
</tr>
<tr>
<td>I</td>
<td>.72</td>
</tr>
<tr>
<td>Mean</td>
<td>78</td>
</tr>
<tr>
<td>SD</td>
<td>.56</td>
</tr>
<tr>
<td>Skin surface area</td>
<td>.10</td>
</tr>
<tr>
<td>Cortical magnification</td>
<td>.78</td>
</tr>
</tbody>
</table>

1. All cortical representations area measures are in rep.3.5
2. Represented cortical area were completely mapped. These values were not included in mean.
3. No area of representations identified at this grade of mapping.
4. Mean of three normal adult monkeys. Values are off.
5. No value obtained or not measured.

### TABLE 1B. Area 3b Squirrel Monkeys

<table>
<thead>
<tr>
<th>Glabrous digits</th>
<th>Palmate digits</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment No.</strong></td>
<td><strong>1</strong></td>
</tr>
<tr>
<td>79-45</td>
<td>.53</td>
</tr>
<tr>
<td>79-30</td>
<td>.90</td>
</tr>
<tr>
<td>79-34</td>
<td>1.00</td>
</tr>
<tr>
<td>79-12</td>
<td>1.80</td>
</tr>
<tr>
<td>79-73</td>
<td>1.00</td>
</tr>
<tr>
<td>Mean</td>
<td>1.54</td>
</tr>
<tr>
<td>SD</td>
<td>.55</td>
</tr>
<tr>
<td>Skin surface area</td>
<td>.97</td>
</tr>
<tr>
<td>Cortical magnification</td>
<td>1.59</td>
</tr>
</tbody>
</table>

1. *P* > *P*<sub>50</sub> sometimes broadly covered both hands; i.e., sites of centers of recognition fields could sometimes not be resolved. In some cases, *P*<sub>50</sub> and *P*<sub>50</sub> represent homologies incompletely mapped. These values were not included in means.

### TABLE 1C. Area 1: Squirrel Monkeys

<table>
<thead>
<tr>
<th>Glabrous digits</th>
<th>Palmate digits</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment No.</strong></td>
<td><strong>1</strong></td>
</tr>
<tr>
<td>79-45</td>
<td>.17</td>
</tr>
<tr>
<td>79-30</td>
<td>.50</td>
</tr>
<tr>
<td>79-34</td>
<td>.32</td>
</tr>
<tr>
<td>79-11</td>
<td>1.24</td>
</tr>
<tr>
<td>79-73</td>
<td>.55</td>
</tr>
<tr>
<td>Mean</td>
<td>.43</td>
</tr>
<tr>
<td>SD</td>
<td>.48</td>
</tr>
<tr>
<td>Skin surface area</td>
<td>.57</td>
</tr>
<tr>
<td>Cortical magnification</td>
<td>.46</td>
</tr>
</tbody>
</table>

1. See footnote to Table 1B.

Split representations of digit 5 have also been seen in other normal monkeys that were mapped less completely.

The skin surface representations of differences between digits or digits and palm varied considerably. The base of the glabrous digit 2 representation in owl monkeys, for example, in some cases bordered a hairy surface represen-
tation of the digit (cases B, P<sub>1</sub>; or the first pad, P<sub>1</sub> (1), P<sub>2</sub> (C, D, O), P<sub>3</sub> or, more equally, P<sub>3</sub> and P<sub>1</sub> (A, E, H) (Figs. 3, 4).

Similar variability was seen in this feature in the squirrel monkey. This can be readily appreciated by scanning the posterior (in the drawing, lower) border of the digit 2 rep-
resentation in the five examples illustrated in Figure 6.
Dorsal Skin Represented
Area 3b (owl monkey)

Fig. 9. All dorsal skin surfaces represented in these relatively completely mapped hand surface representations. The dotted areas indicate the skin surfaces represented in continuous dorsal representations along the lateral and medial aspects of the hand representations. Outlined receptive fields are all fields defined in discontinuous islands of dorsal skin representation within the larger, predominantly glabrous representational zone.

The relationship of the hypobranchial and fourth palmar pads with digits 4 and 5 was highly variable and virtually idiosyncratic in both species.

A number of other examples could be cited; many such topological features, when considered in detail, varied as much.

The skin surface represented along the borders of the hand surface representation

The hand–face border. The glabrous digit 1 margin may be predominant along this border (e.g., owl monkeys B, H; or on the other extreme, not approach the border at all (A). Digit 2 may be represented along part of the border (owl monkeys B, C, G, I), or may not approach within hundreds of microns of it (A, D, E, F, H). Similarly, dorsal digit 2 representations may be along a lengthy border sector (owl monkey I; squirrel monkeys A and Ei; or be nowhere near the border (owl monkeys A, G, H; squirrel monkey D).

The area 3b–area 3a border. This border, along the rostral margin of area 3b, was occupied by representations of digit tips in most monkeys, but dorsal representations (often limited to nail bed fields) were also seen along this line (e.g., owl monkey I; squirrel monkeys, B and Ei. In a few cases (squirrel monkey A), and in several less completely mapped normal cases) palmar fields were also found along a limited sector of the rostral area 3b border.

The area 3b–area 1 border. The exact sequence of skin surfaces along the same glabrous digital border was, again, almost idiosyncratic in detail. In some monkeys, digit sur-
face representations extended down to the borders (e.g., digit 4 in owl monkey I, and several less completely mapped owl monkeys; digits 3 and/or 4 and/or 5 in the squirrel monkeys A, C, Ei. In such instances, the palmar

Fig. 10. Mean areas of representation of the palmar pads in areas 3b and 1 in five adult squirrel monkeys. Abbreviations as in the inset to Figure 3. This vertical line indicates the range of measured areas in these 5 individuals.
INTERNAL MAP ORDER

**Fig. 11.** Internal topography of hand surface maps in three intensively mapped adult owl monkeys. Lines track the centers of receptive fields recorded for all penetrations within 150-μm-wide strips across the hand representation. These strips are aligned in the sagittal plane in the drawings at the left, and in the orthogonal frontal plane in the drawings at the right.

**Fig. 12.** Internal topography of hand surface maps (continued). All skin surfaces represented in all penetrations within 150-μm-wide vertical strips crossing area 3b are indicated by the outlined and dotted areas. Fields from alternating strips are shown, that is, outlined or dotted some represent every fourth cortical strip. Drawings at the left are from rostromedially oriented hands; drawings at the right are from mediolaterally oriented hands.

representation was split, with the most ulnar aspect represented in a separate zone medial to the digital surface representation in such monkeys.

*The hand–wrist border.* Similar individual variability appeared to exist at the hand–wrist border, although this was not completely mapped in all cases of this experimental series.

Thus, nearly all details of area 3b map structure vary in individual monkeys. As will be seen below, an overall continuous internal topography is (with some exceptions) preserved, but regional territorial distributions are highly variable.

**Map variability in area 1**

Variability in area 1 maps of the hand in adult squirrel monkeys is illustrated in Figure 7. Several maps of area 1 in normal owl monkeys (not illustrated) have also been defined in approximately equal detail. As shown in Figure 8, area 1 maps were far more variable than were area 3b maps, and the variable features described for maps of area 3b applied even more emphatically to area 1 maps. For example, note the difference in the overall areas of representation of the hand between the first and third monkeys.
DIFFUSION

The basic organization of the representations of the body surface has been defined in the parietal somatotopy strip in a number of primate species (see Woolsey et al., 1962; Powell and Mountcastle, 1969; Werner and Whitehead, 1969; Pons and Pape, 1972; Paul et al., 1972; Dreyer et al., 1973; Krishnamurti et al., 1976; Merzenich et al., 1978; Sur et al., 1980, 1982; Nelson et al., 1980; Ivanms et al., 1981, 1983; Curtin and Wels, 1981; Carlson and Fitzpatrick, 1982; Fitzpatrick et al., 1982; McKenna et al., 1983). Although individual differences have been noted, none of these studies have dealt directly with map variation. Such comparisons have been difficult because, with only a few recent exceptions, these maps were derived with use of a relatively low resolution, high density, and less complete sampling grid. Further, in most mapping investigations there has been the implicit assumption that the map in one individual applies for all individuals of the same species. Commonly, data from several animals were combined within a single hemispheric or territorial outline representation. A main goal of these studies has been to produce such a composite for each studied species.

This study reveals that when maps are defined in detail, they have striking idiosyncratic features. What might be the meaning of such variation? Variation of this degree constitutes a serious challenge to some conventional views of nervous system organization. In this discussion we first review what varies and what does not vary in these maps; relate these results to those of earlier studies; consider the possible sources of current map variability; consider the implications of the partial representations that are evident for different submodal inputs and for the dorsal of digits; and finally, review the implications of observed map variability for concepts of map generation in development, and for functional cortical operations in adults.

What is constant in cortical maps?

What is variable?

When considered on a large grain, the cortical represen-
tation of the hand in areas 3b and 1, and the digits and palmar pads are represented in an orderly radial-to-ulnar lateral sequence of representations (see Figure 2). The individual digits in different species have been shown to vary considerably. However, in general, the topographic mapping of the hand in areas 3b and 1 is a highly consistent representation of the hand surface. The data from this study, as well as those from the earlier studies, indicate that the basic organization of the hand representation in the parietal somatotopy strip of the monkey is similar across species and that the variability that is observed is primarily due to methodological differences. The implications of these findings for the organization of the hand representation in the parietal cortex of the monkey and other primates are discussed below.
CORTICAL MAP VARIABILITY

largely on two relatively complete maps of the hand, de-

dcribed at one-third to one-fifth of the grain of definition of

the present maps (Mersenich et al., 178). This description of

the internal organization of area 3b (and of area 1) has

been confirmed in the present more complete study, with

three significant exceptions. First, in the more detailed

tmaps, islands of representation of dorsal digital skin sur-

faces have been found amid the large glabrous digital rep-

resentations, in both owl and squirrel monkeys. None were

noted in initial maps. Second, there is substantial individ-

ual variation in the shapes, areas, and, to a lesser extent,

the neighborhood relationships of different skin surfaces,

not fully appreciated in initial studies. Some of these indi-

vidual differences are actually greater than typical inter-


dividual differences between owl and squirrel monkeys.

Third, the dorsal digital surface representation does not

appear to be complete in either area 3b or 1, in at least a

number of intensively studied monkeys.

Surprisingly, since our initial maps were derived in those

and other primate species, investigators using other proce-

dures have failed to confirm this basic organization (Iwa-

mura et al., 81, 83; Mckenna et al., 82; Carlsson et al.,

62). Some investigators have hypothesized that the maps
derived in our studies have been substantially biased by

anesthetic artifacts (Duncan et al., 82; Mckenna et al., 82;

but see accompanying paper, Stryker et al., on this topic,

with our earlier results being interpreted as being other-

wise compatible with a single map of the body extending

across areas 3a, 3b, 1 and 2. Recently, Carlsson et al. (82)

concluded that area 3b contains a representation of the

glabrous surfaces of the digits, while area 1 provides the

dorsal digital representation. We have now mapped the

representation of the hand in area 3b in over 20 owl

and squirrel monkeys, and, in equal detail, in more than

30 additional owl and squirrel monkeys following

restricted peripheral or central lesions. Every one of these

hand maps has been derived on a grain of definition

greater than that in maps generated in any individual

monkey in the contrary studies. Moreover, there are

great technical advantages in defining map structures in

cortical sectors in which the representation is spread

entirely across a flat cortical surface, rather than partially

across a layer of subcortical tissue. Both the owl and

squirrel monkey hand representations offer these advan-
tages. The variation in internal map structure also demon-

strates that any combination of data from different monkeys

to produce a common map of the representation of (e.g., as

in the studies of Whitehead et al., 71; Iwamura et al., 31, 83;

and Mckenna et al., 62) will necessarily result in an obluma-
tion of map detail. The problem of map definition is also

not solved completely by deriving relatively complete maps

in one or two individual monkeys, because of substantial

individual variation.

Another possibility is that the variable maps we see in

the adult animal reflect the fixation of a possibly variable

functional map in early development. Such mechanisms

may have been proposed for visual and vibrissal systems, in

which dramatic alterations in the cortex can be produced

by limiting the early pattern of peripheral input (Woolsey

and Van Essen, 76; Hubel et al., 77; Killackey and Belford,

79; LaVey et al., 80; Woolsey, 80; Mersenich and Van Sluyters,

81; Sterling and Speyer, 82; Simons et al., 84). There is no

reason, however, to expect any particular degree of varia-
tility in any one functional map, and this hypothesis does

not explain findings of adult plasticity studies.

A proposal to account for variability and plasticity of
cortical maps

We propose that there are two major, interlocked sources

of variability in the present maps. First, studies that we have

conducted suggest that these adult cortical maps are shaped

by experience, and subject to alteration by use throughout

What are the sources of cortical map variability?

Why are somatosensory cortical maps so variable?

Inherent errors in mapping procedures are significant, but

they cannot account for most aspects of the variability noted

in this study (see Methods).

The two absolute constancies in the hand maps are 1) at

the largest scale, a constant overall orientation, and 2) at

the very finest scale, a strict internal topography. The vari-

able topologies of digit representation in the maps can be

reconciled with these constancies, at least on a formal level,

by assuming that, after the coarse orientation of the map

is established, the process that gives rise to the fine structure

of maps acts only on the very local scale and does not

include a mechanism for maintaining topology. The next

section presents one proposal for such a process, but any

of a great many mechanisms that maintain the peripheral

neighborhood relations among inputs to the cortex could account

for these findings equally well (for example, Fraser, 80, 85).

The variable areas of digit representation present more

of a problem. One is reluctant to believe that the consider-

able variation in area of cortical representations is a mere

reflection of variation in peripheral innervation. This is

especially the case for the dorsal surfaces of the digits, some

of which appear to lack an area 3b representation entirely.

It is, however, difficult to construct a model that maintains

topographic accuracy but gives rise to representa-
tional areas that do not accurately reflect innervation den-

sity of the input, because the forces that drive such models

toward large-scale organization also tend strongly to spread

out the inputs to uniform density (e.g., Fraser, 80, 85).

The proposal made in the next section is the only model

we know that can easily account for variable area of represen-
tations together with the constancies that are observed

in normal maps, and it has the virtue of accounting as well

for the findings of plasticity experiments.

On the other hand, we know nothing about the genetic or

acquired variability in cutaneous innervation among these

new world monkeys. So it remains possible that the differ-

ences in cortical map area among normal animals do reflect

differences in the periphery. Under this hypothesis, the

normal variability would not result from the mechanisms

that are active in plasticity studies.

Another possibility is that the variable maps we see in

the adult animal reflect the fixation of a possibly variable

functional map in early development. Such mechanisms

may have been proposed for visual and vibrissal systems, in

which dramatic alterations in the cortex can be produced

by limiting the early pattern of peripheral input (Woolsey

and Van Essen, 76; Hubel et al., 77; Killackey and Belford,

79; LaVey et al., 80; Woolsey, 80; Mersenich and Van Sluyters,

81; Sterling and Speyer, 82; Simons et al., 84). There is no

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tility in any one functional map, and this hypothesis does

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A proposal to account for variability and plasticity of
cortical maps

We propose that there are two major, interlocked sources

of variability in the present maps. First, studies that we have

conducted suggest that these adult cortical maps are shaped

by experience, and subject to alteration by use throughout


life (Merzenich et al., '84b; Merzenich, '87). Thus, map structure is substantially altered following peripheral nerve transection (Merzenich et al., '83a,b), digital amputations (Merzenich et al., '84a), or restricted cortical lesions (Jen-
kins et al., '82; Jenkins and Merzenich, '87). Recent experi-
ments have directly revealed changes in map detail resulting from different, usual shapes of the hand by an adult monkey (Jenkins et al., '84, Jenkins and Merzenich, '87). Thus, we hypothesize that details of functional map structure are largely created and are alterable by experience (Merzenich et al., '82b, '84a,b) and that the forms of these adult maps at least to a significant extent reflect the con-
sequences of different lifelong patterns of hand use in these monkeys. Note that, with few exceptions, although map details are substantially variable, internal topographic rel-
ationships and shifting overlap relationships are pre-
erved. We have hypothesized elsewhere that this active ma-
hance of overlap is probably controlled by temporal synchrony or sequencing of inputs (Merzenich et al., '85b, '84a,b; Merzenich, '87). The preservation of overlap relationships in the face of substantial map variability it self constitutes evidence that differences in map detail are largely determined by organizing activities through and after a critical developmental period.

Second, developmental studies indicate that cortical con-
nections are almost entirely set genetically pre-
determined, as had been earlier hypothesized (e.g., see 
Sperry, '60). To the contrary, early addressing of connec-
tions may be guided by cell adhesion molecules that can
effect the generation of only relatively crude local topo-
graphies (see Edelman, '83, for review). Numerous studies in-
clude that these initially crude connections are refined
during an initial period of development (see Harris, '81; 
Sherman and Spear, '82). Both the initial relatively crude
specification of connections and variable early experience
might contribute to variable features of cortical maps re-
corded in adults.

No one has suggested that even after this developmental
shaping there is still a substantial neuroanatomical spread
of inputs in somatosensory cortex, i.e., that the "neuroana-
tomical map" in the adult monkey is crude. Therefore, the
detail of cortical maps is a product of a process of selection
that continues throughout life (Merzenich et al., '84b; Merzenich, '87). By this process, there are very many possible
detailed forms of functional representation that can be created over time. The potential for variability is
limited by the degree of divergence and convergence of
anatomical inputs (Merzenich et al., '84a,b; Merzenich, '87),
but within such limits considerable variation is possible.
This view is consistent with the theory of neuronal group
selection, postulated by Edelman ('82).

In models in which maps are believed to organize along a
gradient (as opposed to their being specified genetically
point by point), it has been argued that one margin of
gradient is likely genetically specified (see Horder and Mar-
tin, '78; Dykes, '76). It is interesting to note, then, that skin
surfaces represented along all borders of the hand surface
representation are highly variable.

What is the significance of the incomplete representation of
dorsal hand surfaces in areas 3b and I? How can evidence for slowly adapting and rapidly adapting columns in area 3b be consistent with evidence for a single, simple representation of
dorsal hand surfaces?

One unexpected feature of these maps is the fragmented
and often incomplete representations of the
dorsal digits in areas 3b and in area I in many individual
monkeys. This disposition suggests that a topographically
continuous or complete overlap representation of these sur-
faced is not prerequisite for what area 3b contributes to
aspects of perception attributable to this field.

Studies of plasticity suggest that the dorsal digital skin
surface representation is special, in several respects. Thus
a) complete and very highly detailed map of the dorsal
digital representation arises in the map after removal of
glabrous digital inputs (Merzenich et al., '83a,b) by dorsal
cutaneous, representation zones have been seen to be oc-
cluded by glabrous digital inputs, following restricted cortical
lesions (Jenkins et al., '82; Jenkins and Merzenich, '87c) in
a few instances, neurons at one recording site have
appeared to switch their receptive fields from glabrous to
dorsal skin following heavy stimulation of the dorsal skin
(unfinished observations).

These findings suggest that both dorsal and glabrous inputs are present and closely overlapping in area 3b. Both
are capable of creating large, detailed maps over this corti-
ical zone; but in the monkeys that we have studied, with their individual histories of hand use, glabrous digital rep-
resentations predominate.

In studies of the distributions of neurons driven by slowly
adapting inputs, several investigators have presented evi-
dence that there are separate, complete representations of
the skin for each submodality class (Sur et al., '81; Dykes and
Gabor, '81). On the other hand, these detailed maps indicate
that there is a single, simple representation of the glabrous
hand surfaces in these fields. In area 3b of monkeys, Sur
and colleagues ('81) have proposed that in layer IV, slowly
adapting (SA) and rapidly adapting (RA) inputs are segre-
gated into narrow alternating bands of partially shifted somatotopic overlap so that overall, SA and RA bands sep-
arately represent the same skin surfaces. However, possibly consistent with the existence of a single overall map, they
believe that these inputs merged into a mixed representa-
tion in deep layers. This proposal is similar to that made for striate cortex in monkeys where occipular dominance bands represent the same visual space individually for the two eyes in layer IV and combine to
form a single binocular representation in other layers. In
dorsal somatosensory maps, only a single highly topog-
ographic map was evident; separate representations were
not apparent. Map reorganization after peripheral lesions
suggest that the boundaries of SA and RA zones may be
subject to change. Thus, we hypothesize, SA and RA bound-
aries may be functionally defined and have diffuse, lateral
sensory aspects of predominant hand use.

Evidence for map variability in other
cortical regions

If map variability is primarily a consequence of differ-
ences in hand use in individual monkeys, then map varia-
bility in other cortical fields might constitute evidence for
the possible extents of use-dependent alterability in these
monkeys. Again, variability in map structure has not been the
primary objective of any earlier studies in cortex. However,
differences have been described in several regions.

In auditory cortical fields, there is substantial variation
in the details of best frequency organization in individual
cats, although the overall pattern of cochleotopic or "tono-
centric" representation is retained (Smith et al., '76;
Peterson et al., '75; 646; Reale and Imig, '80). In the in
frequency dimension of the primary auditory cortex, functional orga-
nization is very highly idiosyncratic (see Merzenich and
Burgo, '73; Imig and Adrian, '77; Imig et al., '77; Schwi-
CORTICAL MAP VARIABILITY

for example, and Cynader, '84; Merzenich et al., '84b). In the cat, for neurons of similar activity of the isoport of AI have highly specific, complex response properties which differ from each other. Neuronal projections from the auditory thalamus are massively convergent and emergent from the field (Coës, '77; Merzenich et al., '84a, '84b; Middlebrooks and Zook, '83).

Other somatosensory zones are likely more variable in representational order than are areas 3b and 1. Thus, for example, raw data from different SH field maps are sub- stantially different in the relatively detailed studies of Robin- son, Burton and Freedman, conducted in macaques and cats (Robinson and Burton, '80a; Freedman, '81; Burton et al., '82). Very great individual differences were noted, in an important study of the somatosensory representation of area 7b and other orthodromic fields in the macaque (Robinson and Burton, '80b; Burton and Robinson, '81).

We have earlier hypothesized that the limits of cortical map alterability are determined by the extents of spread of anatomical inputs (Merzenich et al., '81b, '84b; Merzen- ich, '90). In this vein, the very substantial variation re- corded along the isoport axis of auditory fields and within and area 7 somatosensory fields is consistent with this view, as inputs to all of those cortical zones are more widely convergent-divergent than are to areas 3b and 1.

Variability in visual field organization has been less well studied. There, maps, have as a rule, been defined in coarse grain, as mapping has again been largely directed toward defining visual representational entities, and toward deter- mining the overall grand pattern of retinotopy (e.g., see Zeki, '69, '70; Allman and Koss, '71a, '71b, '74, '75, '76; Tsut et al., '78, '79, '81; Palmer et al., '78). Indeed, individ- ual comparisons are more difficult because of a limitation in the frames of reference for comparing map details.

The representation of the visual field periphery as a variable number of “islands” within areas 18 and 19 in the cat (e.g., Derrington and Farah, '85) cannot be equi- valent to those described herein (also see Tsut et al., '78, '79, '81; Albus and Beckman, '79). It would be surprising if the sources of substantial map variability operating within the somatosensory and auditory cortical fields are not also present within visual cortical areas.

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