

Magnification, Receptive-Field Area, and “Hypercolumn” Size in Areas 3b and 1 of Somatosensory Cortex in Owl Monkeys

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SUMMARY AND CONCLUSIONS

1. Several features of the two complete and separate representations of the contralateral body surface in cortical areas 3b and 1 of somatosensory cortex in owl monkeys were quantitatively studied.

2. Areal magnification factors for different body regions in the two representations were obtained. The glabrous hand and foot regions were found to occupy nearly 100 times more cortical tissue per unit body-surface area than the trunk or upper arm.

3. In the representations of the hand digits, inverse magnification was linearly related to distance from the digit tips.

4. Receptive-field size was found to be proportional to inverse magnification over the entire body-surface representation as well as over the local region of the glabrous hand digits. The relation between receptive-field size and inverse magnification appears to be linear; specification of one would specify the other over the representation in one area.

5. By relating receptive-field overlap to distance separating recording sites, the area of cortex presumed to receive all fibers from any given receptive field was obtained and found to be independent of the body surface represented. Such an area of somatosensory cortex, about 1–1.5 mm in diameter, may be akin to the “hypercolumn” proposed for primary visual cortex (6).

INTRODUCTION

The systematic representation of peripheral receptor surfaces is a basic feature of cortical organization. It has been long appreciated

that the skin surface is represented systematically within at least two representations—SI and SII of somatosensory cortex of mammals (see Refs. 12, 25 for review). In monkeys and the higher primates it has also been recognized that the postcentral parietal representation, SI, includes cytoarchitectonic areas 3a, 3b, 1, and 2 of Brodmann (2) (later Vogt, Ref. 30). In a recent series of mapping experiments, we have shown that each of cortical areas 3b and 1 of somatosensory cortex contains a complete and separate cutaneous representation of the contralateral body surface in owl monkeys (12), macaque monkeys (15, 26), squirrel monkeys (16), and *Cebus* monkeys (4). Each of these two representations within the classical primate SI consists of sectors within which given regions of the skin surface are represented somatotopically (9, 12). These two large cutaneous representations are essentially mirror images of each other.

In any topographical mapping, quantifiable relationships exist between the representation and the sensory epithelium. In the visual system, there have been several attempts at describing these quantifiable relationships. Thus, for example, cortical “magnification” as a function of eccentricity has been used to describe the visual-field representation in area 17 of monkeys (3, 6, 14), the lateral geniculate nucleus of monkeys (11), area 17 of cats (1, 28), areas 18 and 19 of cats (29), and the lateral suprasylvian areas of cats (18). It has been proposed that linear cortical magnification, defined as the one-dimensional quantity millimeters of cortex per degree of visual field represented, varies approximately inversely with eccentricity (3, 6). It has also

been suggested that, in primary visual cortex of monkeys, receptive-field size may be inversely proportional to magnification, i.e., the larger the amount of cortical area devoted to a given region of the visual field, the smaller the receptive fields (6). Magnification factors have been used in the description of somatosensory representations to point out the proportional differences in cortical area for different body regions in the body maps in SI and SII of the gray squirrel (17).

In the representations of the body surface on somatosensory cortex, a number of features similar to those described for the visual-field representations in visual cortex have been noted. For example, relatively sensitive parts of the body surface, like the digit tips, occupy relatively larger areas of cortical tissue (e.g., Ref. 31); and receptive-field sizes vary depending on the body region and the proportion of cortex devoted to that region (e.g., Ref. 13). In this paper we describe quantitatively, for areas 3b and 1 in owl monkeys, the change in cortical magnification as a function of different body regions in general and distance down the hand digits in particular. We show that receptive-field size is proportional to magnification over the entire body-surface representation as well as over the cortical representation of the phalanges of the hand digits. Related to this observation, there is a constant area of cortex (in either area 3b or 1) that represents a given receptive field (or a constant area of cortex representing any given point on the skin) at any place on the skin surface. Such an area of cortex would be akin to the hypercolumn proposed for primary visual cortex by Hubel and Wiesel (6). A visual cortex hypercolumn is the area that contains one set of left and right eye ocular dominance columns or a complete set of orientation columns representing 180° , and thus may form a basic processing unit for any region of the visual field equal to the size of an elementary receptive field. In somatosensory cortex, then, the area of cortex representing a given receptive field completely and, hence, receiving all fibers from such an area of skin, could be expected to contain within it the basic processing capability for the prototypical skin area the size of a receptive field anywhere on the body surface.

A preliminary report of these results has appeared elsewhere (24).

METHODS

The data reported in this paper was obtained from 11 owl monkeys (*Aotus trivirgatus*). Surgical procedures and methods of stimulation and recording have been described by Merzenich et al. (12), where the organization of the body-surface representations in areas 3b and 1 obtained from nine of these experiments have been reported and discussed. Briefly, owl monkeys were anesthetized with ketamine HCl (50 mg/kg), the cortical surface was exposed, and a dam of acrylic was built around the skull opening to hold a pool of silicone over the brain. Recording sites, usually spaced 200–300 μm apart, were marked on an enlarged photograph of the cortical surface. Recordings were usually from, or close to, layer IV, at depths of 700–1,200 μm from the pial surface. In cortex receiving cutaneous input, usually one receptive field was defined for each penetration normal to the cortical surface. Receptive fields were delineated by fine hand-held glass probes and drawn on photographs or drawings of the appropriate body part. Stimulus amplitudes used to define receptive fields did not produce marked skin deformations, but caused enough increased neuronal activity that could be reliably distinguished from background or spontaneous rates of discharge. On the glabrous skin, stimuli consisted of punctate indentations causing dimplings that often were barely visible without magnification. Correlation with accurately measured graded amplitudes of indentation provided by an electromechanical stimulator in two owl monkeys, in which adaptation and receptive-field properties of cortical cells were studied, provided estimates of stimulus indentation depths as between 100 and 300 μm . Stimuli on the hairy skin consisted of deflection of hairs at low to moderate rates, estimated at 1–10 cm/s. Using such stimuli, the areas of skin providing input to single neurons or very small clusters of neurons can be clearly demarcated (13, 20).

The owl monkey was chosen for this study because of its important advantage of lack of a central sulcus. In the other monkeys mapped, at least part of the anterior boundary of area 3b is buried in the central sulcus and the detailed topography of the body representation therein is difficult to define with great spatial accuracy. Penetrations have to be made down the bank of the sulcus, and the recording sites cannot be visualized. Further, the central sulcus itself curves rostrally, so that a nonresponsive recording site in a sulcus penetration need not be rostral to area 3b, but merely deep to responsive cortex. In the owl monkey, on the other hand, the organization of area 3b can be easily determined electrophysiologically, within the limits of accurate control of electrode position and interpenetration distance, all the way to the

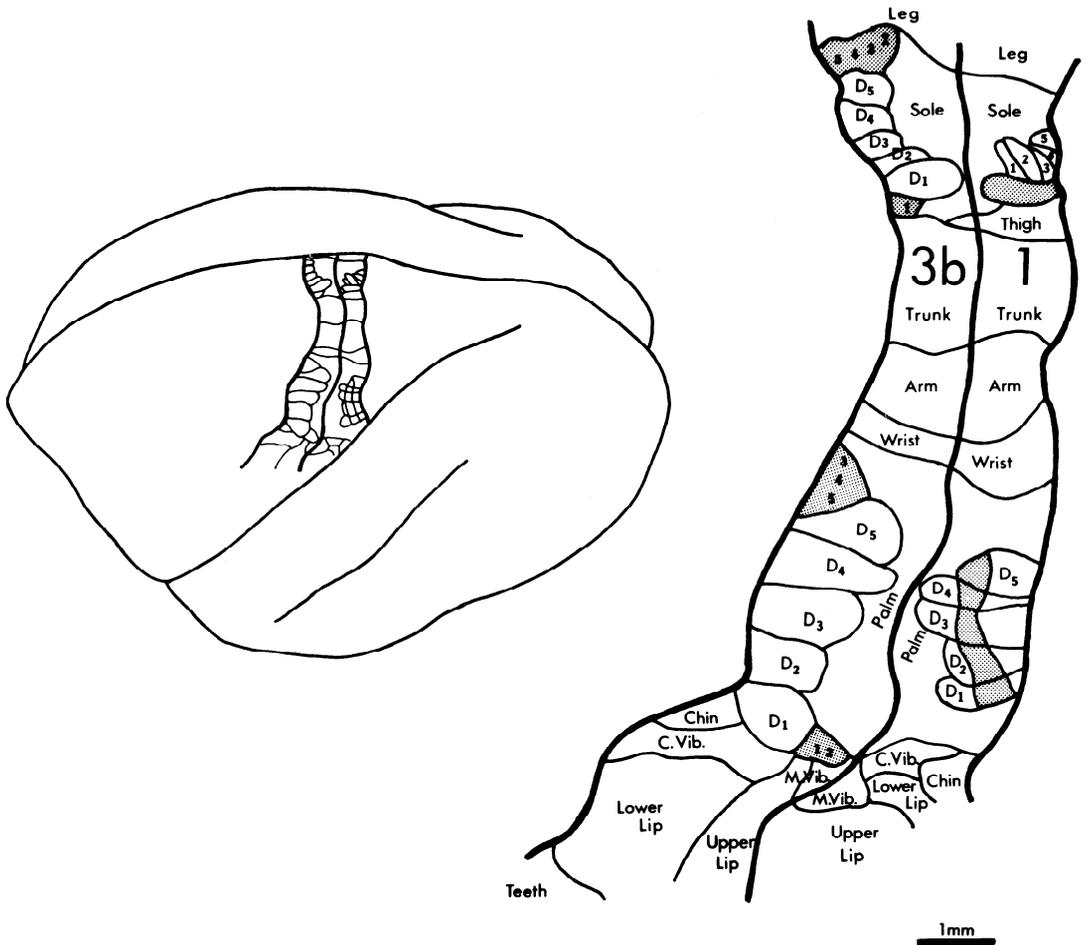


FIG. 1. Representation of the contralateral body surface within cytoarchitectonic areas 3b and 1 in the owl monkey, *Aotus trivirgatus*. Sectors within each map representing different body surfaces are appropriately labeled. Shaded region shows cortex representing dorsal hairy surfaces of fingers and toes. The arm representation can be subdivided into forearm and upper arm representations. (From Merzenich et al. (12). Reprinted with permission from the *Journal of Comparative Neurology*.)

rostral as well as caudal boundary. This completeness is necessary for accurate estimates of cortical magnification. Second, as an issue related to lack of a central sulcus, the boundaries of the two representations in areas 3b and 1 obtained by electrophysiological mapping have been shown to correlate precisely and remarkably with boundaries obtained by independent architectonic examination of sagittal sections (12). However, though cortical representational regions within areas 3b and 1 may be defined and measured very accurately for owl monkeys, observations made in all other monkey species we have mapped indicate that the results derived from the owl monkey apply generally.

Obtaining accurate quantitative values of magnification, receptive-field size, and hypercolumn dimensions requires fine-grain, detailed mapping

of cortex and careful receptive-field delineation on the skin. Our highly detailed mapping studies have allowed accurate measurements of cortical areas representing different skin surfaces. In each experiment, within each representation of the contralateral body on cortex, receptive fields were derived at many hundreds of cortical sites. The representation of the body surface in each of cortical areas 3b and 1 was reconstructed by demarcating sectors of cortex that received cutaneous input from given body parts (Fig. 1). The cortical magnification factor for any skin surface was obtained by dividing its cortical representational area by its skin-surface area. Thus, cortical magnification is the proportional quantity, cortical area per unit body-surface area. For several analyses where a reciprocal relation of magnification

was expected with the variables studied, e.g., distance of portions of the hand digits from the digit tips or receptive-field area over parts of the body surface, inverse magnification, denoting body-surface area per unit cortical area, was used for illustration.

Magnification factors in areas 3b and 1 for separate regions of the body surface, like the hand, foot, trunk, arm, forearm, and wrist, were obtained from the cortical maps over areas 3b and 1 derived in one owl monkey in which 486 penetrations were made in somatosensory cortex (see Fig. 1, taken from Merzenich et al. (12)). The map includes 165 recording sites in the hand region, 107 in the trunk and forelimb, and 122 sites in the foot region. Values of magnification factors were checked against (and found to be close to) values obtained from three other monkeys in which different body regions were mapped completely (but not the entire body surface). Relations between magnification factors and distances from a digit tip and between magnification factors and receptive-field sizes were obtained from these same monkeys. Measurements of receptive-field overlap as a function of cortical distance, needed to estimate hypercolumn size, requires interpenetration spacings of 150–200 μm at least over cortex representing local regions of individual body parts. Such data for the hand digits and palmar pads were obtained from an experiment done specifically to illustrate the fine topography of the hand representation.

Cortical and body-surface areas were obtained from enlarged drawings and photographs (linearly magnified up to 40 \times), using an electronic planimeter. Receptive fields, drawn on enlarged pictures of appropriate body parts during recording, were measured similarly. All measured areas of cortical regions and subregions, body parts, and receptive fields were appropriately scaled.

The sources of error in these procedures should be considered at the outset. With an interpenetration spacing of about 250 μm , there is some error in determining the boundaries of the cortical representations. Areas of skin driving single peripheral afferent fibers vary somewhat with stimulus amplitudes used, especially on the glabrous skin (7). Though it was attempted to map all cortical receptive fields under the same conditions of skin indentation or hair deflection over glabrous and hairy skin, respectively, some errors in precise definition are likely. The effects of ketamine HCl as an anesthetic as well as degree of anesthesia on receptive-field sizes were not systematically studied. Areas of body surfaces with curvature were estimated from planar photographs. The arm area was determined as that of a cylinder whose mean diameter was measured on a photograph, while the forearm area was calculated as that of a conic section with the base diameter given at the elbow and the apex diameter at the wrist.

On the other hand, errors in measurements were minimized by enlarging the cortical representational and body-surface areas. Experimental bias regarding any of the issues being addressed was relatively absent because the data on which this study is based was collected primarily during experiments aimed at defining the separate body representations in areas 3b and 1. The observations described provide orders of magnitude for the features measured. Finally, there is an empirical validity to the numbers that have been obtained, for they confirm and quantify observations that have been seen repeatedly in over 60 experiments in four species of monkeys.

RESULTS

The two separate and complete representations of the contralateral body surface within cytoarchitectonic areas 3b and 1 of the owl monkey are shown in Fig. 1. The representations are approximately mirror images of each other. Hand and foot digits point rostral in area 3b and caudal in area 1. These general features of somatosensory cortical organization are similar for owl monkeys, macaque monkeys, squirrel monkeys, and *Cebus* monkeys (9).

Overall magnification for different body regions

From the representational areas for each body region within the map in area 3b or 1 and the actual skin-surface areas on the body regions, the overall magnification curve for the whole body is obtained and illustrated in Fig. 2. The face and leg representations extend laterally and medially into the sylvian and midsagittal sulci, respectively, and were consequently incompletely mapped. Thus they are excluded from Fig. 2. The hand and foot magnification factors are for glabrous skin. The wrist magnification factors for areas 3b and 1 include the dorsum of the palm because the representation of this skin overlaps extensively with that of the dorsal wrist (12).

Within each representation, cortical magnification obviously varies greatly across different body regions. For example, the glabrous hand or foot representations occupy nearly 100 times more cortical tissue per unit body-surface area than the trunk or upper arm representations in both areas 3b and 1. There are also differences in the representational areas of individual body regions across areas 3b and 1. Except for the wrist, the rep-

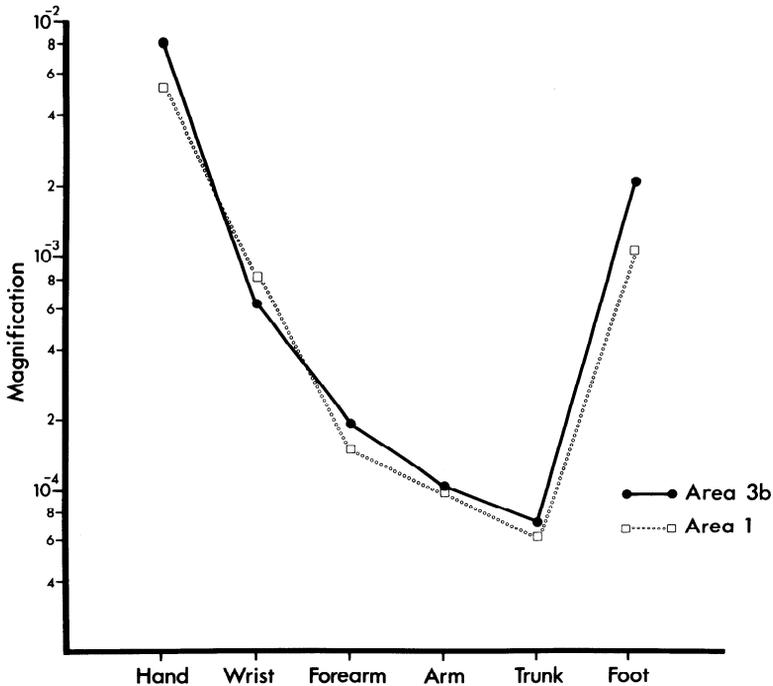


FIG. 2. Graph of magnification for different body regions represented separately in areas 3b and 1. The face and leg were incompletely mapped and are not shown. Magnification is defined as (cortical area)/(body area).

resentation of different body regions in area 3b is larger than that in area 1. This difference in proportional area is exactly as noted by Merzenich et al. (12), as their Table 1 indicates.

As clearly seen in Fig. 2, the intra-areal differences in cortical proportion across different body regions can be much larger than the interareal (3b-1) differences for the same body region. The major difference in proportional area for similar body parts between areas 3b and 1 is that considerably more tissue in area 3b is devoted to the glabrous hand and foot (Fig. 1). More specifically, the glabrous hand and foot digits form the main source of differences in areal proportion across areas 3b and 1, with area 3b containing 2-3 times the area of tissue representing these skin surfaces in area 1. The areas devoted to the palm and sole are more nearly equal. Since the hand and foot magnification factors for areas 3b and 1 shown in Fig. 2 include cortical and skin-surface areas of both the glabrous digits and the glabrous palm or sole, the overall differences in proportion are not as dramatic as they would be for the digits alone.

Magnification functions for hand digits

The difference between the hand digit representations in areas 3b and 1 are readily apparent from Fig. 3A and B. The points of Fig. 3A, which shows inverse magnification (M^{-1}) versus distance from digit tip for area 3b, were obtained by dividing each digit into portions for which the cortical representation of the digit could be validly subdivided. These portions were: distal half of the distal phalanx, proximal half of the distal phalanx, middle phalanx, and proximal phalanx. For each of these skin sectors, inverse magnification was obtained and plotted against the distance of the center of the appropriate portion from its digit tip. There are thus four points each for digits 2-5 and three for digit 1 (which contains only distal and proximal phalanges). These points were best fit by a linear function

$$M^{-1} = 8.93d + 27.69 \quad (1)$$

with a correlation coefficient $r = 0.97$. Exponential, power, inverse, and log tanh functions all yielded higher errors of fit.

In area 1, the representation of each digit is smaller, and hence each digit could only

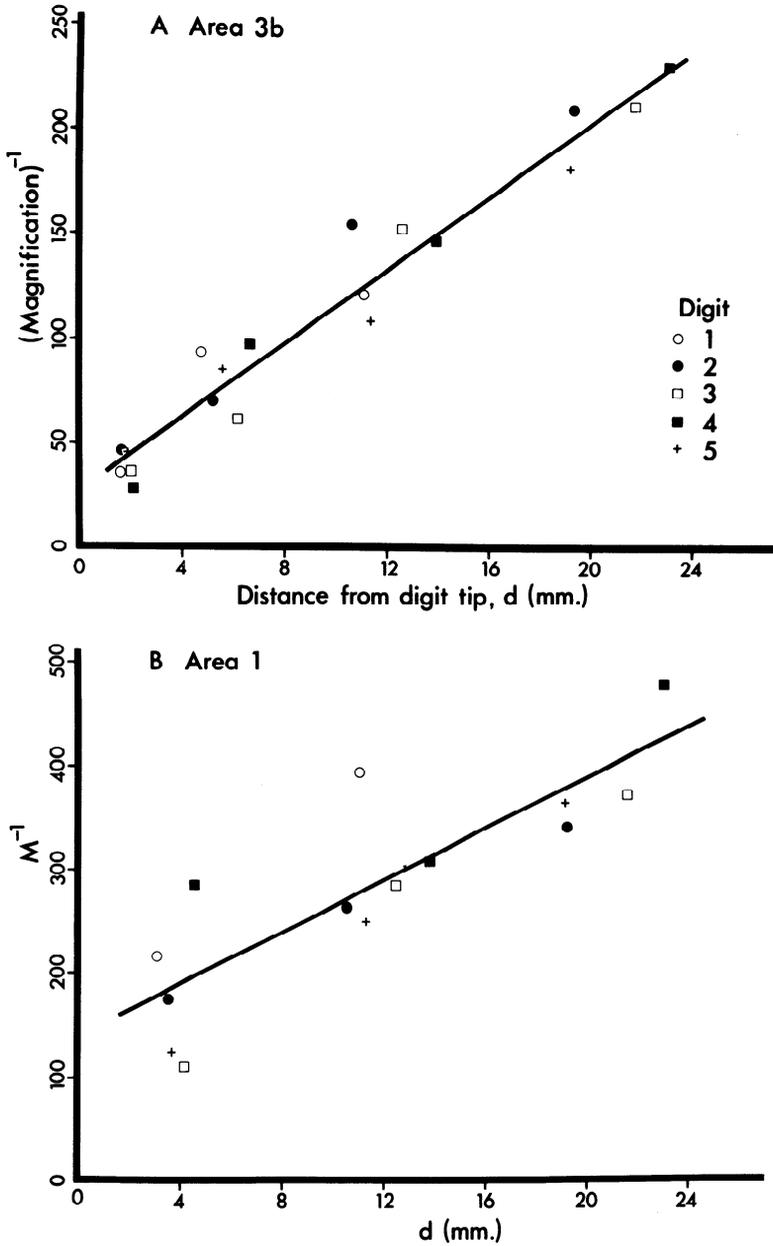


FIG. 3. A: graph of inverse magnification versus distance from digit tip for the representation of the hand digits in area 3b. The procedure for obtaining points is described in the text. The straight line is the best fit to these points, $M^{-1} = 8.93d + 27.69$, $r = 0.97$. B: graph of inverse magnification versus distance from digit tip for the representation of the hand digits in area 1. The straight line is $M^{-1} = 12.39d + 139.98$, $r = 0.84$.

be subdivided into its phalanges for obtaining M^{-1} . The best fit is again with a straight line

$$M^{-1} = 12.93d + 139.98 \quad (2)$$

with $r = 0.84$. The points show a greater variance in Fig. 3B, at least in part, because

the cortical areas are smaller. Also, the values of M^{-1} are almost double for area 1 than for area 3b, indicating that area 3b devotes almost double the amount of cortical tissue to these glabrous digit representations.

It must be noted that *equations 1 and 2* are

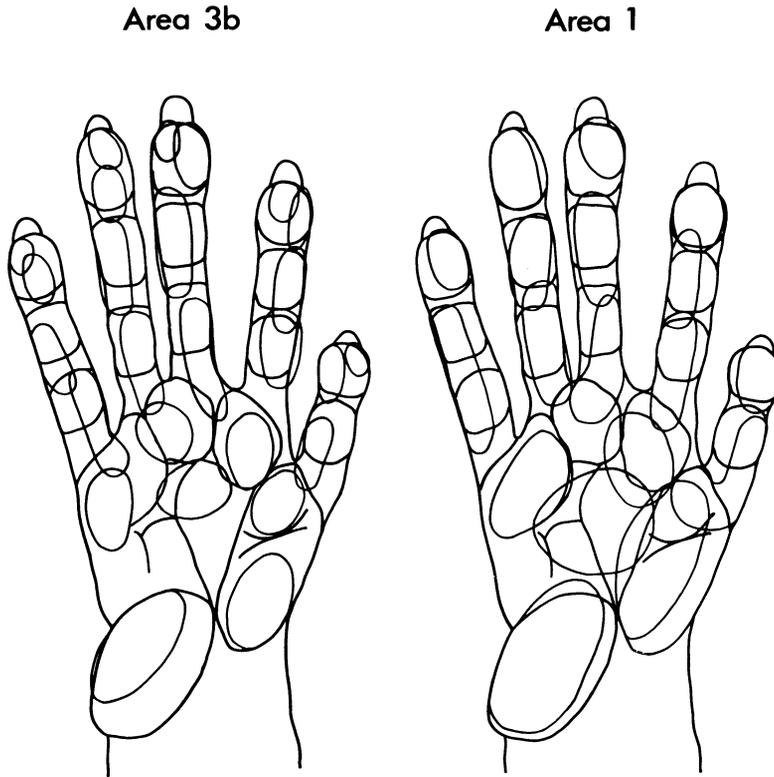


FIG. 4. Typical receptive fields on the glabrous hand. Left: area 3b receptive fields. Right: area 1 receptive fields.

defined only over the ranges of d and M^{-1} that have been obtained and illustrated in Fig. 3A and B. Undoubtedly *equations 1* and *2* are not defined over infinitesimally small values of d , for M^{-1} then could be expected to be close to zero and its relation to d , probably nonlinear.

The magnification function can be interpreted as the Jacobian or mapping function of the hand digits on area 3b or 1. Thus, an equation describing the mapping of the digits from the skin surface to cortex can be derived. Such a derivation stemming from the magnification function of a very detailed map of the hand in area 3b of the owl monkey has been obtained and will be described separately.

Receptive-field area

One of the most common observations in our mapping experiments has been the change in receptive-field size as a function of represented skin locus. Thus, receptive fields are smallest at a digit tip and become progressively larger toward the base of the digit.

Receptive fields also increase in size from the distal to the proximal limb representation, and receptive fields on the upper arm, upper leg, and trunk are the largest in size (Fig. 7). Further, receptive fields for neurons in area 1 (especially those over the glabrous hand and foot) are consistently larger than receptive fields for neurons in area 3b. Typical receptive fields over almost the entire glabrous hand region are illustrated in Fig. 4 where the relatively larger sizes of the receptive fields for area 1 are evident.

Whether or not receptive field area varies in a systematic way over the entire cortical representation in area 3b or 1 can be investigated by plotting the receptive-field areas from different body regions against the magnification factors for these body regions. Figure 5 shows a graph of mean receptive-field area against M^{-1} in area 3b for the six body regions whose magnification factors are shown in Fig. 2. (M^{-1} has been chosen rather than M because both field size and M^{-1} vary in the same direction.) Each point for recep-

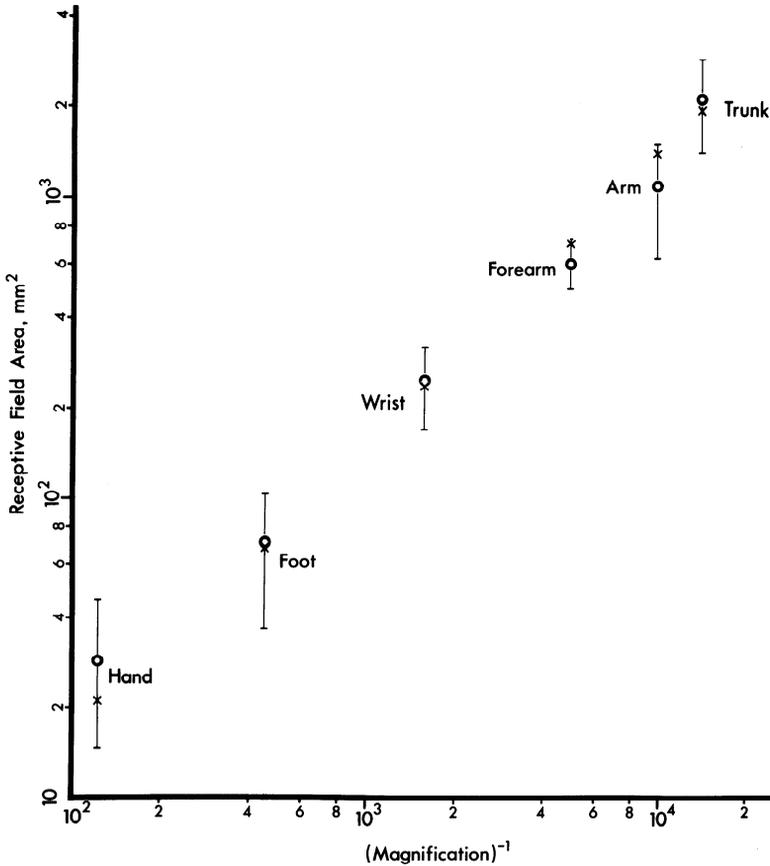


FIG. 5. Mean receptive-field area plotted against inverse magnification for the representational regions of the body surface shown in Fig. 2. Bars bounding open circles represent 1 standard deviation. Crosses represent theoretical values of receptive-field area obtained from equation 3 and M^{-1} values from Fig. 2. See text for details.

tive-field area in Fig. 5 is a mean of all receptive fields over the body region indicated and was obtained in the same experiment as that used for obtaining the magnification factors. All receptive fields are for recording sites within area 3b as architectonically identified. The bars indicate 1 standard deviation around the mean area. The M^{-1} values are the area 3b values from Fig. 2.

As seen clearly from Fig. 5, receptive-field size is, in general, proportional to inverse magnification over the representations of separate skin surfaces in area 3b. The larger the cortical tissue per unit body-surface area devoted to a region of the body surface, the smaller the receptive fields over that body region. The graph of Fig. 5 shows M^{-1} and receptive-field sizes for the area 3b rep-

resentation; it can be shown that a similar relationship also holds for the area 1 representation.

In addition to the relationship between receptive-field size and magnification across the large units of body surface, we can also expect a proportionality over local regions of the body surface. The hand digits provide a particularly clear model for such a demonstration. Magnification varies dramatically from distal to proximal over the digits (Fig. 3); receptive-field sizes vary from the tip to the base of the digits (Fig. 4). Receptive-field areas over different segments of all five digits (included in Fig. 4) have been plotted in Fig. 6 against the magnification factors of these same segments (shown in Fig. 3). The graphs of Fig. 6A and B show that receptive-

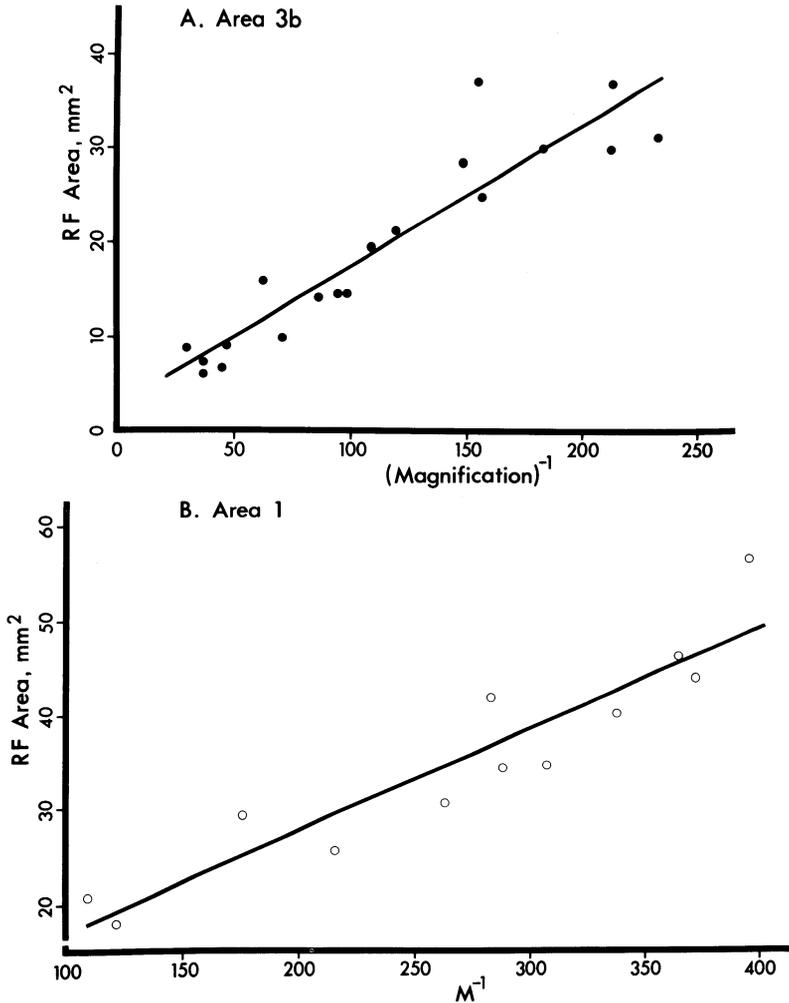


FIG. 6. *A*: graph of receptive field area versus M^{-1} for the area 3b hand digit representation. M^{-1} values are from Fig. 3A. $RF = 0.15M^{-1} + 2.56$, $r = 0.93$. *B*: graph of receptive field area versus M^{-1} for the area 1 hand digit representation. M^{-1} values are from Fig. 3B. $RF = 0.11M^{-1} + 5.78$, $r = 0.93$.

field size and magnification are proportional over the surface of the hand digits, in both areas 3b and 1.

The straight-line best fits to the graphs of Fig. 6A and B are, respectively

$$RF = 0.15M^{-1} + 2.56 \quad \text{for area 3b} \quad (3)$$

and

$$RF = 0.11M^{-1} + 5.78 \quad \text{for area 1} \quad (4)$$

These lines represent fits to data only over the ranges of field size and M^{-1} indicated. In general, any relation between RF and M^{-1} must include the origin, for it would otherwise lead to the absurd result of a nonzero recep-

tive-field area for zero inverse magnification (the case of no skin represented over an area of cortex). However, the relationship between receptive-field size and magnification is probably highly nonlinear for skin surfaces with high magnification (very low M^{-1}).

An important issue inherent in the data of Figs. 5 and 6A is whether the relation that describes the proportionality between receptive-field size and magnification across different body regions in area 3b also describes the proportionality over a local subregion like the hand digits. The existence of such a general relation can be tested simply (at the

level of a first approximation) by obtaining hypothetical receptive-field sizes for the whole body from *equation 3* and comparing them to the experimentally obtained mean values. Extrapolating *equation 3* over the M^{-1} values in area 3b for the entire hand, foot, wrist, forearm, trunk, and arm yields theoretical values of receptive-field size as denoted by crosses in Fig. 5. As is clearly evident, the theoretical and experimentally obtained mean receptive-field areas match rather closely. This implies that there exists, for all of the body representations in area 3b, a general relation between receptive-field size and magnification. Specification of one automatically specifies the other. At a first-order level, the relation is the linear one shown in *equation 3*. Such a general relation may be expected to also hold for the area 1 representation.

The slope of the line relating receptive-field size and M^{-1} represents the nominal cortical area in area 3b that subserves a given receptive field (see DISCUSSION). The total cortical area that is driven from all or any portion of a given receptive field can be obtained directly, as shown below.

Receptive-field shift and hypercolumn size

One of the foundations of the hypothesis of columnar organization of somatosensory cortex is that receptive fields remain spatially localized for a vertical aggregate of cells. This postulate has been amply confirmed by our experiments. But as receptive fields are sampled by transverse (either anterior-posterior or medial-lateral) shifts in recording sites, there is an overall predictable movement of the receptive-field centers. The amount of receptive-field shift as a function of cortical distance may be quantified by measuring the degree of overlap of successive receptive fields defined in nearby penetrations, known distances away from a given receptive field.

Receptive fields from five regions of the body projecting to area 3b and used for these measurements are shown in Fig. 7. In each case, starting with a given receptive field, there are two fields that overlap the first field and that have been recorded at slightly shifted sites in area 3b. The amount of overlap of each of the latter two fields relative to the first is plotted against the cortical distance of each

of the recording sites from the first. The overlap versus distance graph is shown in Fig. 8.

Receptive fields of cells in somatosensory cortex may sometimes show some scatter as a function of depth. As far as can be ascertained, the receptive fields used for overlap measurements are for cells in layer IV. The receptive fields chosen also have to be confined to a body region with approximately uniform magnification so as to not confound absolute field area as a variable. Further, all receptive fields shown in Fig. 7 also probably relate to the same receptor type. The dimensions that are yielded, therefore, form order-of-magnitude estimates for a hypercolumn.

The line of Fig. 8 indicates that, regardless of the body region represented, a cortical displacement of 500–600 μm (560 μm in Fig. 8) is required to shift a receptive field to a nonoverlapping position. The gradient of the overlap versus distance graph should be interpreted as a trend rather than as a rigid shift in receptive field from cell to adjacent cell.

The graph of Fig. 8 represents unidirectional measurements, though both anterior-posterior and medial-lateral cortical sites have been used in constructing it. Assuming cortical symmetry, an area of 1–1.5 mm diameter (approximately 2 times 560 μm , as indicated in Fig. 8) anywhere in area 3b would receive input from the region of a receptive field anywhere on the body surface. Alternately, any point on the skin surface would be represented in a cortical area about 500–600 μm in diameter. Our data indicate a similar area for area 1 also.

The graph of Fig. 8 is obtained from comparison of two partially shifted receptive fields with one reference field. Such data provide, in general, valid estimates of overlap. The extensive or reliable nature of the overlap versus distance relation may be gauged as well by comparing only two adjacent recording sites and receptive fields. These would yield only one point for receptive-field overlap for the measured interpenetration spacing on the overlap versus distance graph. Such a graph obtained for 72 pairs of overlap and cortical distance points is shown in Fig. 9. It includes 24 points for the hand and 16 each for the forelimb, trunk, and foot. These data are, again, consistent with the conclusion drawn from Fig. 8 that receptive fields

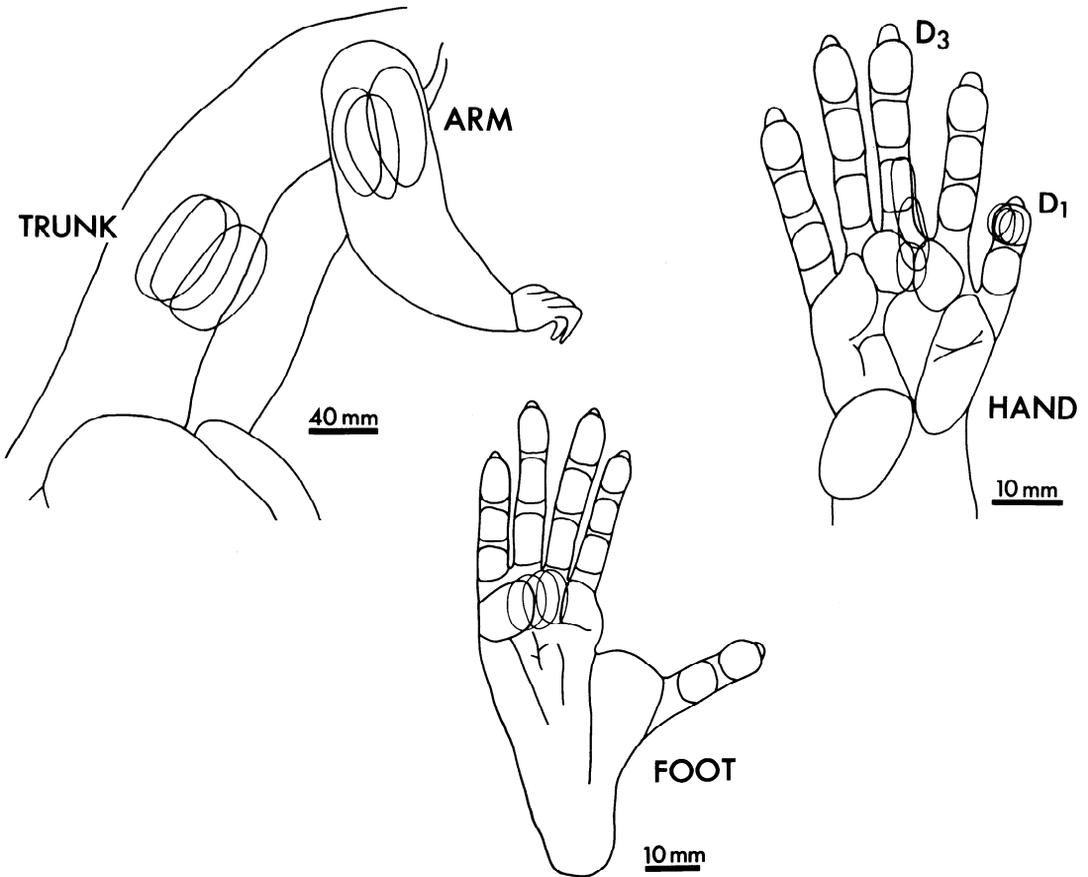


FIG. 7. Typical receptive-field sizes on the hand, arm, trunk, and foot pads. The overlap data shown was used to construct the overlap versus distance graph of Fig. 8.

for recording sites separated by about $600\ \mu\text{m}$ fail to overlap, regardless of position on the body surface.

DISCUSSION

Four main observations are presented in this paper. First, the change in cortical magnification over different body regions has been obtained for areas 3b and 1. Second, inverse magnification has been shown to be linearly related to distance down the hand digits. Third, receptive-field size has been shown to be proportional to inverse magnification over the entire body surface as well as over the local region of the glabrous hand digits. Fourth, by relating receptive-field overlap to distance separating recording sites, an estimation of the area of cortex presumed to receive all fibers from any given receptive

field anywhere on the body surface has been obtained and has been found to be roughly constant.

Magnification function

The linear relation obtained between inverse magnification and distance from a digit tip identifies the mapping of the digits from distal to proximal on each of areas 3b and 1 as a logarithmic function of distance on the digit surfaces from distal to proximal. Such a mapping may also hold for primary visual cortex (21), stemming from the observation of a linear relation between inverse magnification and visual-field eccentricity.

The relation between inverse magnification and distance has been demonstrated here for only the glabrous digits, a local region of the hand surface. Such a relation may also hold for larger regions of the body,

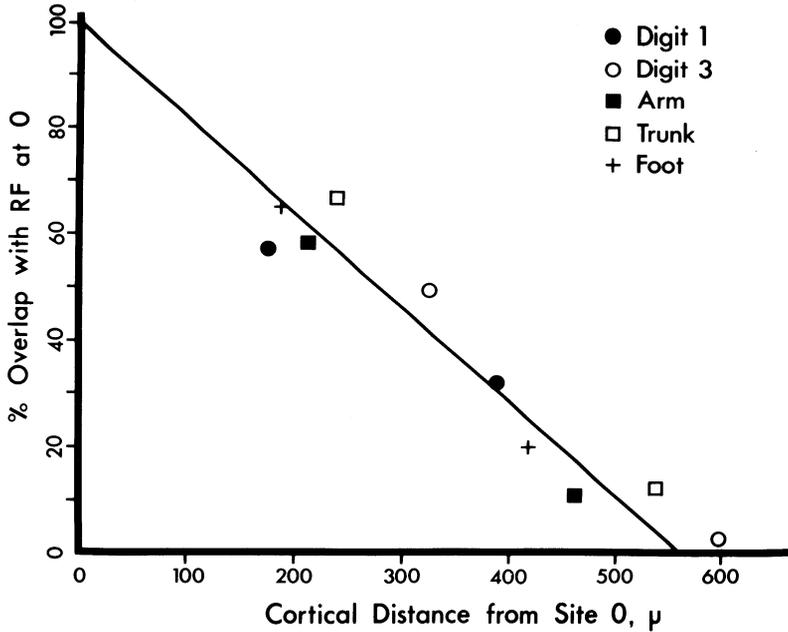


FIG. 8. Overlap of two different receptive fields with a given receptive field on the same body region plotted against distance of the cortical recording sites from the first recording site. Data from Fig. 7. Recording sites in area 3b. $r = 0.96$.

for example, the entire forelimb. Demonstration of any such relation, however, requires extremely fine-grain mapping of the entire forelimb region in one animal so that sectors of cortex representing sufficiently small sectors of the forelimb skin can be accurately defined.

It now appears that the proportional representation of different skin surfaces do not simply reflect peripheral innervation density as once hypothesized (31). Maps in owl monkeys have revealed that the two complete skin-surface representations in areas 3b and 1 have different proportional areas of representation for the same skin surfaces (12). Some of these differences are quantified in Figs. 2 and 3. Similar results have subsequently been derived in all monkeys studied (4, 9, 15, 16, 26). Clearly, areas 3b and 1 cannot simply reflect overall peripheral innervation density, receiving input from identical fiber populations.

Perhaps more compellingly, recent detailed maps of the skin surface in a series of squirrel monkeys have revealed great variation in the area of representation of certain skin surfaces in different individual monkeys of this species (far more marked than that observed in indi-

vidual owl monkeys). Thus, for example, the area of representation of the digits in area 1 varies by a factor of almost five, while the area of the hand surface varies by about 10% (M. M. Merzenich, J. T. Wall, M. Sur, R. J. Nelson, D. J. Felleman, and J. H. Kaas, unpublished observations). This would seem to make it unlikely that there is any simple governing organizational rule (beyond a general trend) between peripheral innervation density and cortical magnification. It is possible that the magnification function in each area reflects input from at least partially separate sets of primary afferents. The resolution of the question, what determines cortical magnification, must await further study.

Cortical magnification and cortical topography

There is a direct relation between cortical magnification and cortical topography in the maps defined within areas 3b and 1 in the owl monkey (as well as in other primates and in the body representation in somatosensory cortex in other animals). In the skin periphery, there are obvious variations in receptor density over different regions of the body.

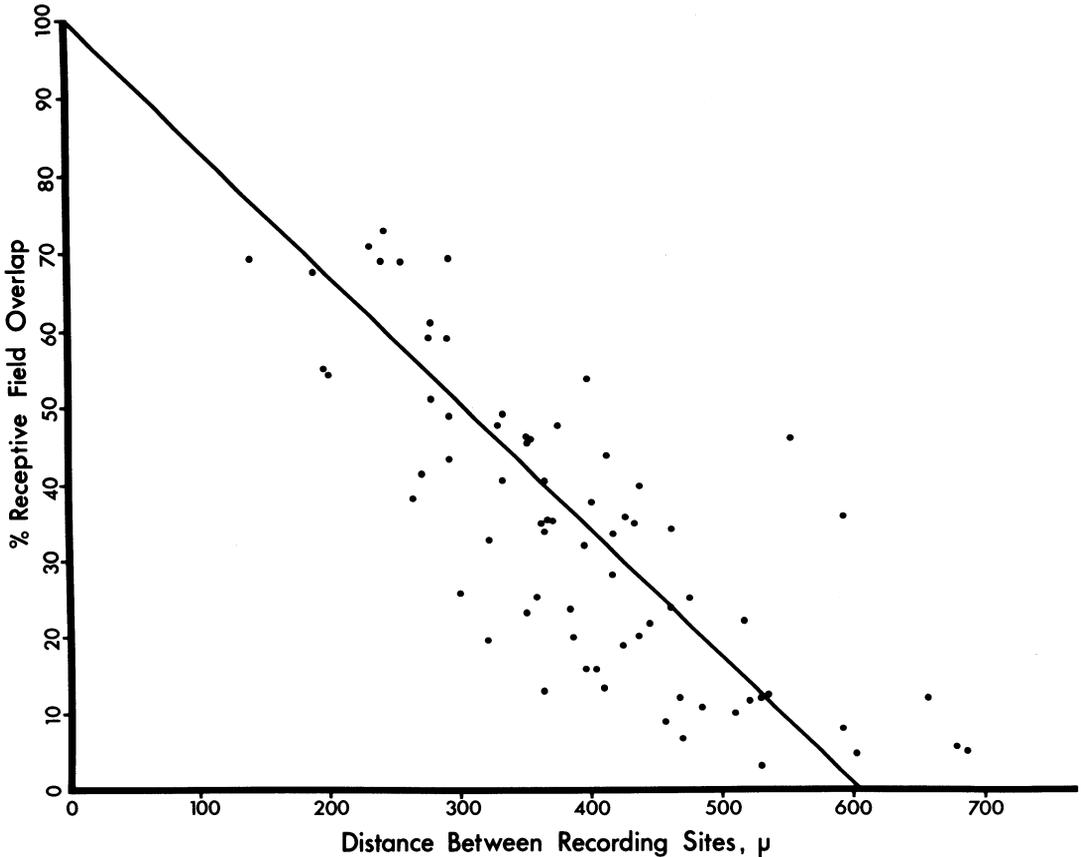


FIG. 9. Overlap of pairs of receptive fields plotted against cortical separation between the recording sites. Data includes receptive fields on the hand, forearm, arm, trunk, and foot. $r = 0.79$.

The glabrous hand and foot contain considerably larger numbers of receptors than the hairy limbs or the trunk. The mapping of the body surface on area 3b or 1 depicts, in a general fashion, the representation of the peripheral receptor surface. If cell density were varying over different parts of somatosensory cortex, there could be a perfect picture of the periphery—a perfect homunculus—on each of areas 3b and 1. In cortex, however, cell density in either area 3b or 1 is largely invariant. Hence different body parts come to occupy varying areas of cortex. (Our conclusion here is identical to that reached by Hubel and Wiesel (6) for the mapping of the retina on primary visual cortex.) However, in the two-dimensional map of the contralateral body surface over each area, disproportionate representation of one region of the body affects topographical relationships of that region with adjacent regions in

the representation. The regions with high cortical magnification—the glabrous hand or foot—cannot maintain the same topography with the rest of the forelimb or hindlimb that exists on the skin. There are thus numerous discontinuities in receptive-field progression in crossing the borders of the glabrous hand and foot representations, especially at the lateral extent of the representations (12). Regions with more equal magnification factors—the forearm, arm, trunk, or leg—may maintain topography across the local regions of representation (15, 16, 27). In the same manner, topography within each region of representation is strongly dependent on the relative enlargements or magnifications of different subregions represented. In the glabrous hand representation in area 3b in the owl monkey, for example, the magnification of the digits and the rostral pads forces the thenar and hypothelar eminences to be rep-

resented far apart on cortex. In the macaque monkey, the "pad split" of the hand is even more severe (9, 15).

Based on these considerations of topography within sectors of the cortical map, exemplified by the body representation on somatosensory koniocortex of the galago (27), it has been proposed that the representation can be characterized as a few blocks, each of which is internally somatotopic and may contain one or more individual body regions. In galagos, the map consists of four blocks representing the head, hand, foot, and the hairy body surface, including the limbs and trunk. Such a framework provides a general description of a cortical map tied to two essential descriptors—somatotopy and magnification; for clearly, the body regions within a block are regions with similar magnifications.

Finally, there are two obvious types of departure from point-to-point correspondence between the skin surface and the cortical representation in either area 3b or 1 in monkeys or over parietal somatosensory cortex of other animals (15). First, points (skin areas) that are adjacent on the skin may be represented at nonadjacent points on cortex. Second, points that are adjacent on cortex may represent nonadjacent skin areas. Examples of the first are the split between the thenar and hypothenar pad and splits across the arm or leg skin (9, 12, 15, 25–27). An example of the second is the adjacent cortical representation of the (glabrous and hairy) thumb or radial pads of the hand and the face (Fig. 1). None of these particularities is predicted by dermatomes (12, 17).

It has been shown how, in representing a nonuniform receptor sheet on the two-dimensional plane of cortex, varying magnification is necessary and is sufficient to cause departures from strict adjacency relationships. In addition, physical three-dimensional skin surfaces like the arm and leg have to be split to be overlaid on a two-dimensional surface (25). Due at least in part to the same reason, the dorsum of the hand or foot digits, along with the dorsum of the palm or sole, are represented separately from the ventrum representations. These two features, varying magnification and splits in three-dimensional surfaces, may account in large measure for the nontopography observed in the maps and

express what is to some degree intuitive—that a vital reason for the departures from strict somatotopy observed in the cortical maps, and hence a determinant of the map itself, is the essential nature of cortex as a two-dimensional rather than a three-dimensional transformational surface.

Receptive-field area and magnification

One of the most important observations in this study is the proportional relationship between receptive-field area and magnification in the somatosensory cortex. The smaller the area of cortex per unit body-surface area devoted to a given region or subregion of the body surface, the larger are the receptive fields on that part of the body surface. Coupled to this expected result is the particular form of the relation—a linear one—between field size and inverse magnification. The linear relation has been indicated by the data over the hand digits in each of the two representations (Fig. 6), and the same relation appears to describe the proportionality between receptive-field size and inverse magnification for the representation of all body parts, including the foot, wrist, forearm, arm, and trunk in the same area (as demonstrated for the area 3b representation in Fig. 5). Specification of either receptive-field size or magnification specifies the other, for a given body representation.

Not only does the proportionality between receptive-field area and magnification hold within each cortical area, it probably holds in a general way across areas 3b and 1. Magnification factors for the same body region are generally lower for area 1; receptive fields are correspondingly larger. These results are again evident from Figs. 4 and 6. Our data are not extensive enough to allow us to compare Fig. 6A and B directly and to evaluate whether the two slopes, for example, should be the same or different. Such a comparison would make sense only if exactly the same receptor population that projected to area 3b also projected to area 1. However, it appears likely that the inputs to areas 3b and 1 are not identical. For example, as mentioned earlier, the same skin surfaces have different magnification factors in the two areas. Anatomical studies of the connections of areas 3b and 1 with the ventroposterior lateral (VPL) nucleus suggest there must be some

differences in the inputs to these areas (8, 10). Studies of neuron properties in areas 3b and 1 indicate that there are differences in the receptor inputs to the two areas (19, 20, 23).

Our results do suggest a greater convergence from peripheral fibers to area 1 cells than area 3b cells. Multiplication of the slopes of the lines of Fig. 6A and B by the cell densities of layer IV in areas 3b and 1 would yield the nominal numbers of cells in each area that relate to given receptive fields. Since the cell density of layer IV in area 1 is lower than that of area 3b (20) and the slope of the line of Fig. 6B (0.11 mm^2) is lower than that of Fig. 6A (0.15 mm^2), fewer cells in area 1 than in area 3b must subservise receptive fields typical to each area. Of course area 1 cells have, in general, larger receptive fields over the same body surface than area 3b cells. These observations lead to the inference that area 1 cells process information from larger numbers of peripheral fibers than area 3b cells. Yet, again, this hypothesis must be moderated by the uncertainty in knowing the degree of common afferent input to the two cortical areas. The linear relations of Fig. 6A and B and the extrapolations on Fig. 5 also imply that there is a constant number of cells in each of areas 3b or 1 that receive input from a patch of skin the size of a receptive field or, equivalently, that a constant number of cells are excited by a point stimulus anywhere on the skin surface.

Finally, the linear relations between receptive-field area and inverse magnification and between inverse magnification and distance down a digit imply that there is also a linear relation between receptive-field size and distance of the field from a digit tip. Such a relation for area 3b, for example, is

$$\text{RF} = 1.34d + 6.71 \quad (5)$$

Equation 5 is also defined only over the ranges of distance and field area that equations 1 and 3 are defined. The relation above is in full agreement with the finding of Mountcastle and Powell (13) of a linear variation of receptive-field area with distance from the tip of the forelimb of macaque monkeys.

Hypercolumn of somatosensory cortex

A hypercolumn, as defined by Hubel and Wiesel (6) and adopted by us, is the area of

cortex representing any region of the sensory surface equal to the size of a receptive field. It has been shown that such an area of cortex in area 3b, independent of the skin surface represented, is 1–1.5 mm in diameter.

There are several issues that relate to the hypercolumn hypothesis and its dimensions. First, the hypercolumn is basically a theoretical construct; it does not necessarily imply that area 3b is actually carved up into pieces 1–1.5 mm in diameter. The major usefulness of such a hypothesis and of knowing its dimensions is that it specifies the area in which all incoming fibers from a prototypical skin region the size of a receptive field must lie. If there are different types of afferent input to a given area (for example, from slowly adapting and rapidly adapting receptors to area 3b (13, 19, 20)), and the skin surface is to be represented in the context of each afferent type, these types of fibers must be present in an area of cortex the size of a hypercolumn. Hence, all initial processing related to skin regions the size of a receptive field must be taking place in such an area. Thus, even though a hypercolumn may not be a concrete entity, it provides a basis for thinking concretely about cortical microorganization. And though a hypercolumn itself may not be discrete, it must contain within it several types of discrete substructures or columns, based on 1) different types of afferent input, and 2) products of different types of processing in a given area. Ultimately, such discrete substructures may be aligned together in slabs, as in the ocular dominance and orientation columns of primary visual cortex (5, 6) and in the slowly adapting and rapidly adapting columns of area 3b (23). This study proposes that the place to look for such entities would be over an area 1–1.5 mm in diameter anywhere in area 3b, for such an area of cortex would be a prototypical input and processing area.

A second issue relates to the dimensions of the hypercolumn as obtained here. That the size of cortical tissue that would represent a given receptive field completely is independent of the skin region represented is a direct consequence of the unique relationship between receptive-field size and magnification. The slope of the line relating receptive-field size and M^{-1} in area 3b (0.15 mm^2), however, represents only the nominal

cortical area that would relate to a given receptive field. The slope is, in fact, equal to the entire area of cortex driven by a given point on the skin surface. The slope value of 0.15 mm^2 corresponds to a circular area of cortex about $450 \mu\text{m}$ in diameter. This derived value corresponds remarkably with the value of $500\text{--}600 \mu\text{m}$ obtained by relating receptive-field overlap to distance separating cortical recording sites in area 3b (Figs. 8, 9).

Finally, the hypercolumn dimensions refer to the area of cortex in area 3b that relates to a given receptive field. The mapping of the skin surface on cortex is, specifically, an area of skin to a point on cortex (each cell in layer IV, for example, has a receptive field) and a point on the skin to an area of cortex (there is overlap of receptive fields for adjacent cortical cells). The hypercolumn dimensions express the relation of an area

of skin to an area of cortex, the generalized form of the mapping (22). The area of cortex that represents any point on the skin is an area $500\text{--}600 \mu\text{m}$ in diameter, obtained directly from Figs. 8 and 9. This is one-quarter the hypercolumn size, as a receptive field is represented completely over the sum of the cortical areas for the four diametrically spaced points that bound the field.

ACKNOWLEDGMENTS

The authors thank Dr. Francis H. C. Crick for his comments on an earlier version of the manuscript, and C.-S. Lin and R. J. Nelson for their help in collecting data.

This work was supported by National Science Foundation Grant BNS 81824 to J. H. Kaas and National Institutes of Health Grant NS 10414 to M. M. Merzenich.

Received 3 October 1979; accepted in final form 25 February 1980.

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